



Revisiting the phylogenetic relationships, biogeography, and taxonomy of spider monkeys (genus *Ateles*) in light of new molecular data



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ABSTRACT

Spider monkeys (*Ateles*) are one of the most endangered groups of primates in the Neotropics. The genus is widely distributed from Mexico to the north of Bolivia and includes many morphologically distinct forms in terms of pelage color and patterning. The taxonomy, phylogenetic relationships, and biogeographic history of the genus have been subject to much debate, making scientific communication difficult and creating challenges for conservation actions. We extracted DNA from samples of all currently recognized species of spider monkeys collected from across the geographic range of the genus, sequenced ~3.5 kilobases of coding sequence from the mitochondrial genome, and used this large dataset to (a) infer the phylogenetic relationships among the different forms of spider monkeys, (b) evaluate whether currently recognized species of spider monkeys form reciprocally monophyletic groups that are concordant with contemporary classifications, and (c) estimate divergence dates among the different lineages of *Ateles*. We found that all proposed species of spider monkeys for which we have samples from multiple localities indeed appear to form monophyletic groups. However, in contrast to previous studies, several of our analyses robustly inferred *Ateles marginatus* from northeast Brazil as the sister taxon to all other spider monkeys. A Bayesian dating analysis suggests that the most recent common ancestor of extant *Ateles* dates to ~6.7 Ma, in the late Miocene, and most species-level splits within the genus took place in the late Pliocene, suggesting that the modern diversity in spider monkeys cannot be explained principally by isolation and divergence of populations in forest refugia during the Pleistocene. Based on our new phylogenetic inference and dating analysis, we propose a revised biogeographic scenario for the evolution of this genus.

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1. Introduction

Spider monkeys (*Ateles*) are one of the most endangered primates in the Neotropics, primarily due to habitat destruction and hunting (Mittermeier et al., 1989; Peres and Palacios, 2007; Rylands et al., 1997; Zaldivar et al., 2004). The classification, phylogenetic relationships, and biogeographic history of taxa within this genus have been discussed and revised multiple times with little consensus (Collins, 1999; Collins and Dubach, 2000b; Froehlich et al., 1991; Kellogg and Goldman, 1944; Nieves et al., 2005) (Table 1), which makes scientific communication difficult and creates challenges for the design and implementation of conserva-

tion policy. Distributed widely from Mexico to the north of Bolivia, the genus *Ateles* encompasses many morphologically distinct forms in terms of pelage color and patterning (Collins, 2008; Kellogg and Goldman, 1944). Those differences have sometimes been used as diagnostic characteristics to differentiate species and subspecies (Groves, 2001; Kellogg and Goldman, 1944; Hershkovitz, 1977). Other researchers, however, have questioned the use of pelage characteristics to define *Ateles* taxonomy and have instead used phylogenetic methods to try to infer the evolutionary relationships among the different spider monkey taxa. These phylogenetic studies have utilized morphological, cytogenetic, and molecular characters, but have found little consensus; different studies have reconstructed very different phylogenetic relationships, suggested alternative taxonomic arrangements, and proposed various biogeographic hypotheses to explain the origins and spread of spider monkeys (Collins and Dubach, 2000a; Froehlich et al., 1991; Groves, 2001; Medeiros et al., 1997; Nieves et al., 2005).

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Table 1
Alternative classifications that have been proposed for the taxonomy of extant spider monkeys. Different taxonomists have advocated dividing the genus into anywhere between one and seven different species. For this paper, we follow the taxonomy of Groves (2001).

Kellogg and Goldman (1944) (4 species)	Hernandez-Camacho and Cooper (1976) (1 species)	Froehlich et al. (1991) (3 species)	Medeiros et al. (1997) (4 species)	Collins and Dubach (2000a) (4 species)	Groves (2001) (7 species)
<i>A. paniscus</i>	<i>A. paniscus</i>	<i>A. paniscus</i>	<i>A. paniscus</i>	<i>A. paniscus</i>	<i>A. paniscus</i>
<i>A. p. paniscus</i>					
<i>A. p. chamek</i>		<i>A. belzebuth</i>	<i>A. belzebuth</i>	<i>A. belzebuth</i>	<i>A. chamek</i>
<i>A. belzebuth</i>					<i>A. belzebuth</i>
<i>A. b. marginatus</i>					<i>A. marginatus</i>
<i>A. b. hybridus</i>		<i>A. geoffroyi</i>	<i>A. hybridus</i>	<i>A. hybridus</i>	<i>A. hybridus</i>
<i>A. fusciceps</i>			<i>A. geoffroyi</i>	<i>A. geoffroyi</i>	<i>A. fusciceps</i>
<i>A. f. fusciceps</i>					
<i>A. f. robustus</i>					
<i>A. geoffroyi</i>					<i>A. geoffroyi</i>

Here, we revisit the issue of *Ateles* phylogenetics and biogeography and offer a new hypothesis for the evolutionary history of the genus. Our analysis differs from previous ones in that it encompasses a wider number of putative taxa sampled from across the geographic distribution of the genus, takes advantage of longer genetic sequences (~3.9 kb of primarily coding mtDNA sequences), and uses improved methods of phylogenetic inference. Using these sequence data, we also estimate the times of divergence of the major clades of spider monkeys and use those data to consider alternative biogeographic scenarios.

1.1. Brief overview of spider monkey taxonomy and phylogeny

The first comprehensive taxonomic review of spider monkeys was done by Kellogg and Goldman (1944) (Table 1) and was based solely on morphological characteristics, such as pelage color and hair length, as well as cranial measurements. The authors divided spider monkeys into four allopatric species: (1) *Ateles geoffroyi*, (with nine subspecies, confined to Mesoamerica); (2) *Ateles fusciceps* (with two subspecies, distributed along the Pacific coast of northwestern South America); (3) *Ateles belzebuth* (with three subspecies, distributed throughout the Amazon Basin and northern Colombia), and (4) *Ateles paniscus* (with two subspecies, one found north of the Amazon River in the Guianas and one located south of the Amazon River in the central and southwestern Brazilian Amazon as well as Bolivia and Peru) (Kellogg and Goldman, 1944). Later morphology-based taxonomies offered a somewhat different view of spider monkey taxonomic diversity. For example, Hernandez-Camacho and Cooper (1976) argued that all spider monkeys should be classified in a single, highly variable species, *Ateles paniscus*.

Froehlich et al. (1991) conducted the first explicitly phylogenetic analysis of the spider monkeys using 50 cranial and dental characters scored for seven putative taxa of *Ateles*. They concluded that the genus could be divided into three clades, merging some of the taxa previously recognized as distinct by Kellogg and Goldman (1944): Clade 1 consisted of Kellogg and Goldman's (1944) *A. p. paniscus*; Clade 2 comprised *A. hybridus* – which Kellogg and Goldman (1944) had included as a subspecies within *Ateles belzebuth* – as well as the Mesoamerican and Pacific coast forms (*A. geoffroyi*, *A. fusciceps* = *A. fusciceps fusciceps*, and *A. robustus* = *A. fusciceps rufiventris*); and Clade 3 consisted of the all the northwestern, southwestern, central, and southeastern Amazonian forms, which correspond to contemporary *A. belzebuth* plus Kellogg and Goldman's (1944) *A. p. chamek* and *A. b. marginatus* (Table 1). Froehlich et al. (1991) also suggested that all the South American forms comprise an interbreeding ring species, as they found a morphological cline ranging from the Guianas to Venezuela (Froehlich et al., 1991).

Since the mid-1990s, various types of genetic rather than morphological data have been used to revisit the evolutionary

relationships among the spider monkeys. For example, Medeiros et al. (1997) used karyotype data to divide the spider monkeys into four karyomorphs ([1] *A. geoffroyi* + *A. hybridus*; [2] *A. fusciceps* + *A. rufiventris*; [3] *A. belzebuth* + *A. chamek* + *A. marginatus*; and [4] *A. paniscus*), a schema similar to that of Froehlich et al. (1991), apart from the positions of *A. hybridus* and *A. paniscus*. Medeiros et al. (1997) also proposed that *A. chamek* represents the most basal form of the genus, which they argued originated in the southwestern Amazon basin and extended eastwards and northwards, giving rise to *A. marginatus* in the central Amazon and to *A. belzebuth* in the northwest. The authors also concluded that *Ateles fusciceps* (including *A. rufiventris*) may be reproductively isolated from *A. geoffroyi* and *A. hybridus* and therefore considered a different species (Fig. 1) (Medeiros et al., 1997).

Shortly thereafter, Collins and Dubach (2000b) used DNA sequence data from the mitochondrial control region and cytochrome *c* oxidase subunit II (COII) gene to investigate the phylogenetic relationships among *Ateles*. Their research incorporated many of the same putative subspecies and species included in the present study; however, importantly, the western Amazonian form, *Ateles belzebuth*, was missing from their analysis. Collins and Dubach (2000b) also concluded that the genus could be divided into four distinct clades, but, contrary to the findings of Medeiros et al. (1997), they argued that *A. paniscus* was the basal sister taxon to all other spider monkeys and that *A. hybridus* was closely related to a clade formed by *A. fusciceps*/*A. geoffroyi* and *A. chamek*/*A. marginatus*. They also argued that *A. chamek* and *A. marginatus* did not represent different groups, at least based on the mitochondrial regions sequenced in their study, while *A. hybridus* was suggested to be a unique phylogenetic lineage. Finally, Collins and Dubach (2000b) concluded that *Ateles geoffroyi* and *A. fusciceps robustus* were closely related sister taxa, and they thus considered them to belong to the same species but different subspecies (Fig. 1) (Collins and Dubach, 2000b).

More recently, Ruiz-Garcia and Alvarez (2003) used RFLPs from mtDNA to infer the phylogenetic histories of six genera of Neotropical monkeys. These researchers found two mtDNA haplotypes within the taxon *Ateles fusciceps*, which they argued could indicate the existence of two distinct evolutionary lineages and possibly two subspecies: *A. f. rufiventris* and *A. f. robustus*. Also, due to the detection of common microsatellite alleles (unpublished data) between northern populations of *A. fusciceps* and *A. hybridus*, they suggested that some degree of gene flow might occur between these two putative species (Ruiz-Garcia and Alvarez, 2003).

Finally, Nieves et al. (2005) used a combination of cytogenetic and mtDNA sequence data to explore the relationships between species of spider monkeys. The authors used samples from six putative species of *Ateles* to construct a chromosome-based phylogeny (*Ateles hybridus*, *A. geoffroyi rufiventris*, *A. marginatus*, *A. belzebuth*, *A. chamek*, and *A. paniscus*) but incorporated only three

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