

# Phylogenetic relationships and divergence times among New World monkeys (Platyrrhini, Primates)

Juan C. Opazo<sup>a</sup>, Derek E. Wildman<sup>a,b,c</sup>, Tom Prychitko<sup>d</sup>, Robert M. Johnson<sup>e</sup>,  
Morris Goodman<sup>d,\*</sup>

<sup>a</sup> Center for Molecular Medicine and Genetics, School of Medicine, Wayne State University, Detroit, MI 48201, USA

<sup>b</sup> Department of Obstetrics and Gynecology, Wayne State University, School of Medicine, Detroit, MI 48201, USA

<sup>c</sup> Services in support of the Perinatology Research Branch, NICHD/NIH, Detroit, MI 48201, USA

<sup>d</sup> Department of Anatomy and Cell Biology, School of Medicine, Wayne State University, Detroit, MI 48201, USA

<sup>e</sup> Department of Biochemistry and Molecular Biology, School of Medicine, Wayne State University, Detroit, MI 48201, USA

Received 28 July 2005; revised 7 November 2005; accepted 9 November 2005

Available online 15 May 2006

## Abstract

Orthologous sequences of six nuclear genes were obtained for all recognized genera of New World monkeys (Primates: Platyrrhini) and outgroups to evaluate the phylogenetic relationships and to estimate divergence times. Phylogenetic relationships were reconstructed by maximum parsimony, maximum likelihood, and Bayesian approaches. All methods resolved with 100% branch support genus-level relationships, except for the grouping of *Aotus* as a sister taxa of *Cebus* and *Saimiri*, which was supported by low bootstrap percentages and posterior probability. All approaches depict three monophyletic New World monkey families: Atelidae, Cebidae, and Pitheciidae; also within each family, all approaches depict the same branching topology. However, the approaches differ in depicting the relationships of the three families to one another. Maximum parsimony depicts the Atelidae and Cebidae as sister families next joined by the Pitheciidae. Conversely, likelihood and Bayesian phylogenetic trees group families Atelidae and Pitheciidae together to the exclusion of Cebidae. Divergence time estimations using both local molecular clock and Bayesian approaches suggest the families diverged from one another over a short period of geological time in the late Oligocene–early Miocene.

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**Keywords:** New World monkeys; Phylogeny; Divergence times; South America

## 1. Introduction

New World monkeys (NWMs) represent a monophyletic group, which inhabit South and Central America. Extant NWM species are assigned to the Infraorder Platyrrhini and Superfamily Ceboidea, which in turn divides into three families (Atelidae, Cebidae, and Pitheciidae) and 14–15 genera (Goodman et al., 1998, 1999; Wildman and Goodman, 2004). The phylogenetic relationships among NWMs have been extensively investigated using nucleotide

sequences from different genomes (nuclear and mitochondrial) and other kinds of markers like short interspersed elements (SINEs) (Ray et al., 2005). Nevertheless, despite these different studies, there still are some unresolved issues. The branching order of the three families has not been confidently resolved. Some evidence suggests that the first split separated Pitheciidae from the other two families (Fig. 1A) (Prychitko et al., 2005; Ray et al., 2005; Steiper and Ruvolo, 2003; von Dornum and Ruvolo, 1999). Conversely, families Atelidae and Pitheciidae as the sister group of Cebidae has also been proposed (Fig. 1B) (Canavez et al., 1999a; Harada et al., 1995; Porter et al., 1997a). The phylogenetic relationships among different genera of the families Atelidae ((*Lagothrix*, *Brachyteles*), *Ateles*), *Alouatta*) and

\* Corresponding author. Fax: +1 313 577 3125.

E-mail address: [mgoodwayne@aol.com](mailto:mgoodwayne@aol.com) (M. Goodman).

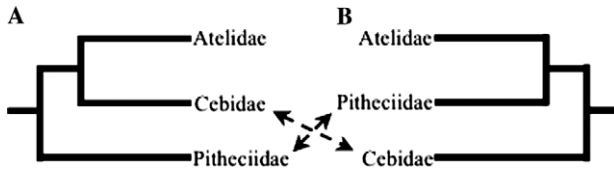


Fig. 1. Schematic representation of the two hypotheses proposed to explain the phylogenetic relationships at the familial level among New World Monkeys. (A) The first hypothesis suggests an initial split between Pitheciidae and the remaining platyrrhines, grouping Atelidae and Cebidae together. (B) The second hypothesis groups Atelidae and Pitheciidae as the sister group of the family Cebidae.

Pitheciidae (*Cacajao*, *Chiropotes*, *Pithecia*, *Callicebus*) are well characterized (Canavez et al., 1999a; Goodman et al., 1998; Harada et al., 1995; Horovitz et al., 1998; Meireles et al., 1999; Porter et al., 1997a,b, 1999; Schneider et al., 1993; von Dornum and Ruvolo, 1999); however, based on mitochondrial (COII and control region) and nuclear (aldolase A) sequences, one recent article suggests that within the family Atelidae a trichotomy among *Brachyteles*, *Lagothrix*, and *Ateles* should still be recognized (Collins, 2004). On the other hand, morphological data suggest *Ateles* and *Brachyteles* as a sister group of *Lagothrix* (Rosenberger, 2002). Within family Cebidae, most molecular phylogenetic studies agree that genera within the subfamily Callitrichinae group as follows, (*Callimico*, *Callithrix*, *Leontopithecus*, *Saguinus*) (Canavez et al., 1999a,b; Chaves et al., 1999; von Dornum and Ruvolo, 1999). However, some articles have reported alternative topologies, grouping *Leontopithecus* and *Saguinus* as a sister taxa (Goodman et al., 1998; Harada et al., 1995; Porter et al., 1997b, 1999; Schneider et al., 1993). A sister-group relationship between *Saimiri* and *Cebus* is well supported (Canavez et al., 1999a,b; Harada et al., 1995; Horovitz et al., 1998; Porter et al., 1997a,b, 1999; von Dornum and Ruvolo, 1999;

Steiper and Ruvolo, 2003). Nevertheless, the phylogenetic position of *Aotus* is still unclear, some studies have shown *Aotus* as a branch in a cebid polytomy (Schneider et al., 1993; Singer et al., 2003; von Dornum and Ruvolo, 1999), as a sister clade of the subfamily Callitrichinae (Goodman et al., 1998; Harada et al., 1995; Porter et al., 1997a,b, 1999) or as sister of all other extant Cebidae (Horovitz et al., 1998). On the other hand, morphological evidence has shown *Aotus* and *Callicebus* as either a sister group of *Saimiri* or of the subtribe Pitheciina (Rosenberger, 2002).

There is now DNA sequence data available for NWM genera from six nuclear genomic loci. In the present study, we concatenate the six loci and align the orthologous sequences among 15 NWM genera. Our objective is to estimate both phylogenetic relationships and divergence times among these NWMs. Accordingly, we have produced some sequences to fill gaps in the database.

2. Materials and methods

Sequences from ε-globin (HBE), interphotoreceptor retinol binding protein (IRBP), von Willenbrand factor (vWF), β2-microglobulin (B2M), β-globin (HBB), and glucose-6-phosphate dehydrogenase (G6PD) genes were obtained for all genera of NWMs and outgroups from GenBank (Table 1). For the vWF gene, we conducted PCRs for species of the genera *Brachyteles* (DQ129680), *Chiropotes* (DQ129681), *Pithecia* (DQ129682), and *Saimiri* (DQ129683) (Table 1). We used vWF-8 and vWF-10 primers (Chaves et al., 1999) under the following conditions: 30 cycles of denaturation, 94 °C, 1 min; annealing, 52 °C, 1 min; and extension 72 °C, 3 min; initial denaturation at 94 °C for 2 min and extension at 72 °C for 10 min were conducted. For the β-globin gene, we conducted PCRs for species in *Brachyteles* (DQ145531), *Cacajao* (DQ145529), *Chiropotes* (DQ145530), *Leontopithecus*

Table 1  
Accession numbers of all sequences and taxa used in this study

Genus	ε-Globin	G6PD intron 4	G6PD intron 5	β2-Microglobulin	IRBP	vWF	β-Globin
<i>Alouatta</i>	L25370	AF028473	AF028497	AF032048	U18602	AF092837	AY279110
<i>Aotus</i>	L25371	AF028475	AF028500	AF032093	U18601	AF092812	AY279113
<i>Ateles</i>	L25369	AF028477	AF028501	AF032087	U18603	AF092813	AY279117
<i>Brachyteles</i>	L25366	AF028478	AF028502	AF032051	U18605	This study	This study
<i>Cacajao</i>	L25365	AF028484	AF028508	AF032078	U19748	AF092814	This study
<i>Callicebus</i>	L25359	AF028483	AF028507	AF069326	U18609	AF092815	AY279119
<i>Callimico</i>	L25364	AF028486	AF028510	AF032039	U19749	AF092826	AY279118
<i>Callithrix</i>	L25363	AF028488	AF028512	AF068767	U18606	AF092828	AY279111
<i>Cebus</i>	U18608	AF028479	AF028503	AF032018	U18607	AF092822	AY279115
<i>Chiropotes</i>	L25360	AF028487	AF028511	AF032075	U18612	This study	This study
<i>Lagothrix</i>	L25358	AF028489	AF028513	AF032054	U18614	AF092830	AY279114
<i>Leontopithecus</i>	L25357	AF028490	AF028514	AF032036	U19751	AF092832	This study
<i>Pithecia</i>	L25356	AF028492	AF028516	AF032072	U18615	This study	AY279112
<i>Saguinus</i>	L25355	AF028493	AF028517	AF032024	U19752	AF092836	This study
<i>Saimiri</i>	U18618	AF028496	AF028520	AF068765	U18619	This study	AY279116
Outgroups							
<i>Homo</i>	NG000007	X55448	X55448	M17987	J05253	AC006576	WGS
<i>Macaca</i>	M81364	456149763	460044619	AY091962	402318992	AY434057	X05665
<i>Tarsier</i>	M81411	NA	NA	NA	NA	NA	M33973
<i>Otolemur</i>	U60902	NA	NA	NA	NA	NA	M61740

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