



# How many genera and species of woolly monkeys (Atelidae, Platyrrhine, Primates) are there? The first molecular analysis of *Lagothrix flavicauda*, an endemic Peruvian primate species



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## ABSTRACT

We sequenced *COI* and *COII* mitochondrial genes of 141 Neotropical woolly monkeys to provide new insights concerning their phylogeography and phylogenetic relationships. For the first time, eight individuals of the endemic and extremely rare Peruvian yellow-tailed woolly monkey (*flavicauda*) were sequenced at these genes and compared with other *Lagothrix* taxa (*poeppigii*, *lagotricha*, *lugens* and *cana*). There were four main results. (1) *L. flavicauda* showed a gene diversity of zero, whereas *poeppigii* and *lugens* showed high levels of gene diversity and *lagotricha* and *cana* showed more modest levels of gene diversity. The absence of gene diversity found for *L. flavicauda* strongly supports that it is one of the 25 more endangered primates on earth; (2) Our genetic distance and phylogenetic analyses, which included many cases of genetic introgression and recent hybridization, suggest that all woolly monkeys could be included in one unique genus, *Lagothrix*, divided into two species: *L. flavicauda* and *L. lagotricha*. The last species is divided into at least four subspecies. Our molecular results agree with Fooden's (1963) classification, but do not support the classification proposed by Groves (2001). (3) *Poeppigii* was the first taxon within *L. lagotricha* to experience a mitochondrial haplotype diversification, while *cana* and *lagotricha* experienced more recent mitochondrial haplotype diversification; (4) *Poeppigii* and *lagotricha* were the taxa which showed the greatest evidence of population expansions in different Pleistocene periods, whereas *lugens* experienced a population declination in the last 25,000 YA.

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## 1. Introduction

*Lagothrix* (E. Geoffroy, 1812) is one of four Neotropical Primate genera of the Atelidae family—containing the largest living primates in Latin America. These primates have distinct thick woolly fur (woolly monkeys), strong prehensile tails and occupy a critically important niche linked to the successful dispersal and recruitment of trees (Levi and Peres, 2013). Thus, their conservation is of prime concern, not just for sake of the woolly monkeys themselves, but also for the preservation of Amazonian forests. Rightly so, conservation biology depends on the identification and description of species and agreed upon taxonomic categories. However, unfortunately, there is general disagreement among primatologists over the taxonomy of *Lagothrix*. It is our intention to resolve this debate by the presentation of new molecular findings.

Here, we begin with a brief review of the literature regarding taxonomic characters of *Lagothrix*. A more detailed review along with references are provided in Table 1. Fooden (1963) determined that this genus was integrated by two species: *L. flavicauda* (yellow-tailed woolly monkey), an endemic species in Peru, and *L. lagotricha* (Humboldt's woolly monkey), distributed in Colombia, Venezuela, Ecuador, Peru, Brazil and recently discovered in Bolivia (Wallace and Painter, 1999).

Ever since Alexander von Humboldt provided the first description of the yellow-tailed woolly monkey in 1812, there have been consistent changes in its taxonomy. During this time it has been redefined, placed together with *Ateles*, separated from *L. lagotricha*, and even considered as a full genus (Table 1). These variations in taxonomy may be due to the lack of molecular data needed to help determine the relationship of *flavicauda* with other *Lagothrix* and *Atelidae* taxa.

Taxonomic questions of this species are further complicated because of the difficulty in finding samples. It has a very limited

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**Table 1**  
Chronology of taxonomy regarding the yellow-tailed woolly monkey.

Date	Author(s)	Summary
1812	von Humboldt	Analyzed skins and determined yellow-tailed woolly monkey to be <i>Simia flavicauda</i>
1927(a,b)	Thomas	Redefined the yellow-tailed woolly monkeys as <i>Oreonax hendeei</i>
1963	Fooden	Combined <i>Simia flavicauda</i> and <i>Oreonax hendeei</i> into a single species called <i>Lagothrix flavicauda</i>
2001	Groves	Based on an examination of skulls from museums, <i>Lagothrix flavicauda</i> is grouped with <i>Ateles</i> and considered separate from <i>Lagothrix lagotricha</i> . <i>Flavicauda</i> was considered a full genus called <i>Oreonax flavicauda</i>
2008(a,b)	Rosenberger	<i>Oreonax</i> is not different from <i>Lagothrix</i> . The yellow-tailed woolly monkey is renamed as <i>Lagothrix flavicauda</i>

geographic distribution in the Peruvian premontane, montane and cloud forests between 1500 and 3000 m above sea level (masl). Many of these areas are inaccessible and the species has an extremely small population size. The species probably has a distribution in the Peruvian Departments of Amazonas, San Martín, Huánuco, Loreto and La Libertad as predicted by an ecological model (Pacheco et al., 2007). However, the species presence has only been verified in two Peruvian Departments, Amazonas and San Martín (DeLuycker, 2007; Shanee et al., 2008). Leo Luna (1989) did report nine locations where this species was present in the 1980s; however, its presence could not be demonstrated in other areas where this species was previously reported during the 1970s and 1980s (Pedro Ruiz Gallo; Yambrasbamba, Gira-Sisa Reserve, Shimbayacu). More recently, DeLuycker (2007) and Shanee et al. (2008) showed a detailed study where this taxon is distributed (Table 2).

No thorough censuses have been carried out of this taxon, but Nowak (1999) estimated that there were less than 250 individuals (although this number could be somewhat greater) in the wild.

Also, there are no individuals of this species found in any of the world's public zoos. This species is listed as Critically Endangered by IUCN in 2014 and it is classified as one of the 25 most endangered primate taxa (Mittermeier et al., 2007).

Humboldt's Woolly monkey (*Lagothrix lagotricha*) has also undergone taxonomic changes since its first description by Humboldt in 1812. Its taxonomy is based on Fooden's analysis of 312 specimens (Fooden, 1963). He identified four different subspecies within *Lagothrix lagotricha*: *L. l. lugens*, *L. l. lagotricha*, *L. l. poeppigii*, and *L. l. cana*. Their distributions and phenotypes are described in Table 3. Groves (2001), however, elevated these *L. lagotricha* taxa to the status of different species. Thus, this author considered the existence of two woolly monkey genera, *Oreonax*, with a unique species, *O. flavicauda*, and *Lagothrix* with four species: *L. lugens*, *L. lagotricha*, *L. poeppigii* and *L. cana*.

Only two molecular studies have been published to help resolve the systematics questions regarding the woolly monkeys (Botero et al., 2010; Ruiz-García and Pinedo 2010).

Botero et al. (2010) analyzed 16 samples collected from Colombian zoos. Unfortunately, as often occurs with these kind of samples, the authors could not determine the exact geographical origins of their exemplars. Additionally, only phenotype individuals belonging to *lugens* and *lagotricha* were enclosed in their study. The authors sequenced two mitochondrial genes (*mtCOII* and the *mt D-loop*), analyzed the karyotypes, and provided three main and important conclusions. They determined that there were no significant differences in the variation of karyotype frequency at chromosomes 4, 7 and 24 between *lugens* and *lagotricha*. This finding supported a subspecies status rather than a species status for these *Lagothrix* taxa. They obtained a similar conclusion when they constructed and analyzed a Bayesian tree with *lugens* and *lagotricha* haplotypes intermixed. The authors also detected a very recent split between *lugens* and *lagotricha* at the beginning of the Holocene.

Ruiz-García and Pinedo (2010), analyzed the mitochondrial *COII* gene (*mtCOII*) of 97 *Lagothrix lagotricha* specimens, belonging to the

**Table 2**  
Geographic distribution of yellow-tailed woolly monkey in Peru.

Distribution	References
<ul style="list-style-type: none"> <li>• Nine locations within two Peruvian Departments               <ol style="list-style-type: none"> <li>1. Between Pongo de Rentema and Bagua</li> <li>2. Two points in the Ulcubamba River</li> <li>3. Two points between the Chiriago and Mayo Rivers</li> <li>4. One point west of Chachapoyas</li> <li>5. One point between Rioja and Mendoza</li> <li>6. Two points in the Southwestern area of the San Martín</li> <li>7. Department Frontier with La Libertad near Achiras and Paulina</li> </ol> </li> </ul>	Leo Luna (1989)
<p><i>Wide areas</i></p> <ul style="list-style-type: none"> <li>• Three or four regions within two Peruvian Departments (Amazon and San Martín Departments)               <ol style="list-style-type: none"> <li>1. Colan Cordillera (641 km<sup>2</sup>)</li> <li>2. Upper Mayo River (1820 km<sup>2</sup>)</li> <li>3. Abiseo River National Park (2740 km<sup>2</sup>)</li> <li>4. Maybe, Laguna de los Cóndores</li> </ol> </li> </ul>	DeLuycker (2007)
<p><i>Precise areas</i></p> <ul style="list-style-type: none"> <li>• Five locations within the Amazon Department               <ol style="list-style-type: none"> <li>1. Santa Rosa</li> <li>2. Shipasbamba</li> <li>3. Abra Patricia</li> <li>4. Gocta</li> <li>5. La Perla de Limasa</li> </ol> </li> <li>• Three locations within the Martín Department               <ol style="list-style-type: none"> <li>1. Paitoja</li> <li>2. Colca</li> <li>3. Nuevo Mendoza</li> </ol> </li> </ul>	Shanee et al. (2008)

*lugens*, *lagotricha*, *poeppigii* and *cana* taxa. This study produced several important findings. *Poeppigii* and *lugens* showed the highest levels of gene diversity, whereas *lagotricha* and *cana* showed the lowest. The authors also suggested that an ancestor of *poeppigii* was a possible candidate for the beginning of the diversification of *L. lagotricha*. They also detected different mitochondrial lineages within *poeppigii* and *lugens* and even hybrid individuals between *lagotricha* and *lugens*, between *lagotricha* and *poeppigii* and between *lugens* and *poeppigii*. Also, all of their samples came from the wild and hybridization was considered to be natural among these taxa. Such an interpretation suggests that these taxa are subspecies and not full species as claimed by Groves (2001). The beginning of the mitochondrial haplotype diversification in *L. lagotricha* began around 2.5 MYA—coinciding with the beginning of the Pleistocene. Lastly, the authors' data supports haplotype diversification within *poeppigii* and *lugens* during the first and second Pleistocene glacial periods and the diversification of *lagotricha* and *cana* during the third and fourth Pleistocene glaciations. Their results agree quite well with the results reported in the previous mentioned work of Botero et al. (2010). That is, both taxa are subspecies and not full species such as suggested by Groves (2001).

In this study, we sequenced two mitochondrial genes, the cytochrome c oxidase subunits I and II (*mt COI* and *COII*). The

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