



## NEW INSIGHTS ON THE PHYLOGENETIC RELATIONSHIPS OF THE TWO GIANT EXTINCT NEW WORLD MONKEYS (PRIMATES, PLATYRRHINI)<sup>1</sup>

(With 1 figure)

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**ABSTRACT:** The phylogenetic position of the genera *Caipora* and *Protopithecus* within the Platyrrhini was investigated within a cladistic framework based on morphological characters with emphasis on patterns of tooth variation. A data matrix of 102 characters and 23 terminal taxa was subjected to analysis using a branch and bound option of the PAUP 4.0 Software. As a result, 40 equally most parsimonious trees were obtained. A strict consensus of these trees yielded a topology with 15 components with five unresolved trichotomies. The phylogenetic results show that the giant monkeys *Caipora* and *Protopithecus* should be recognized as typical atelins, belonging to the tribe Atelini, being both closely related to *Ateles*. The cranio-dental evidence supporting the Atelini clade are: 1) a rounded basal portion of the incisors; 2)  $I_{1-2}$  similar in size (height); 3) hypocone smaller than protocone in  $M^2$  and similar in size in  $M^1$ ; 4) metacone smaller than paracone in  $M^{1-2}$ ; 5) metacrista developed in  $M^{1-2}$ ; and 6) postglenoid foramen reduced. Based on this phylogenetic data, the taxonomical interpretation that indicates *Protopithecus* as a member of Alouattini is refuted.

**Key words:** *Protopithecus*, *Caipora*, Platyrrhini, primates, phylogenetics, tooth morphology.

**RESUMO:** Novos dados sobre as relações filogenéticas de dois macacos gigantes extintos do Novo Mundo (Primates, Platyrrhini).

A posição filogenética de *Caipora* e *Protopithecus* dentro de Platyrrhini foi investigada a partir de uma abordagem cladística baseada em caracteres morfológicos, com ênfase nos padrões de variação dentária. Uma matriz de dados com 102 caracteres e 23 táxons terminais foi submetida a uma análise de parcimônia usando a opção *branch and bound* do Programa PAUP 4.0. Como resultado desta análise, foram obtidas 40 árvores igualmente parcimoniosas. O consenso estrito das árvores resultou numa topologia contendo 15 componentes, sendo cinco tricotomias não resolvidas. De acordo com os resultados *Caipora* e *Protopithecus* são reconhecidos como atelinos, pertencentes a Tribo Atelini, ambos filogeneticamente associados ao gênero *Ateles*. As evidências crânio-dentárias que suportam o clado Atelini são as seguintes: 1) porção basal dos incisivos abaulada; 2)  $I_{1-2}$  similares em tamanho (altura); 3) hipocone menor que o protocone em  $M^2$  e com tamanho similar em  $M^1$ ; 4) metacone menor que o paracone em  $M^{1-2}$ ; 5) metacrista desenvolvida em  $M^{1-2}$ ; e 6) forame pós-glenóide reduzido. Baseado nestas informações, a interpretação taxonômica de *Protopithecus* como membro de Alouattini é refutada.

**Palavras-chave:** *Protopithecus*, *Caipora*, Platyrrhini, primatas, sistemática filogenética, morfologia dentária.

### INTRODUCTION

Primates are primarily arboreal placental mammals presently distributed along tropical forests of Africa, Asia, Central and South America. During the Tertiary epochs, however, their geographical distribution extended through major parts of the European and the North American continents (SZALAY & DELSON, 1979). Among living primates, Eusimiiformes (*sensu* GROVES, 2001; "Anthropoids" in FLEAGLE,

1988; KAY, ROSS & WILLIAMS, 1997; and ROSS, 2000) comprise the most specious and studied primate group that encompasses Old World monkeys and apes (Catarrhini) and New World monkeys (Platyrrhini).

Platyrrhine monkeys represent at least 30% of the living primate species (MITTERMEIER *et al.*, 1988). Living platyrrhines are found from southern Mexico to northern Argentina, but paleontological records have been encountered in Patagonia and as far north as to the Greater

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Antilles (HOROVITZ & MACPHEE, 1999). These mammals inhabit remarkably different ecological niches, and show great variability in size, diet, and ecological adaptations. They range from the 100g *Callithrix (Cebuella) pygmaea* (Spix, 1823) to the 14kg *Brachyteles arachnoides* (E.Geoffroy, 1806).

A series of morphological attributes, shared by all species of the group, sustains an uncontroversial monophyletic status for the group (e.g., KAY, ROSS & WILLIAMS, 1997). Conversely, historical relationships within platyrrhines remain the focus of heated debates. Part of the problem lies in the fossil record that, until about fifty years ago, was limited to a few fossil fragments, many assigned to the genus *Homunculus* Ameghino, 1891. At the present time, a few hundred specimens are catalogued and classified into approximately twenty genera (MCKENNA & BELL, 1997; TEJEDOR, 1998). Most of these fragments, however, are represented by isolated maxillary and mandibular fragments. A formal cladistic analysis including most of these fossil taxa was performed by HOROVITZ (1999).

There are, however, two remarkably complete and well preserved platyrrhine skeletons that have been recently discovered. They are the largest known specimens of New World monkeys: *Caipora bambuorum* Cartelle & Hartwig, 1996 and *Protopithecus brasiliensis* Lund, 1838. These atelid monkeys were found next to one another in a cave in the Northeastern Brazil, in the State of Bahia (HARTWIG, 1995; CARTELLE, 1996; CARTELLE & HARTWIG, 1996; HARTWIG & CARTELLE 1996).

*Caipora* is hypothesized to have weighed approximately 20kg (CARTELLE, 1996; CARTELLE & HARTWIG, 1996). According to the authors, this species resembles atelin monkeys in both cranial and postcranial features, but it is distinctive in having a more spherical neurocranium with a much larger braincase and skeleton. They also indicated that the *Caipora* skeleton and teeth are more similar to *Ateles* E. Geoffroy, 1806 than to any other living platyrrhine genera (CARTELLE & HARTWIG, 1996).

*Protopithecus* is also remarkable for its large size, which is calculated to be a gigantic 25kg (CARTELLE, 1996; HARTWIG & CARTELLE, 1996). *Protopithecus* is also unquestionably supported as an atelid, but within atelids it exhibits a puzzling mosaic of characters with a cranial morphology that resembles alouattins and a

postcranial skeleton similar to atelins (HARTWIG, 1995; CARTELLE & HARTWIG, 1996; HARTWIG & CARTELLE, 1996). This evolutionary puzzle was left unresolved by Cartelle and Hartwig, but they did suggest the possibility that typical atelin postcranial adaptations to suspensory locomotion may be a primitive condition for the ateline radiation (CARTELLE & HARTWIG, 1996; HARTWIG & CARTELLE, 1996). By suggesting that, the authors implied that the cranial similarities that *Protopithecus* shares with howler monkeys (i.e., Alouattini) are to be interpreted as evidence favoring a close phylogenetic relationship of this giant monkey with the alouattines.

Here, we present the first formal phylogenetic study relative to the emergence of these two extinct species within platyrrhines. We hope to shed some light on the puzzle concerning the cladistic position of these giant monkeys within platyrrhines. In this first evaluation, we have focused on patterns of variation observed in the masticatory apparatus, while supplemental morphological information was gathered from HOROVITZ (1999). In future studies we expect to present more comprehensive assessments to platyrrhine phylogeny and evolution.

## MATERIAL AND METHODS

Following MCKENNA & BELL (1997), the 20 genera are representing the terminal taxa of the present phylogenetic study. These include the two giant fossil species and two other extinct taxa (†), plus all currently recognized extant platyrrhini genera: *Alouatta* Lacépède, 1799; *Aotus* Illiger, 1811; *Ateles* E. Geoffroy, 1806; *Brachyteles* Spix, 1823; *Cacajao* Lesson, 1840; *Caipora*† Cartelle & Hartwig, 1996; *Callicebus* Thomas, 1903; *Callimico* Miranda-Ribeiro, 1911; *Callithrix* Erxleben, 1777; *Carlocebus*† Fleagle, 1990; *Cebuella* Gray, 1866; *Cebus* Erxleben, 1777; *Chiropotes* Lesson, 1840; *Lagothrix* E.Geoffroy, 1812; *Leontopithecus* Lesson, 1840; *Pithecia* Desmarest, 1804; *Protopithecus*† Lund, 1838; *Saguinus* Hoffmannsegg, 1807; *Saimiri* Voigt, 1831; and *Stirtonia*† Hershkovitz, 1970.

The genus *Callithrix* presents interesting taxonomical questions. GROVES (2001), for example, divides *Callithrix* into the following subgenera: *Cebuella* Gray, 1866; *Mico* Lesson, 1840 (= *argentata* group of HERSHKOVITZ, 1977

and VIVO, 1991); and *Callithrix* Erxleben, 1777 (= *jacchus* group of HERSHKOVITZ, 1977 and VIVO, 1991). Here we adopt MCKENNA and BELL's classification in order to evaluate the controversial taxonomic status of *Cebuella*, and two *Callithrix* species were included as terminal taxa, representing the subgenera *Mico* and *Callithrix*. Unfortunately, however, no specimens of *Callithrix humilis*, only recently recognized as the new genus *Callibella* (VAN ROOSMALEN & VAN ROOSMALEN, 2003), were included in the material examined.

*Carlocebus* and *Stirtonia* were included in the analysis based on the fact that they are among the few available platyrrhine fossils represented by relatively complete upper and lower jaws with teeth in good conditions (see APPENDIX I for a detailed list of the material examined). The inclusion of these two fossil taxa has implied a minimal number of missing data cases to the analysis regarding the evaluation of the tooth morphology. Dental terminology is based on HERSHKOVITZ (1977).

The platyrrhines used as reference material in this study are from the following collections: Museu Nacional, Rio de Janeiro (MN); Museu de Zoologia da Universidade de São Paulo (MZUSP); Museu Paraense Emilio Goeldi (MPEG); and Instituto de Geociências da Universidade Federal de Minas Gerais (IGC-UFMG). Illustrations of *Carlocebus* and *Stirtonia* published by SZALAY & DELSON (1979); HERSHKOVITZ (1970); SETOGUCHI, WATANABE & MOURI (1983); KAY *et al.* (1987); KAY, MADDEN & GUERRERO-DÍAZ (1989) and FLEAGLE (1990) were consulted.

We employed standard cladistic procedures (FARRIS, 1983) in order to carry out the phylogenetic analysis. The *branch and bound* algorithm was applied using the PAUP\* 4.0 b10 program (SWOFFORD, 2002), and Bremer indices were calculated to evaluate branch stability.

The characters selected for this study were chosen in order to represent in detail the full range of patterns of variation in platyrrhine tooth morphology. We employ this strategy in the interest of developing a starting point for a better assessment of the taxon's paleodiversity. A total of 102 unordered characters were the basis of the study, distributed across 23 taxa, with two non-platyrrhines anthropoid outgroups added: *Aegyptopithecus* Simons, 1965 which is a basal anthropoid representative, and one cercopithecoid catarrhine, *Pygathrix* E. Geoffroy, 1812.

## RESULTS

### TOOTH MORPHOLOGY: PATTERNS OF VARIATION

Even though platyrrhines are known to have rich diversity in their tooth morphology (HERSHKOVITZ, 1977; ROSENBERGER, 1981), most have retained the primitive dental formula of anthropoid primates – upper jaw with I<sup>1</sup>, I<sup>2</sup>, C, P<sup>2</sup>, P<sup>3</sup>, P<sup>4</sup>, M<sup>1</sup>, M<sup>2</sup> and M<sup>3</sup>, and lower jaw with I<sub>1</sub>, I<sub>2</sub>, C, P<sub>2</sub>, P<sub>3</sub>, P<sub>4</sub>, M<sub>1</sub>, M<sub>2</sub> and M<sub>3</sub>. Third molars are absent in callitrichines and *Xenothrix* Williams and Koopman, 1952 which is not included here. They generally have also maintained a quadritubercular upper molar crown pattern, except in the tritubercular callitrichines.

Since the 80's, a number of authors have been using dental features in their phylogenetic analyses of New World monkeys, such as ROSENBERGER (1977, 1981), KAY (1990); MACPHEE *et al.* (1995); KAY & MELDRUM (1997); HOROVITZ & MACPHEE (1999); HOROVITZ (1999); and GUEDES (2000). In the following we provide a general summary of the information on tooth morphology based on our direct observation of the specimens. Nearly half of the characters here hypothesized represent original data and/or reformulations of previously proposed characters. The other half is nearly identical to the information presented by HOROVITZ (1999). The details of such character formulations are a subject of a future, broader study on the evolution of the New World monkeys. A synthetic list of the characters formulated for this study is presented below:

- 1) Upper incisors, relative position: 0 – incisors placed in a wide U-shape liked dental arch; 1 – incisors placed in a narrow V-shape liked dental arch.
- 2) I<sup>1</sup>, development of the metastyle: 0 – absent; 1 – present (Note: The metastyle may be reduced in some species of *Callithrix* group *jacchus*).
- 3) I<sup>2</sup>, development of the parastyle and metastyle: 0 – absent; 1 – parastyle and metastyle present (Note: Metastyle is rounded in all platyrrhine genera except *Callithrix* and *Cebuella*, where it is cuspidiform).
- 4) Upper incisors, anteroposterior inclination in relation to the sagittal plane of the palate (labial face): 0 – incisors have a perpendicular position in relation to the sagittal plane of the palate; 1 – incisors have a anterior inclination in relation to the sagittal plane of the palate; 2 – incisors

- have a drastic inclination, almost parallel to the sagittal plane of the palate.
- 5) Upper incisors, development of the basal portion (buccal): 0 – weakly developed; 1 – developed, curve (rounded). (Note: A more basal portion analogous to the protocone, considered by HERSHKOVITZ (1977) as the protocone, may also be present independently of the entocingulum development).
  - 6) Upper incisors, spatial orientation of the crowns: 0 – crowns are oriented to the posterior portion of the palate, almost in lateral alignment; 1 – I<sup>1</sup> crown is oriented to the posterior portion of the palate and I<sup>2</sup> crown is somewhat rotated internally; 2 – crowns are rotated to the internal region, anteriorly (I<sup>1</sup> slightly rotated and I<sup>2</sup> more accentuated way). (Note: Although incisors of *Callithrix* and *Cebuella* are organized in two rows, one composed by the central incisors and another composed by the lateral ones, crowns of lateral incisors are oriented internally to the tooth row, in a convergent direction. In *Leontopithecus* incisors are displaced in two rows also but they are oriented relative to the posterior region of the palate).
  - 7) I<sup>1-2</sup>, development of an accessory cusp (protocone): 0 – no cusp or accessory crest is developed at the entocingulum; 1 – a cusp is developed in I<sup>1</sup> and is vestigial or absent in I<sup>2</sup>; 2 – a cusp is developed in both I<sup>1-2</sup>.
  - 8) Upper incisors, relative dimensions of the paracone: 0 – the maximum length is similar to the maximum width; 1 – the maximum length is bigger than the maximum width.
  - 9) Premaxilla, development of the anterior portion (lateral view from the labial face): 0 – without any anterior projection of the premaxilla; 1 – with a drastic anterior projection of the premaxilla, from a transversal axis at the base of nasal bone.
  - 10) Upper incisors, relative size: 0 – both incisors similar in size; 1 – I<sup>1</sup> bigger than I<sup>2</sup> (Note: This size relationship among upper incisors is independent from the shape, even when central and lateral incisors are differently shaped).
  - 11) Upper incisors, development of the crown (paracone): 0 – low crowns; 1 – high crowns.
  - 12) Development of crests over the palatine bone in the region of the major palatine foramen: 0 – absent; 1 – present, but reduced; 2 – present, well developed.
  - 13) I<sub>2</sub>-C, relative position: 0 – teeth separated by a diastema; 1 – teeth in contact.
  - 14) I<sub>1-2</sub>, relative size: 0 – both teeth similar in size; 1 – I<sub>1</sub> smaller than I<sub>2</sub>.
  - 15) Lower incisors, dorsoventral dimensions of the occlusal buccal surface: 0 – short paraconid; 1 – elongated paraconid; 2 – more prolonged paraconid.
  - 16) Lower incisors, development of the buccal base of the paraconid: 0 – reduced or absent in I<sub>1-2</sub>; 1 – reduced or absent in I<sub>1</sub> and developed in I<sub>2</sub>; 2 – developed in both incisors.
  - 17) I<sub>2</sub>, development of a projection at the supra-distal (lateral) portion of the paraconid: 0 – absent; 1 – present.
  - 18) Lower incisors, morphological general pattern of the crown: 0 – spatulate; 1 – bunodont; 2 – presenting a shape almost cylindrical, with I<sub>2</sub> in a caniniform trend (Note: Platyrrhine lower incisors are spatulate in general, with a variable degree of spatulation where pitheciins have the most extreme condition. Morphology of lower incisors of *Cebuella* is similar to those ones in *Callithrix* with the exception of I<sub>2</sub> being more caniniform and both incisors being more cylindrical and sharp – in *Callithrix* only I<sub>2</sub> is cylindrical. This trend to the cylindrical shape is the result of a condition where the I<sub>2</sub> buccal surface has a perpendicular position relative to I<sub>1</sub>, with an apparent twist internally to the tooth row).
  - 19) I<sub>2</sub>, curvature of the internal surface: 0 – teeth without any apparent anterior curvature; 1 – teeth curved anteriorly.
  - 20) Lower incisors, angle of projection in relation to its insertion axis over the mandible: 0 – non-evident anterior projection of the incisors; 1 – incisors drastically projected anteriorly.
  - 21) I<sub>2</sub>, development of the distal border of the metacingulid: 0 – vestigial or absent; 1 – present.
  - 22) Development of the basal region of the lower incisors at the buccal surface: 0 – basal portion of incisors without any evidence of a developed conid; 1 – protoconid developed, forming a conid at the buccal extremity of the incisors.
  - 23) Lower incisors, displacement: 0 – incisors located in V-shaped, in alignment with the rest of dental row; 1 – incisors displaced in a narrow arch; 2 – incisors aligned among themselves and displaced in a wider dental arch.
  - 24) Lower incisors, development of parastylid (mesostylid) and distostylid: 0 – absent; 1 – present.
  - 25) I<sub>2</sub>, paraconid relative width: 0 – narrow; 1 – enlarged.

- 26) Upper canine, entocingulum development: 0 – vestigial or absent; 1 – present.
- 27) Upper canine, parastyle and metastyle development: 0 – both parastyle and metastyle reduced or absent; 1 – parastyle absent, metastyle present; 2 – both parastyle and metastyle present.
- 28) Lower canine, entocingulid development at the anterior region of the buccal surface: 0 – vestigial or absent; 1 – present (Note: This is a sexually dimorphic character in both *Cebus* and *Saimiri*).
- 29) Lower canine, entocingulid development at the posterior region of the buccal surface: 0 – vestigial or absent; 1 – present, weakly developed; 2 – present, well developed.
- 30) Shape of the canines viewed from the labial surface: 0 – triangular, in a conical shape; 1 – pyramidal, laterally compressed (“pitheciine pattern”); 2 – cylindrical.
- 31) Lower canines, lateral projection: 0 – without any apparent lateral projection; 1 – with a slight lateral projection; 2 – canines extremely projected laterally.
- 32) C-P<sub>2</sub>, relative position: 0 – teeth in contact; 1 – teeth separated by a diastema (Note: This is a variable condition in some species of *Callithrix*, *Saguinus* and *Aotus*. In species of *Pithecia*, *Chiropotes* and *Cacajao* all degrees can be found, from teeth in contact to total separation of teeth by different diastema sizes).
- 33) Premolars and molars, texture of the external layer of the enamel: 0 – smooth surface; 1 – crenulated surface (Note: In *Callicebus* there are different degrees of crenulation of the enamel).
- 34) P<sup>2</sup>, protocone development: 0 – vestigial or absent; 1 – developed.
- 35) P<sup>3-4</sup>, protocone relative development: 0 – present, developed; 1 – reduced or absent.
- 36) Upper premolars, relative size (labial surface): 0 – all premolars have the same height; 1 – P<sup>2</sup> is the biggest tooth of the series; 2 – P<sup>4</sup> is the biggest tooth of the series.
- 37) Premolars, relative position of the protocone: 0 – protocone has an anterior position in all premolars; 1 – protocone has a mesial position in P<sup>2</sup> and an anterior position in P<sup>3-4</sup>; 2 – protocone has a more mesial position in all premolars, parallel to the paracone.
- 38) Lower premolars, entocingulid development: 0 – reduced or absent; 1 – present, developed.
- 39) Upper molars, hypocone relative position: 0 – hypocone aligned to the protocone; 1 – hypocone located more buccally to the protocone (not aligned).
- 40) Upper molars, mesostyle development: 0 – absent; 1 – present.
- 41) M<sup>1-2</sup>, entocingulum development: 0 – reduced or absent; 1 – developed.
- 42) M<sup>1-2</sup>, relative size of hypocone and protocone: 0 – hypocone and protocone have similar size in both molars; 1 – hypocone and protocone have similar size in M<sup>1</sup> and hypocone is smaller than protocone in M<sup>2</sup>; 2 – hypocone is smaller than protocone in both molars; 3 – hypocone is absent.
- 43) M<sup>1-2</sup>, relative size of metacone and paracone: 0 – metacone and paracone have similar size in both molars; 1 – metacone and paracone have similar size in M<sup>1</sup> and metacone is smaller than paracone in M<sup>2</sup>; 2 – metacone is smaller than paracone in both molars.
- 44) M<sup>3</sup>, development: 0 – M<sup>3</sup> bigger than M<sup>1</sup>; 1 – M<sup>3</sup> smaller than M<sup>1</sup>, until its half-size; 2 – M<sup>3</sup> reduced, smaller than half-size of M<sup>1</sup>; 3 – M<sup>3</sup> absent.
- 45) M<sup>1-2</sup>, epimetacrista development: 0 – developed; 1 – reduced or absent.
- 46) Upper molars, metaconule development: 0 – vestigial or absent; 1 – present.
- 47) M<sup>1-2</sup>, paracone and metacone relative position: 0 – cones somewhat separated by a space; 1 – cones presenting a contact at their internal bases; 2 – both internal cusp walls are in full contact, and the basal portions are immersed each other.
- 48) Upper molars, prehypocrista development: 0 – vestigial or absent; 1 – present, reduced.
- 49) Upper molars, general shape pattern of the cusps: 0 – typically cuspidiform (sharp), high; 1 – rounded, typically bunodont; 2 – the cusps are low, not detached from the crown.
- 50) Upper molars, preprotocrista development: 0 – present; 1 – vestigial or absent (Note: This crest appears to present a trend to reduction in *Platyrrhini*).
- 51) Upper molars, postprotocrista type of contact: 0 – it is connected to the hypocone; 1 – it is extended to the distal portion of the metacone base, oriented to the metacingulum; 2 – it is connected directly to the metacone (hypometacrista).
- 52) Upper molars, entocingulum development: 0 – reduced or absent; 1 – developed, forming a detached border (Note: This character is variable among *Callicebus* species).

- 53)  $P_2$ , metaconid development: 0 – vestigial or absent; 1 – present.
- 54) Lower molars, general shape of the cusps (talonid and trigonid depth): 0 – cylindrical cusps (high crown); 1 – elongated cusps, cuspiform (high crowned); 2 – bunodont cusps, rounded (low crown); 3 – cusp reduced and practically non-detached from the crown.
- 55) Lower molars, epiprotocristid development: 0 – well developed; 1 – poorly developed (reduced).
- 56)  $P_3$ , entoconid and hypoconid development: 0 – vestigial or absent; 1 – present.
- 57)  $P_4$ , entoconid and hypoconid development: 0 – both conids developed; 1 – developed entoconid and reduced hypoconid; 2 – both conids vestigial or absent.
- 58)  $P_3$ , metaconid development: 0 – present; 1 – absent.
- 59) Lower premolars, relative size: 0 –  $P_2$  is the biggest tooth in the size-decreasing premolars series; 1 –  $P_2$  is the biggest tooth of the series, and  $P_{3-4}$  are of similar size; 2 – all three premolars have similar height.
- 60)  $M_{1-2}$ , hypoconulid development: 0 – developed in both molars; 1 – developed in  $M_1$  and vestigial or absent in  $M_2$ ; 2 – vestigial or absent in both molars.
- 61) Lower premolars, buccal projection of the talonid: 0 – non-evident; 1 – evident.
- 62) Lower premolars, basal portion development (labial surface): 0 – absence of a projection of the labial wall; 1 – presence of a curved prominence at the basal portion of the labial wall.
- 63)  $M_{1-2}$ , relative size of entoconid and hypoconid: 0 – entoconid bigger than hypoconid; 1 – entoconid with similar size in relation to the hypoconid; 2 – entoconid smaller than hypoconid.
- 64)  $M_{1-2}$ , entocristid development connecting entoconid to metaconid: 0 – deep, forming a “V” shape; 1 – flat.
- 65) Lower molars, pre-hypocristid relative position: 0 – it connects to the trigonid external wall and does not expand to the crown; 1 – it extends to the molar crown and is connected to the talonid internal wall.
- 66)  $M_3$ , development: 0 –  $M_3$  is the biggest tooth in a decreasing series; 1 –  $M_3$  has similar size of  $M_{1-2}$ ; 2 –  $M_3$  is the smallest tooth in an increasing series; 3 –  $M_3$  absent.
- 67) Lower molars, protoconid / hypoconid relative height: 0 – both cuspids similar in height; 1 – hypoconid lower than protoconid.
- 68) Lower molars, relative width of trigonid and talonid (labio-buccal axis): 0 – both similar in width; 1 – talonid larger than trigonid.
- 69)  $P_2$ , entocingulid development: 0 – developed; 1 – absent.
- 70) Lower molars, relative position of protoconid and metaconid: 0 – both cuspids aligned; 1 – metaconid placed more distally in relation to the protoconid.
- 71) Lower molars, paraconid development: 0 – present; 1 – vestigial or absent.
- 72)  $M_3$ , epi-hypocristid development: 0 – present; 1 – vestigial or absent.
- 73)  $P_2$ , inclination of the labial wall towards the interior part of the arch: 0 – non-evident; 1 – evident.
- 74) Lower molars, development of a fossa between the labial cusps: 0 – present; 1 – vestigial or absent.
- 75) Mandible, relative position of coronoid and condylar processes: 0 – one process away from another one; 2 – processes placed closer to each other.
- 76) Mandible, relative height between coronoid and condylar process: 0 – coronoid process slightly higher than the condylar process, but similar in general aspect; 1 – coronoid process higher than the condylar process; 2 – coronoid process lower than the condylar process.
- 77) Mandibular ramus, shape of the ventro-distal border: 0 – rectangular; 1 – rounded; 2 – rounded and with a distal projection.
- 78) Mandible, angular process development: 0 – vestigial or absent; 1 – detached as an extremity (Note: This character is variable in *Aotus* specimens).
- 79) Mandible, development of the symphyseal region: 0 – with a narrow area of contact; 1 – with a wide area of contact, resulting in a relatively wide anterior surface.
- 80) Mandible, *ptergoideus internus* area of insertion: 0 – poorly detached, without any external marks; 1 – well developed and forming a detached concavity, visible from the external mandible surface.
- As previously mentioned, other non-dental morphological characters gathered from the literature by HOROVITZ (1999), except the last two, were included in the data matrix in order to allow a broader morphological context to our analysis. These characters are the following:
- 81) Offspring per birth, number: 0 – one; 1 – two.

- 82) Lumbar vertebrae, number: 0 – more than five; 1 – five or fewer.
- 83) External thumb: 0 – absent or reduced; 1 – present.
- 84) Tail, ventral glabrous surface: 0 – absent; 1 – present.
- 85) Claws on manual and pedal digits except hallux: 0 – absent; 1 – present.
- 86) Postglenoid foramen: 0 – absent; 1 – reduced; 2 – large.
- 87) Middle ear, pneumatization of anteroventral region: 0 – absent; 1 – present.
- 88) Middle ear, paired prominences on cochlear housing: 0 – absent; 1 – present.
- 89) Pterygoid fossa, depth: 0 – deep; 1 – shallow.
- 90) Canal connecting sigmoid sinus and subarcuate fossa: 0 – absent; 1 – present.
- 91) Vomer, exposure in orbit: 0 – absent; 1 – present.
- 92) Temporal emissary foramen: 0 – present and large; 1 – small or absent.
- 93) Eyeball physically enclosed: 0 – absent; 1 – present.
- 94) Cranial capacity: 0 – less than 15cm<sup>3</sup>; 1 – more than 15cm<sup>3</sup>.
- 95) Zygomatic arch, ventral extent: 0 – below plane of alveolar level; 1 – above plane of alveolar level.
- 96) Pterion region, contacts: 0 – zygomatic-parietal; 1 – frontal-alisphenoid.
- 97) Infraorbital foramen, vertical position relative to the maxillary cheek teeth in Frankfurt plane: 0 – above interval between (or caudal to) M<sup>1</sup> and P<sup>4</sup>; 1 – above interval between P<sup>4</sup> and P<sup>3</sup>; 2 – above (or rostral to) anteriormost premolar.
- 98) Zygomaticofacial foramen, size relative to maxillary M<sup>1</sup> breadth: 0 – small; 1 – large.
- 99) Number of premolars: 0 – two; 1 – three.
- 100) Carpometacarpal joint of thumb: 0 – non-saddle; 1 – saddle.
- 101) Orientation of the nares: 0 – parallel (narrow nose); 1 – lateral (broad nose).
- 102) Cheek, development: 0 – absent; 1 – present.

#### PARSIMONY ANALYSIS

The data matrix (APPENDIX II) built with these 102 characters and the 23 terminal taxa was submitted to a *branch and bound* algorithm. The results generated 40 equally parsimonious trees with a length of 290 steps, and consistency and retention indices of 0.483 and 0.677, respectively

(complete statistics of the analysis are available upon request). A strict consensus of these 40 trees was retrieved, yielding a tree with 15 components (clades), with five unresolved trichotomies (Fig.1).

In the consensus tree in figure 1, two major clades diverge from the platyrrhine basal node. One includes Cebinae and Callitrichinae, representing the family Cebidae. The other represents the family Atelidae, composed of Pitheciinae and Atelinae, with Alouattini and Atelini as sister taxa within the later. Among cebids, Cebinae is formed by a trichotomous clade joining *Cebus*, *Saimiri*, and *Carlocebus*. They are phylogenetically related to the branch that joins *Aotus* as the sister taxon of *Callicebus*. The Callitrichinae clade has *Callimico* rooted at the basal node and then *Saguinus* as the next basal taxon, followed by *Leontopithecus*. *Leontopithecus* is the sister taxon of the clade represented by a polytomy with the three subgenera of *Callithrix*: *Cebuella*, *Mico*, and *Callithrix*. The two clades that stand as particularly well supported with Bremer values equal or higher than five are the Callitrichinae and Pitheciinae. Since the fossils in question are atelids, more information is provided here on the morphological basis of their interrelationships. Atelidae is composed of the pitheciine and ateline clades. The former is subdivided into two clades: the first one is represented by a polytomy with *Alouatta*, *Brachyteles*, and *Stirtonia*, and another one has *Lagothrix* rooted at the basal node as sister of a trichotomy with *Ateles*, *Caipora*, and *Protopithecus*. The synapomorphies, consistency indices and transformations for each character supporting Atelinae are: 13 (0.25; 0†1), 16 (0.33; 0†2), 25 (0.50; 0†1), 26 (0.40; 0†2), 36 (0.33; 1†2), 57 (0.40; 0†1), 59 (0.33; 0†2), 62 (0.33; 0†1), 79 (0.25; 1†0), 82 (1.00; 0†1), 84 (1.00; 0†1), 92 (0.67; 1†0), 97 (0.50; 2†1), and 98 (0.33; 0†1). On the other hand, the tribe Alouattini is supported by the following synapomorphies: 10 (0.50; 1†0), 39 (0.33; 0†1), 40 (0.33; 0†1), 46 (0.40; 0†1), 47 (0.33; 2†0), 51 (0.67; 2†1), 52 (0.50; 0†1), 61 (0.50; 0†1), 64 (0.33; 1†0), 66 (0.60; 2†0), 68 (0.25; 0†1), and 73 (0.33; 1†0). Our analysis, therefore, shows that the two giant fossil platyrrhines are closely related to *Ateles* and fall within the tribe Atelini, along with *Lagothrix*. The following six apomorphic characters support the monophyly of the tribe Atelini: 5 (0.50; 0†1), 14 (1.00; 1†0), 42 (0.75; 2†1), 43 (0.33; 1†2), 45 (0.25; 1†0), and 86 (0.50; 0†1). The clade composed by the two giant fossils and *Ateles* is supported by the following eight

transformation series: 18 (0.50; 0†1), 49 (0.67; 0†1), 53 (0.33; 0†1), 54 (0.60; 0†2), 63 (1.00; 0†2), 71 (0.25; 0†1), 72 (0.33; 1†0), and 83 (0.50; 1†0). According to the alternatives observed among the 40 equally parsimonious trees, *Ateles* consistently occupies a sister position either to *Caipora* or *Protopithecus*.

DISCUSSION

The cladistic patterns that arose from our analysis of platyrrhine relationships agree well with previous morpho- and molecular-based arrangements proposed. This is especially true for the following:

1) The affinities between *Cebus* and *Saimiri* is an outcome that reinforces relationships proposed by ROSENBERGER (1981), BARROSO *et al.* (1997), HARADA *et al.* (1995), PORTER *et al.* (1997), HOROVITZ *et al.* (1998), CANAVEZ *et al.* (1999) and HOROVITZ (1999).

2) *Aotus* and *Callicebus* as sister taxa (ROSENBERGER, 1981; FORD, 1986; SORCI *et al.*, 1997); conversely, *Carlocebus* emerged as a component of the clade Cebinae, in contrast with HOROVITZ's proposal (1999) that places *Carlocebus carmemensis* together with the calitrichines. However, much is need to know about the taxonomical status of the two species currently recognized as part of the genus *Carlocebus* (*C. carmemensis* and *C. intermedius*).

3) The monophyletic status of Callitrichinae is well corroborated, with *Callimico* rooted at the basal node, followed by *Saguinus* and *Leontopithecus* (ROSENBERGER, 1981; FORD, 1986; KAY, 1990) and the "Callithrix" clade, encompassing the subgenera *Cebuella*, *Mico*, and *Callithrix* (BARROSO *et al.*, 1997).

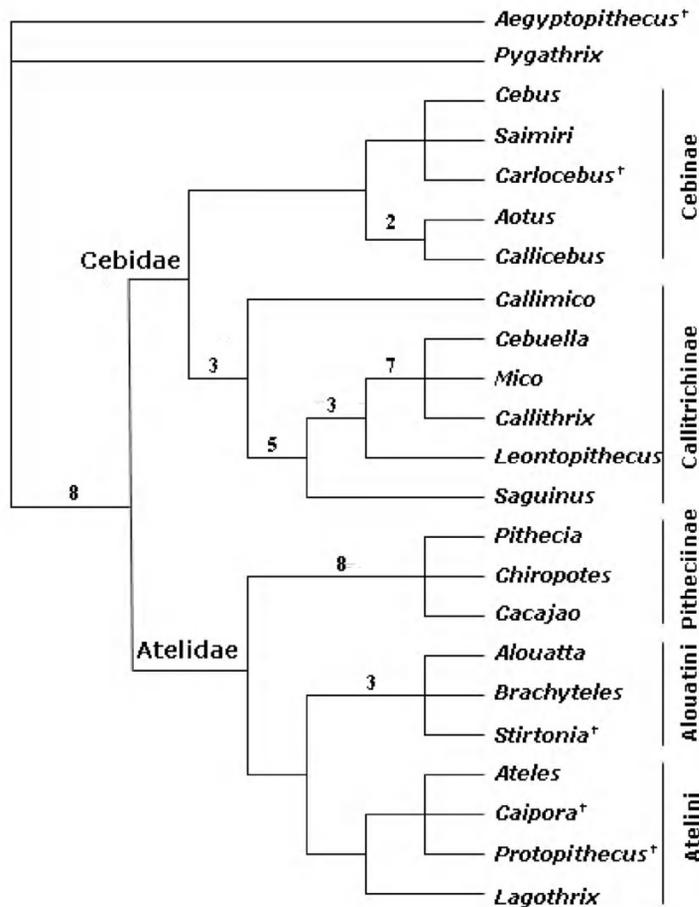


Fig.1- Strict consensus tree of 40 equally parsimonious trees showing relationships within the platyrrhines (CI= 0.483; RI= 0.677). Bremer support is indicated for clades with values higher or equal to 2.

- 4) The monophyletic status of Atelidae is pointed out, as widely accepted in the current literature.
- 5) Subfamily Pitheciinae, with *Pithecia*, *Chiropotes* and *Cacajao*, has received full support from all sources of data. On the other hand, our analysis does not confirm the position of *Callicebus* at the subfamily's basal node, as many have recently found.
- 6) The monophyly of Atelinae is indicated, as widely supported by various studies.
- 7) *Alouatta* and *Stirtonia* have close affinities as alouattines, as is widely agreed. Conversely, the idea that *Brachyteles* is more closely related to the Alouattini than to *Ateles* has not received much support, with a few exceptions (KAY, 1990; MACPHEE *et al.* 1995).
- 8) Close affinities between *Ateles* and *Lagothrix* are pointed out (KAY, 1990; MACPHEE *et al.*, 1995).

Our results, which are largely based on dental morphology, are in agreement with CARTELLE & HARTWIG (1996) and HARTWIG & CARTELLE (1996) to the extent that *Caipora* and *Protopithecus* should be recognized as atelines and that *Caipora* is closely related to *Ateles*. However, our data provides no support for the interpretation of *Protopithecus* being an alouattin. We suspect that more progress on uncovering the phylogenetic relationships of these unique giant monkeys will be possible as we untangle the mosaic pattern found in their craniodental and postcranial structures.

To conclude, these two unique giant Brazilian subfossil monkeys, *Caipora* and *Protopithecus*, offer a special opportunity for new phylogenetic and paleontological enterprises to be undertaken, which will definitely open new avenues for the understanding of the New World monkeys' evolutionary history.

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## APPENDIX I

## SPECIMENS EXAMINED

- Alouatta belzebul* (Linnaeus, 1766) – BRASIL, MARANHÃO, Imperatriz: MN21089 (♀ ).  
*Alouatta caraya* (Humboldt, 1812) – BRASIL, MATO GROSSO, Alto Xingu: MN11704 (♀ ).  
*Alouatta seniculus* (Linnaeus, 1766) – BRASIL, PARÁ, Almeirim: MN2774 (♂ ); BRASIL, RORAIMA, Boa Vista: MN21129 (♀ ), MN 23155 (♂ ).  
*Aotus infulatus* Kuhl, 1820 – BRASIL, MATO GROSSO: MN2701 (sex indet.).  
*Aotus nigriceps* Dollman, 1909 – BRASIL, RONDÔNIA, Rio Jamari: MN28495 (♂ ).  
*Aotus vociferans* (Spix, 1823) – BRASIL, AMAZONAS, Rio Purus: MN2695 (♀ ).  
*Ateles paniscus* (Linnaeus, 1758) – BRASIL, AMAZONAS, Paraná do Manhãna: MN2500 (♀ ); BRASIL, AMAZONAS, Norte do Rio Amazonas: MN6035 (♂ ), MN6037 (♀ ); BRASIL, AMAZONAS, Fonte Boa: MN21058 (♀ ); BRASIL, MATO GROSSO, Rio Jaurú: MN506 (♀ ); BRASIL, MATO GROSSO, Alto Tapajós: MN32701 (♂ ); BRASIL, MATO GROSSO, Cáceres: MN33615 (sex indet.); unknown locality: MN1093 (sex indet.), MN2476 (♂ ).  
*Brachyteles aracnoides* (E. Geoffroy, 1806) – BRASIL, RIO DE JANEIRO, Parati: MN8513 (♀ ), MN6699 (♂ ), MN7724 (♂ ); unknown locality: MN8514 (♂ ), MN30188 (♂ ).  
*Cacajao calvus* (I. Geoffroy, 1847) – BRASIL, AMAZONAS, Paraná do Manhãna: MN2444 (♀ ), MN2452 (♀ ).  
*Cacajao melanocephalus* (Humboldt, 1811) – VENEZUELA, Serra do Imery: MN2437 (♂ ), MN2439 (♀ ).  
*Callicebus moloch* (Hoffmannsegg, 1807) – COLOMBIA: MN2486 (sex indet.); BRASIL, AMAZONAS, Aripuanã: MN2480 (sex indet.); BRASIL, PARÁ, Vila Braga: MN2472 (♂ ); BRASIL, PARÁ, Santarém: MN11592 (♀ ), MN11593 (♂ ); BRASIL, PARÁ: MN21062 (♂ ); unknown locality: MN414 (sex indet.).  
*Callicebus personatus* (E. Geoffroy, 1812) – BRASIL, ESPÍRITO SANTO, São Domingos: MN21053 (♂ ); BRASIL, ESPÍRITO SANTO: MN30181 (♂ ).  
*Callicebus torquatus* (Hoffmannsegg, 1807) – BRASIL, AMAZONAS, Foz do Castanho: MN2482 (sex indet.); BRASIL, AMAZONAS, Fonte Boa: MN21047 (♂ ).  
*Callimico goeldii* (Thomas, 1904) – BRASIL, ACRE, Porongaba, margem direita do Alto Rio Juruá: MPEG22969 (♂ ); PARÁ, BRASIL: MN23736 (♂ ); BRASIL, Rio Juruá, Seringal Oriente, próximo à Vila Taumaturgo: MPEG214 (♂ ); Rio Yaco, cabeceira do Rio Purus: MPEG443 (♂ ); unknown locality: MUZUSP 11355 (♂ ).  
*Callithrix argentata* (Linnaeus, 1766) – BRASIL, PARÁ, Piquiatuba: MN5946 (♀ ); BRASIL, PARÁ, Cametá: MN5954 (♂ ); BRASIL, MATO GROSSO, Córrego do Cabral: MN2855 (sex indet.); BRASIL, MATO GROSSO, São Luiz de Cáceres: MN5845 (♂ ).  
*Callithrix aurita* (E. Geoffroy, 1812) – BRASIL, MINAS GERAIS, Além Paraíba: MN1354 (♀ ), MN1355 (♂ ).  
*Callithrix flaviceps* (Thomas, 1903) – BRASIL, ESPÍRITO SANTO, Santa Teresa: MN5875 (♀ ); MN178 (sex indet.): unknown locality.  
*Callithrix geoffroyi* (Humboldt, 1912) – BRASIL, MINAS GERAIS, Conceição do Mato Dentro: MN13481 (♂ ), MN13482 (♀ ); BRASIL, ESPÍRITO SANTO, Morro da Argola: MN3958 (♂ ), MN3962 (♀ ), MN3970 (♂ ).  
*Callithrix humeralifer* (Humboldt, 1812) – BRASIL, AMAZONAS, Lago do Baptista, Rio Amazonas: MN5944 (♀ ), MN5948 (♂ ); BRASIL, PARÁ, Rio Tapajós, Vila Braga: MN2838 (♀ ), MN2839 (♂ ).  
*Callithrix jacchus* (Linnaeus, 1758) – BRASIL, SERGIPE, Cristinópolis: MN30541 (♂ ), MN30544 (♀ ); BRASIL, RIO DE JANEIRO, Parque Nacional da Tijuca: MN5570 (♀ ); unknown locality: MN5566 (sex indet.).  
*Callithrix penicillata* (E. Geoffroy, 1812) – BRASIL, BAHIA, Barreiras: MN4260 (♀ ), MN4261 (♂ ); BRASIL, BAHIA, Ilhéus: MN8527 (♂ ), MN8535 (♂ ), MN8538 (♀ ); BRASIL, MINAS GERAIS, Uberaba: MN7565 (♀ ); BRASIL, MINAS GERAIS, Araguari: MN7566 (♂ ).  
*Cebuella pygmaea* (Spix, 1823) – PERU, LORETO, Territorio Yahuas: MN2781 (♂ ), MN2782 (♂ ); PERU, IQUITOS: MPEG 201 (♀ ), MPEG 848 (♂ ); PERU, CHIMBOTE, Rio Solimões: MPEG 283 (♂ ); BRASIL, AMAZONAS, Alto Solimões: MN11910 (♂ ); ACRE, OCIDENTE, margem direita, Alto Rio Juruá: MPEG 22951 (♀ ); unknown locality: MN2783 (sex indet.).  
*Cebus apella* (Linnaeus, 1758) – BRASIL, PARÁ, Paragominas: MN23336 (sex indet.), MN23337 (sex indet.); BRASIL, PARÁ, Nova Timboteua: MN23344 (♀ ), MN23346 (♀ ); BRASIL, RIO DE JANEIRO, Parque Nacional de Itatiaia: MN21171 (♂ ).  
*Cebus olivaceus* Schomburgk, 1848 – BRASIL, RONDÔNIA, Boa Vista: MN23525 (F), MN23526 (♂ ).  
*Chiropotes albinasus* (I. Geoffroy and Deville, 1848) – BRASIL, PARÁ, Serra do Cachimbo: MN21067 (♀ ), MN25718 (♀ ).

- Chiropotes satanas* (Hoffmannsegg, 1807) – BRASIL, RORAIMA, Parecis: MN454 (♂); BRASIL, AMAZONAS, Rio Catrimani: MN2909 (♂); BRASIL, PARÁ, Nova Timboteua: MN21056 (♀).
- Lagothrix lagothricha* (Humboldt, 1812) – BRASIL, AMAZONAS, Baixo Solimões: MN2722 (♂); BRASIL, AMAZONAS, São Manoel: MN2729 (♀); unknown locality: MN518 (♀), MN30196 (♂), MN30198 (sex indet.).
- Leontopithecus crhysomelas* (Kuhl, 1820)– BRASIL, BAHIA, Ilhéus: MN8518 (♂); BRASIL, BAHIA, Pontal: MN8521 (♀).
- Leontopithecus rosalia* (Linnaeus, 1766)– BRASIL, RIO DE JANEIRO, Marica: MN3964 (♂), MN3965 (♀), MN3966 (♂); unknown locality: MN186 (sex indet.), MN5491 (♀).
- Pithecia irrorata* Gray, 1842 – BRASIL, AMAZONAS, Rio Purus: MN3317 (♀); BRASIL, AMAZONAS, São Manuel: MN3339 (♂).
- Pithecia monachus* (E. Geoffroy, 1812) – BRASIL, AMAZONAS, Fonte Boa, Rio Solimões: MN3312 (♀); unknown locality: MN7662 (sex indet.).
- Saguinus bicolor* (Spix, 1823) – BRASIL, AMAZONAS, Manaus, Flores: MN23859 (sex indet.), MN23862 (sex indet.); unknown locality: MN2864 (sex indet.).
- Saguinus fuscicollis* (Spix, 1823) – COLOMBIA, CAQUETA, Rio Mecaya: MN24797 (♀); RORAIMA, UHE Samuel: MN28483 (♂), MN28484 (♀); BRASIL, AMAZONAS, Rio Juruá: MN5934 (♀), MN5937 (♂); BRASIL, AMAZONAS, Rio Juruá, Lago Grande: MN5956 (♂); BRASIL, AMAZONAS, Rio Juruá, Santo Antônio: MN5957 (♀); BRASIL, AMAZONAS, Tefé, Mata Patrimônio: MN23848 (♂); BRASIL, AMAZONAS, Coari: MN23850 (♂); BRASIL.
- Saguinus geoffroyi* (Pucheran, 1845) – COLOMBIA, UNGUIA, Choco: MN24771 (♂).
- Saguinus imperator* (Goeldi, 1907) – BRASIL, AMAZONAS, Rio Juruá, Santo Antônio: MN5929 (♂), MN5930 (♀).
- Saguinus labiatus* (Humboldt, 1812) – BRASIL, AMAZONAS, Rio Purus: MN2481 (♀), MN2482 (♂).
- Saguinus leucopus* (Günther, 1876) – COLOMBIA, PURI, Antioquia: MN28845 (♂).
- Saguinus midas* (Linnaeus, 1758) – BRASIL, AMAPÁ, Serra do Navio: MN20546 (♀), MN20547 (♂); BRASIL, AMAZONAS, Fonte Boa: MN23853 (♀), MN23854 (♂); BRASIL, PARÁ, Paragominas: MN23830 (♀), MN23831 (♂).
- Saguinus pileatus* (I. Geoffroy and Deville, 1848) – BRASIL, AMAZONAS, Tefé: MN23846 (♀), MN23847 (♀).
- Saimiri sciureus* (Linnaeus, 1758) – BRASIL, AMAPÁ, Oiapoque: MN20592 (♂); BRASIL, AMAPÁ, Rio Tracajatuba: MN20563 (♂); BRASIL, AMAZONAS, Lago do Batista: MN6056 (sex indet.), MN6079 (♂); BRASIL, PARÁ, Nova Timboteua: MN23532 (sex indet.).
- Pygathrix* sp. – unknown locality: MN61604 (sex indet.).
- Tarsius* sp. – unknown locality: MN2711 (♂).

## EXTINCT SPECIES

- Caipora bambuorum* Cartelle & Hartwig, 1996 – BRASIL - BAHIA: Campo Formoso, Toca da Boa Vista (type-locality) – (40°51'39"W, 10°09'36"S); Pleistocene: IGC-UFMG 05. Material: caudal vertebrae, incomplete pelvis and scapula, long bones from both upper and lower limbs, carpals, metacarpals, tarsals and phalanges. Skull (maxilla with I<sup>1</sup>-P<sup>3</sup>; right P<sup>4</sup>; left M<sup>1</sup>; right M<sup>2</sup>; M<sup>3</sup>) and mandible (with right I<sub>1-2</sub>; C-P<sub>2</sub>; right P<sub>3</sub>; P<sub>4</sub>-M<sub>1</sub>; left M<sub>2</sub>; M<sub>3</sub>).
- Protopithecus brasiliensis* Lund, 1838 – BRASIL - BAHIA: Campo Formoso, Toca da Boa Vista (type-locality) – (40°51'39"W, 10°09'36"S); Pleistocene: IGC-UFMG 06. Material: several vertebrae, scapulae, long bones from upper and lower limbs, carpals, metacarpals, tarsals, metatarsals, phalanges, skull (maxilla containing I<sup>1</sup>-C; P<sup>3</sup> isolated; left P<sup>4</sup>; part of left M<sup>1</sup>; left M<sup>2</sup>; M<sup>3</sup>) and mandible (with I<sub>1</sub>-C; right P<sub>2</sub>; P<sub>3</sub>-P<sub>4</sub>).
- Carlocebus carmenensis* Fleagle, 1990 –Pinturas Formation, SANTA CRUZ PROVINCE, ARGENTINA; Lower Miocene. (FLEAGLE, 1990).
- Carlocebus intermedius* Fleagle, 1990 – Pinturas Formation, SANTA CRUZ PROVINCE, ARGENTINA; Lower Miocene. (FLEAGLE, 1990).
- Stirtonia tatacoensis* Hershkovitz, 1970 – LA VENTA, COLOMBIA; Middle Miocene. (HERSHKOVITZ, 1970; SETOGUCHI *et al.*, 1983; KAY *et al.*, 1987; 1989).
- Stirtonia victoriae* Kay *et al.*, 1987 Locality – LA VENTA, COLOMBIA; Middle Miocene. (KAY *et al.*, 1987).
- Aegyptopithecus zeuxis* Simons, 1965 – Fayum Depression, EGYPT; Middle Oligocene. (SZALAY & DELSON, 1979).





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