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# The Current Status of the New World Monkey Phylogeny[*]

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## ABSTRACT

Four DNA datasets were combined in tandem (6700 bp) and Maximum parsimony and Neighbor-Joining analyses were performed. The results suggest three groups emerging almost at the same time: Atelidae, Pitheciidae and Cebidae. The total analysis strongly supports the monophyly of the Cebidae family, grouping *Aotus, Cebus* and *Saimiri* with the small callitrichines. In the callitrichines, the data link *Cebuela* to *Callithrix,* place *Callimico* as a sister group of *Callithrix/Cebuella,* and show *Saguinus* to be the earliest offshoot of the callitrichines. In the family Pithecidae, *Callicebus* is the basal genus. Finally, combined molecular data showed congruent branching in the atelid clade, setting up *Alouatta* as the basal lineage and *Brachyteles-Lagothrix* as a sister group and the most derived branch. Two major points remain to be clarified in the platyrrhine phylogeny: (i) what is the exact branching pattern of *Aotus, Cebus, Saimiri* and the small callitrichines, and (ii), which two of these three lineages, pitheciines, atelines or cebids, are more closely related?

**Key words:** New World monkeys, Platyrrhine, Taxonomy, Molecular, Evolution

## INTRODUCTION

The systematics of New World monkeys has been a subject of strong debate during the last three decades. The main protagonists and their taxonomic proposals are: Simons (1972), Hershkovitz (1977), Rosenberger (1981), Ford (1986), and Kay (1990). All of these proposals are based mainly on morphological or ecological studies. The majority of the authors agree with the existence of three monophyletic clades: the large monkeys with a prehensile tail, a group constituted by *Alouatta, Ateles, Lagothrix*, and *Brachyteles*; the seed predator monkeys, consisting of *Pithecia, Chiropotes*, and *Cacajao*, and the small clawed monkeys, composed of the *Saguinus, Leontopithecus, Callithrix*, and *Cebuella* genera. However, they disagree in relation to the branching order among these three major clades, within the ateline and callitrichine clades, and also on the placement of *Saimiri, Cebus, Aotus, Callicebus,* and *Callimico.*

Hershkovitz (1977), placed the small *Callimico* in its own family Callimiconidae, based on its controversial features: this genus shares small body size and the presence of claws instead of nails with the callitrichines, and single pregnancy and the presence of a third molar with the remaining platyrrhine lineages. On the other hand, based on those ambiguous affinities, other morphologists place *Callimico* as the first callitrichine offshoot to diverge from the common ancestor (Rosenberger 1981, Ford 1986, Kay 1990). *Cebus* and *Saimiri* are considered

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by Ford (1986) as the earliest offshoot lineages of the New World primate radiation, but Kay (1990), places *Cebus* as the basal platyrrhine and *Saimiri* as a sister group of the callitrichines. Conversely, Rosenberger (1981) considers *Cebus* and *Saimiri* as sister groups of the callitrichines. The position of the *Callicebus* genus has been also controversial. According to Kay (1990) *Callicebus* is the most basal of the callitrichine tree, and Ford (1986) places *Callicebus* together with *Cebus* and *Saimiri* as the most basal clade of the platyrrhines. However, Rosenberger & Coimbra-Filho (1984) and Rosenberger *et al*. (1990) argued that *Callicebus* and *Aotus* are sister lineages linked to the pitheciine clade. In a more drastic point of view, Tyler (1991) suggested that *Aotus* must be removed from the ceboid clade and placed in a sister group of the entire Anthropoidea. Supporting this proposal, Tejedor (1998) additionally pointed out that *Aotus* and *Callicebus* are ancient taxa and suggested that they have a common ancestor. His belief is based on the assumption that the two Miocene genera, *Homunculus* and *Carlocebus*, show many primitive characters shared by both *Aotus* and *Callicebus*.

The authors also disagree on the internal arrangements within atelines and callitrichines. In the ateline clade the four genera are arranged in three different ways: *Ateles* and *Brachyteles* as sister groups (Rosenberger 1981), *Brachyteles, Lagothrix* and *Ateles* in a non-resolved trichotomy (Ford 1986), and two clades composed of *Ateles-Lagothrix* and *Alouatta-Brachyteles* (Kay 1990). Inside the callitrichines, most of the authors consider the gumivorous *Cebuella* and *Callitrix* as the most derived lineages. For *Saguinus* and *Leontopithecus* there are two proposals: one places *Leontopithecus* as a sister group of *Callithrix-Cebuela* (Rosenberger 1981) and the other places *Saguinus* as a sister group of the gumivorous monkeys (Ford 1986, Kay 1990).

## THE MOLECULAR DATA

Molecular data suitable to cladistic analysis of the New World monkeys were first obtained at the beginning of the 90's, being the first DNA dataset of aligned sequences of the nuclear epsilon globin gene involving all 16 platyrrhine genera and was published by Schneider *et al*. (1993). Subsequently, a series of datasets was generated, some including all extant New World primate genera (Schneider *et al*. 1996, Canavez *et al*. 1999a, von Dornam & Ruvolo 1999, Goodman *et al*. 1998), while others concentrated on particular clades (Canavez *et al*. 1999b, Chaves *et al*. 1999, Meireles *et al*. 1999, Porter *et al*. 1997a b, Porter *et al*. 1999, Pastorini *et al*. 1998, Tagliaro *et al*. 1997).

Table I summarizes the results involving four nuclear datasets (IRBP, EPSILON, G6PD, and $\beta$-2M) for all extant New World primates, and additional molecular data (vWF, upstream region EPSILON, $\gamma$-Globin, ND4, and tRNA) including specific clades. The four DNA datasets (EPSILON, IRBP, G6PD and $\beta$-2M) were combined in tandem to perform a total analysis using Maximum parsimony (MP) and Neighbor-Joining (NJ) approaches utilizing PAUP version 4.0b3a (Swofford, 1998). Figure 1 shows the consensus tree. Percentages at nodes indicate bootstrap support for that particular node, while nodes with stars mean 99-100% bootstrap support. The branch lengths of the Neighbor-Joining tree (Saitou & Nei, 1987) were estimated by the least-squares method referred to in Takezaki *et al*. (1995). MP and NJ trees were almost identical, differing only in the placement of *Aotus*. The MP tree placed *Aotus* as the basal lineage of the Callitrichine clade, while NJ showed *Aotus* to occur in an unresolved trichotomy with the *Cebus-Saimiri* clade and the callitrichines.

The four nuclear genes ($\beta$-2M, EPSILON, G6PD, and IRBP) analyzed separately are not congruent with regards to the close relationship among the three major clades (pitheciine, ateline, callitrichine). EPSILON and $\beta$-2M support a pitheciine-ateline clade, whereas G6PD groups the ateline with the callitrichine clade, and IRBP shows the pitheciine clade to be closer to the callitrichine clade. The topology resulting from the total analysis, favors the

**TABLE I**

**DNA Studies that Elucidate New World monkeys Phylogeny**

| GENES | Kb | AUTHORS | Pitheciine-Ateline-Cebid relationship | *Aotus*, *Cebus* and *Saimiri* as closely linked to callitrichines | *Callicebus* as basal genus of the pitheciine clade | *Lagothrix* and *Brachyteles* as sister group in the ateline clade | Callitrichine clade | |
|---|---|---|---|---|---|---|---|---|
| | | | | | | | *Saguinus* as basal genus | *Callimico* and *Callithrix* as sister group |
| | | | BS% | BS% | BS% | BS% | BS% | BS% |
| EPSILON | 1,8 | Schneider *et al*. 1993 | PA=79 | 94 | 99 | 86 | 77[*] | 69 |
| IRBP | 1,9 | Schneider *et al*. 1996 | PC=96 | 99 | 100 | 77 | 100 | 84[**] |
| G6PD | 1,2 | Von Dorman & Ruvolo, 1999 | AC=40 | 83 | 78 | 72 | 100 | 80 |
| B2M | 1,7 | Canavez *et al*. 1999a | PA=72 | 56 | 87 | 96 | 100 | 92 |
| vWF | 0,7 | Chaves *et al*. 1999 | | | | | 98 | 84 |
| EPSILON and 5' region | 1.8 to 4.3 | Porter *et al*. 1997a | PAC=100 | 100 | | | | |
| EPSILON 5' region | 1.2 – 1.4 | Porter *et al*. 1999 | | | 100 | | | |
| ND4, tRNAs | 0,8 | Pastorini *et al*. 1998 | | | | | 81[*] | 80 |
| Gamma-Globin | 9,6 | Meireles *et al*. 1999 | | | | 100 | | |

BS: Bootstrap Support. Bootstrapping involves creating a new data set by sampling N characters randomly with replacement, so that the resulting data set has the same size as the original, but some characters have been left out and others are duplicated. The random variation of the results from analyzing these bootstrapped data sets can be shown statistically to be typical of the variation that you would get from collecting new data sets (Felseinstein, 1985).

PA = Pitheciines × Atelines; PC = Pitheciines × Cebids; AC = Atelines × Cebids; PAC = unresolved trichotomy

[*] *Saguinus and Leontopithecus* as sister group

[**] *Callimico and Leontopithecus* as sister group of *Callithrix*

ateline-pitheciine clade, but the bootstrap support is not strong (78%) in the MP tree. In addition, Porter *et al*. (1997b)'s analysis using 5'upstream region of epsilon gene in selected primates taxa showed the three major clades in an unresolved trichotomy. The poor resolution of the phylogenetic reconstruction of the three major platyrrhine lineages, resulting from the most robust molecular dataset so far available for the New World monkeys, strongly suggests that the pitheciines, atelines and cebids emerged at almost the same time in the platyrrhine radiation. These lineages are named by Schneider *et al*. 1996, Schneider & Rosenberger 1996 and Goodman *et al*. 1998, as the Atelidae, Pitheciidae and Cebidae families.

In the Pitheciidae family the four nuclear genes and the joint DNA analysis significantly placed *Callicebus* as a sister group of the traditional pitheciines, *Pithecia*, *Chiropotes* and *Cacajao* (bootstrap values ranging from 78 to 100%). These results were reinforced by the complementary study of Porter *et al*. (1999) encompassing more than 4 Kb of the epsilon globin gene and its upstream region.

The joint analysis strongly supports the monophyly of the Cebidae family, grouping *Aotus*, *Cebus*, and *Saimiri* with the small callitrichines (bootstrap values from 83 to 100%). Additionally, three of the four nuclear genes (IRBP, G6PD, $\beta$-2M), and

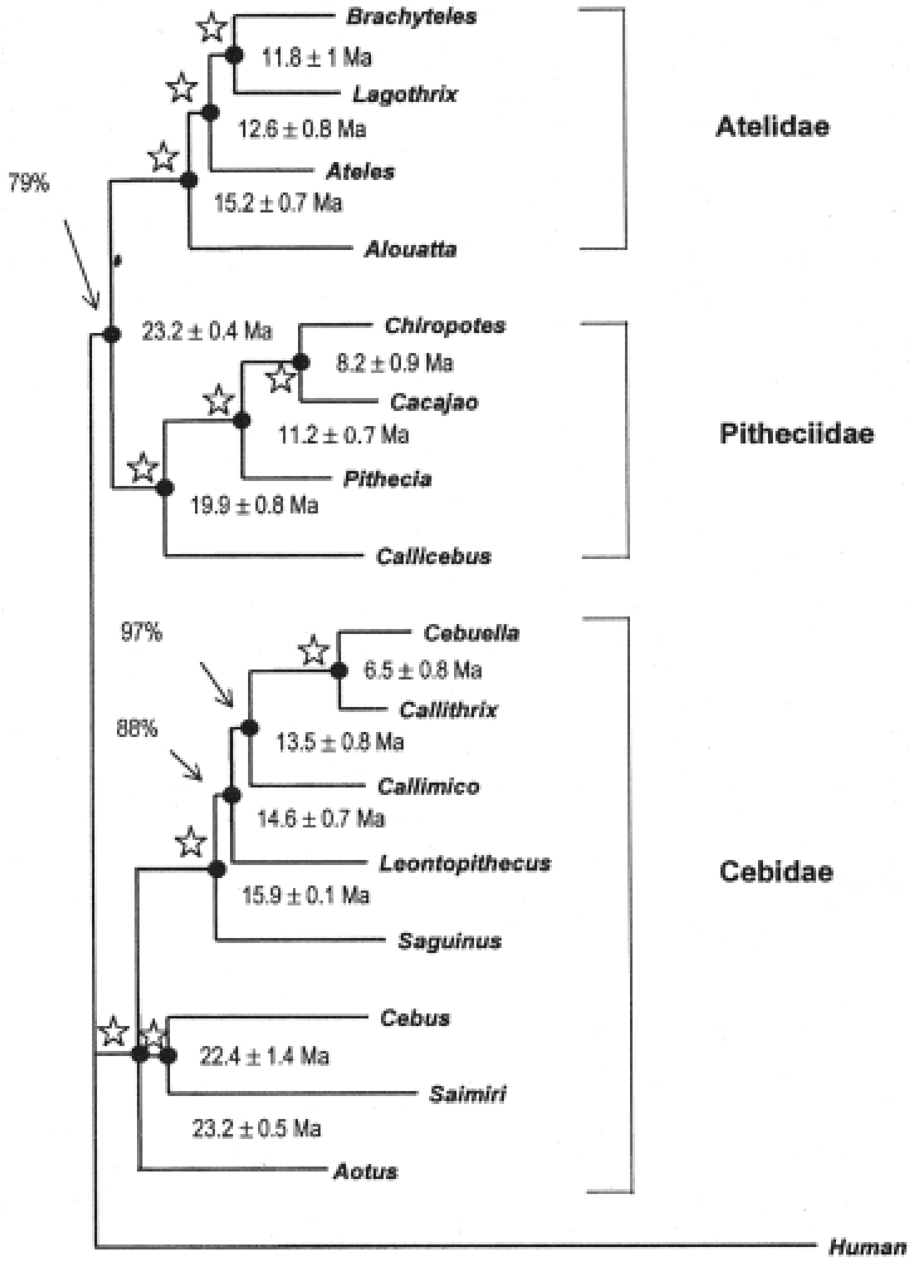

Fig. 1 – Phylogenetic tree found for the 17 sequences of the $\beta$2-M, EPSILON, G6PD and IRBP genes aligned in tandem. Branch lengths and standard deviations were estimated based on least-squares method described in Takezaki *et al*. (1995). Divergence times were estimated using the local molecular clock strategy as described in Schneider *et al*. (1993). MP Bootstrap values at the nodes were obtained in 1000 replicates. Stars at nodes means BS of 99-100%. The length and Consistency index of the MP tree was 2855 and 0.83, respectively.

the epsilon upstream region of Porter *et al*. (1997a, 1999) also indicate a close relationship between *Cebus* and *Saimiri*. Among the callitrichines, additional molecular data of Pastorini *et al*. (1998) using mitochondrial DNA; Chaves *et al*. (1999), Canavez *et al*. (1999a b), using nuclear DNA (intron 11 of von Willebrand, $\beta$-2-microglobulin genes), strongly supported the reclassification of Cebuela as belonging to the *Callithrix* genus (See also Porter *et al*. 1997b, Barroso *et al*. 1997) and also significantly placed *Callimico* as a sister group of *Callithrix*, contrary to the traditional view of *Callimico* as being basal to the callitrichines. Five of the six genes, and the joint analysis placed *Saguinus* as the basal genus of the callitrichine tree with significant bootstrap values (98-100%). Finally, four nuclear genes and the joint analysis showed a congruent branching pattern in the atelid clade, placing *Alouatta* as the most basal lineage and *Brachyteles* from the Atlantic forest) and *Lagothrix* (from the Amazonian forest), as sharing the last common ancestor (bootstrap values ranging from 78 to 100%), contrasting to the widely disseminated view that *Ateles* and *Brachyteles* share the last common ancestor in the ateline clade. Furthermore, as shown in Table I, the investigation by Meireles *et al*. (1999), encompassing more than 9 Kb of the gamma globin gene complex strongly supports the *Lagothrix-Brachyteles* clade (bootstrap value of 100%).

If, at the intergeneric level, the phylogenetic ties are almost elucidated, the same does not occur at the subgeneric level. In almost all polyspecific genera, the relationships among species are highly controversial. The callitrichines are the most investigated group until now at the intrageneric level. In the *Callithrix* genus there are two well defined groups: a jacchus group with an eastern geographic distribution (Atlantic forest), and an argentata group from the Amazonian region. DNA data from Tagliaro *et al*. (1997), Chaves *et al*. (1999) and Canavez *et al*. (1999a b), suggest that the Amazonian *Callithrix pygmaea* and *C. argentata* are closely related species, as expected in view of their geographic distribution. On the other hand, the molecular data does not support the recognition of the Amazonian *C. humeralifera* and the recently described species *C. mauesi* as distinct taxa (Tagliaro *et al*. 1997). Furthermore, in the jacchus group, which has a high diversity of morphotypes, Tagliaro *et al.* (1997) using highly variable mitochondrial DNA data, found that the *C. jacchus, C. kuhli, C. penicillata*, and *C. geoffroyi* species are very similar and that *C. aurita* is the earliest branch of the Atlantic forest group. In addition, the genetic divergence values between species of the *Callithrix* genus are very small, suggesting that speciation in this group is a very recent event.

## THE AGES OF THE PLATYRRHINE CLADES

Following Avise & Johns (1999), divergence times were used to construct a provisional age-related classification of the New World monkeys (Table II). Using the catarrhine-platyrrhine split at 40 Ma (Mega annum) in the middle Eocene, according to Goodman *et al*. (1998, 1999), we estimate that the platyrrhine families, as total groups (Total groups includes all members of the crown group, the stem of the last common ancestor (LCA) and all extinct taxa) originated in the middle to late Oligocene epoch at 26 Ma.

According to our estimates, based on the joint molecular analysis of the combined nuclear genes and calibrating the molecular clock for the emergence of the families at the Oligocene-Miocene boundary (26 Ma), it appears that the Cebidae family split into the subfamilies Cebinae Aotinae at 22-23 Ma, each one with single extant monogeneric tribes (Cebini for *Cebus* and Aotini for *Aotus*). In the early to middle Miocene (16-13 Ma), the basal callitrichines branched into monogeneric subtribes Saguinina (*Saguinus*), Leontopithecina (*Leontopithecus*), *Callimiconina* (*Callimico*), and Callitrichina (*Callithrix*).

According to our proposal, all the members of the Pitheciidae family are grouped in a single subfamily, Pitheciinae, that split at 19 Ma into two

**TABLE II**

**Provisional age-related New World monkeys Classification**

| | |
|---|---|
| Infraorder Platyrrhini | |
| Superfamily Ceboidea (26 Ma) | |
| Family **Cebidae** (23 Ma) | |
| Subfamily Cebinae (22 Ma) | |
| Tribe Cebini | |
| | *Cebus* Erxleben 1777 |
| Tribe Saimiriini | |
| | *Saimiri* Voigt 1831 |
| Subfamily Aotinae | |
| | *Aotus* Illiger 1811 |
| Subfamily Callitrichinae | |
| Tribe Callitrichini (16 Ma) | |
| Subtribe Saguina | |
| | *Saguinus* Hoffmannsegg 1807 |
| | *Leontopithecus* Lesson 1840 |
| Subtribe Callimicomina | |
| | *Callimico* Thomas 1913 |
| Subtribe Callitrichina | |
| | *Callithrix* Erxeeben 1777 |
| Family **Pitheciidae** | |
| Subfamily Pitheciinae (20 Ma) | |
| Tribe Callicebini | |
| | *Callicebus* Thomas 1903 |
| Tribe Pitheciini | |
| Subtribe Pitheciina (11 Ma) | |
| | *Pithecia* Desmarest 1820 |
| Subtribe Chiropotina (8 Ma) | |
| | *Chiropotes* Lesson 1840 |
| | *Cacajao* Lesson 1840 |
| Family **Atelidae** | |
| Subfamily Atelinae (15 Ma) | |
| Tribe Alouattini | |
| | *Alouatta* Lacépède 1799 |
| Tribe Atelini (13 Ma) | |
| Subtribe Atelina | |
| | *Ateles* É. Geoffroy 1806 |
| Subtribe Brachytelina (12 Ma) | |
| | *Brachyteles* Spix 1831 |
| | *Lagothrix* É Geoffroy 1812 |

tribes: the monogeneric Callicebini, with the subtribe Callicebina (*Callicebus*), and the Pitheciini with two subtribes, Pitheciina (*Pithecia*) and Chiropotina (*Chiropotes* and *Cacajao*).

For the Atelidae family, we estimate that at about 15 Ma the early atelines divided into two tribes: Alouattini (genus *Alouatta*) and Atelini, this later tribe splitting in the middle to late Miocene (13 Ma) into two subtribes, Atelina (*Ateles*) and Brachytelina (*Lagothrix* and *Brachyteles*).

The branching events suggested for the Pitheciidae and Atelidae families are in agreement with fossil data. The existence of *Stirtonia, Cebupithecia*, and *Nuciruptor* fossils (related to *Alouatta*, pitheciines and a sister group of pitheciines, respectively) in the middle Miocene scenario, indicates that the stem lineage of pitheciines and atelines were present at that time (Horowitz 1999). However, additional reliable fossil data are necessary to illuminate several other branching points in the New World monkey phylogenetic tree.

In summary, three evolutionary lineages are strongly established for the New World monkeys: atelines, pitheciines, and cebids. However, two major points regarding the branching patterns of the most ancient lineages remain to be clarified: (i) what is the exact branching pattern of *Aotus, Cebus, Saimiri* and the small callitrichines?; and (ii), which two of these three lineages, pitheciines, atelines or cebids, are more closely related?

On the other hand, at the subgeneric level, all the platyrrhine genera deserve to be well investigated. Our preliminary estimates indicate that the majority of the speciation processes seem to have occurred in the Pliocene-Pleistocene scenario (5 Ma or less). However, because the internodes are usually very small when species and populations are compared, even using highly variable mitochondrial DNA, to better understand the recent evolutionary processes of the New World monkeys, a global approach using geomorphology, biogeography, traditional morphology, behavior and cytogenetics, in association with DNA sequencing, should be advocated.

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