OREONAX – NOT A GENUS

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Abstract

We summarize our re-examination and extension of the Groves (2001) parsimony analysis of Woolly monkeys, genus *Lagothrix*, which led him to conclude that the species *flavicauda* is not most closely related to *lagotricha* but to *Ateles*, the Spider monkeys. As a consequence, Groves further proposed that the Yellow-tailed woolly monkey should be assigned to a separate genus, *Oreonax*, previously erected by Oldfield Thomas (1927). Our analysis, while closely following his methods, samples a greater diversity of species and sub-species representing all the living ateline genera and makes minor revisions in Groves' data matrix of craniodental characteristics. With this broader analysis we show that Groves' cladistic results cannot be replicated except by duplicating his study using only a restricted range of taxa. A more wide ranging taxonomic sampling fails to link consistently *flavicauda* and other ateline species, in any particular cladogram topology, while the overall craniodental morphology of *flavicauda* does not separate it from *lagotricha*. Groves' cladistic conclusion is likely to be an artifact stemming from a chance combination of the particular taxa used as a study group and selection of characters that may not be appropriate in intergeneric comparison. There is thus no justification for recognizing *Oreonax* as a distinct genus, and its usage should be rejected.

Key Words: Primates, Atelidae, *Lagothrix*, *Oreonax*, *Lagothrix flavicauda*, Yellow-tailed woolly monkey, cladistics, parsimony, classification.

Resumen

Presentamos abreviadamente nuestra re-examinación y extensión del análisis de parsimonia de Groves (2001) de los monos lanudos, género *Lagothrix*, que le llevaron a concluir que la especie *flavicauda* no esta más cercanamente relacionada con *lagotricha* pero si con *Ateles*, los monos araña. En consecuencia, Groves propuso que el mono lanudo de cola amarilla debería ser asignado a un género aparte, *Oreonax*, previamente erigido por Oldfield Thomas (1927). Nuestro análisis cuidadosamente siguió sus métodos, e incluye una mayor diversidad de especies y subespecies que representan todos los géneros vivientes de Atelinos, y hace revisiones menores en la matriz de Groves de datos de características craneodentales. Con este más amplio análisis mostramos que los resultados cladísticos de Groves no pueden ser replicados excepto al duplicar su estudio utilizando solamente un rango restringido de taxa. Un muestreo taxonómico de rango mucho más amplio falla en articular consistentemente a *flavicauda* y otras especies de atelinos, en cualquier cladograma topológico en particular, mientras que la morfología craneodental general de *flavicauda* no la separa de *lagotricha*. La conclusión cladística de Groves es probablemente una idea derivada de una combinación azarosa de los taxa particulares utilizados como un grupo y la selección de caracteres que parecen no ser apropiados para las comparaciones entre géneros. Por lo tanto no hay justificación para reconocer *Oreonax* como un género distinto, y su uso debería ser rechazado.

Palabras Clave: Primates, Atelidae, *Lagothrix*, *Oreonax*, *Lagothrix flavicauda*, mono lanudo de cola amarilla, cladística, parsimonia, clasificación.

Introduction

The alpha taxonomy of living New World monkeys is experiencing an extreme makeover. The turning point behind this new perspective may be taken as the publication of Groves' (2001) book "Primate Taxonomy." After decades of consolidation and stability beginning in the late 1940s, largely based on the contributions of Philip Hershkovitz, recent treatments have promulgated quite a different picture of platyrrhine biodiversity. Contemporaries of Hershkovitz working under a similar paradigm, such as Napier and Napier (1967) and Napier (1976) who, like Groves, surveyed the systematics of all primates, recognized 64 and 67 platyrrhine species, respectively. Groves recognizes 112. The difference is remarkable, and it has large implications for systematics, evolutionary theory and conservation. The difference results largely from elevating subspecies-level taxa to full species rank. As far as we are aware, this move-

ment toward split taxonomies (i. e., as in the traditional distinction of "lumpers" and "splitters") has not been scrutinized scientifically by primatologists.

Groves's platyrrhine classification (2001, and references therein) is also a departure in the number of modern platyrrhine genera recognized, three more than the authoritative and widely accepted works of the Napiers (Napier and Napier, 1967; Napier, 1976) and Hershkovitz (e.g., 1977). One of these is *Oreonax*, the genus which Groves (2001) revived for a species of Woolly monkey, *flavicauda*, that had fallen into synonymy decades ago. The purpose of this report is to explain that the analysis which led Groves (2001) to raise the rank of the species *L. flavicauda* to the genus level is flawed, making his phylogenetic interpretation and taxonomic decision unjustified.

Groves' study was based on an algorithmic cladistic analysis of 20 craniodental characteristics involving five ateline species, one (none were identified by species name) taken from each living genus – *Alouatta, Lagothrix, Ateles, Brachyteles* – and a pair of species representing *Lagothrix* (explicitly *lagotricha* and *flavicauda*). In a complimentary analysis, he also added the Brazilian subfossils *Caipora* and *Protopithecus*, but this aspect did not add meaningfully to the results. The character state data was analyzed under parsimony criteria using PAUP (Swofford, 1993). Groves found that the species *flavicauda* was more closely related to *Ateles* sp. than to *L. lagotricha*. Having thus discovered that *Lagothrix* is non-monophyletic, Groves elected to remove *flavicauda* to the genus *Oreonax*.

Methods

As explained more fully elsewhere (Matthews and Rosenberger, in press), we replicated Groves' (2001) study and his results, and then extended his methodology to include more taxa belonging to the genera he studied in order to see if it produced a stable outcome that was consistent with his findings. We also made slight modifications in his dataset that are fully justified and explained in Matthews and Rosenberger. The taxonomic distribution of the original set of craniodental characters are listed in tabular form in these sources. This direct test is a more challenging one than a critique in which we would have developed an entirely independent analysis, or if we had introduced new types of data. We showed that a large variety of minimal-

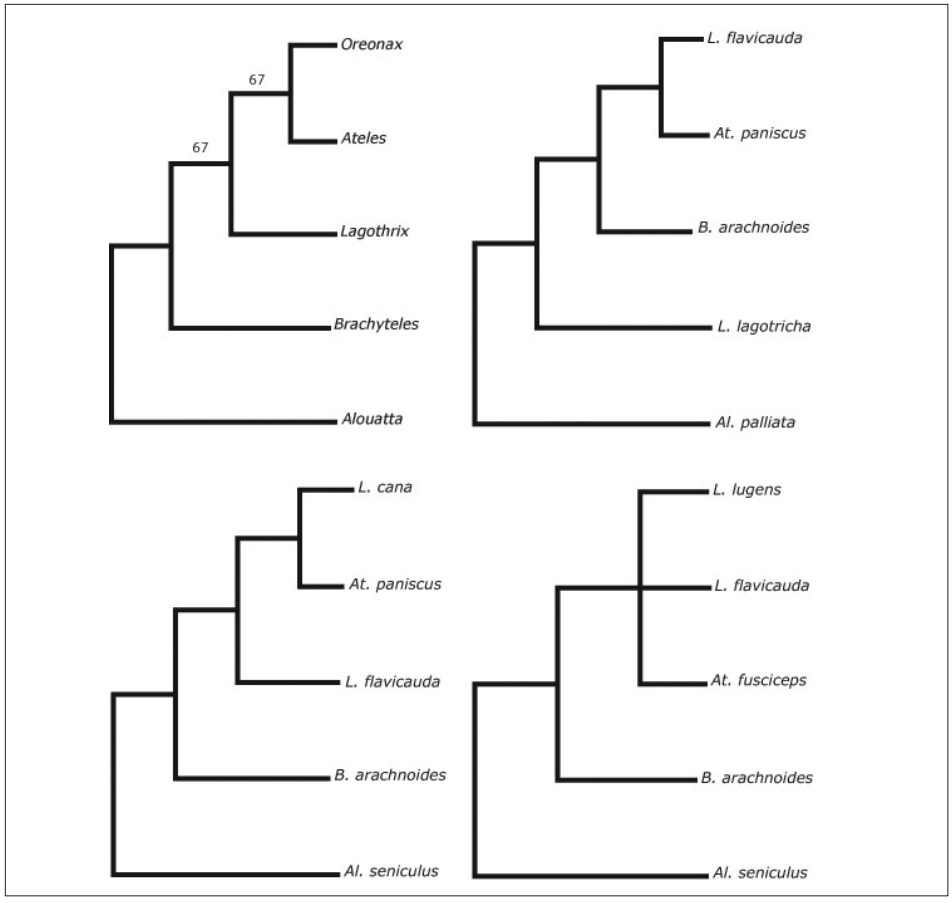

Figure 1. Four different parsimonious cladograms (from Matthews and Rosenberger, in press) based on the data and methods of Groves (2001), as explained in the text. All use five ateline species as the study group, one each from *Alouatta*, *Lagothrix* and *Ateles* and two for *Lagothrix*, *flavicauda* and one other. Fig. 1a is a tree that we generated which replicates Groves's result, his basis for resurrecting *flavicauda* as Genus *Oreonax* Thomas. The three alternatives, and several others (Matthews and Rosenberger, in press), were obtained using different combinations of five species drawn from the four ateline genera. The absence of a stable, replicable cladistic result indicates the Groves's tree is an artifact of taxonomic sampling.

length, incongruent parsimonious cladograms can be generated by varying the number and taxonomic composition of species included as in-group taxa, the very ones whose interrelationships are being tested.

Results

There is no solid evidence that *Lagothrix*, as classically constituted, is paraphyletic; there is no solid evidence that *flavicauda* is closer cladistically to Spider monkeys than to the Common woolly monkey. Figure 1 shows a sample of cladograms that we generated by analyzing the Groves (2001) characters with a more recent version of PAUP* (Swofford, 2002); additional examples appear in Matthews and Rosenberger (in press). Several points need to be made: 1) when replicating Groves' protocols as precisely as possible, we obtain the same tree (Fig. 1A), 2) when adding new ateline taxa to the sample, but still maintaining his 5 species / 20 character matrix, the results diverge from Groves' result and the monophyly and interrelationships of the ateline genera begin to vary in unstable ways (Fig. 1B-1D), 3) the driving force behind these variations appears to be the taxonomic composition of the five species defined as the in-group, or study group. Cladograms resembling the outcome Groves found occurred only under specific conditions, when they included *L. lagotricha* and *Alouatta seniculus* in the study group. For example, when we substituted *L. lagotricha* with another Woolly monkey taxon (*poeppigii*, *cana* or *lugens*) in combination with *flavicauda*, the monophyly of *flavicauda* and *Ateles* sp., the crux of Groves' new findings, was broken.

Discussion and Conclusion

These results reflect an underappreciated shortcoming of algorithmic parsimony analysis and possibly of cladistic analyses in general (including likelihood and Bayesian approaches), that topologies generated from some character sets are highly sensitive to the taxonomic composition of the study sample. Collins (2003) found essentially the same thing in his molecular study of ateline intergeneric relationships. The outcomes varied as he sampled more and different species within the genera. Similar results were also obtained by Sargis (2007) and Silcox (2007) using morphological data in studies involving the relationships of primates to other orders of mammals. Thus the constraints that drive taxonomic sampling to skew cladistic analyses with programs like PAUP appear to occur irrespective of data type and taxonomic level.

Regarding *Oreonax*, we offer some additional thoughts on why Groves' (2001) study may have been problematic from the outset. First there is a practical issue in the nature of the craniodental material Groves used that raises some questions. *Lagothrix flavicauda* is poorly represented in museum collections (Mittermeier et al., 1977). Groves' samples of skulls were the only two specimens in the collections of the American Museum of Natural History (AMNH) and in the United States. They are curiously different in morphology from the holotype and others in the Natural History Museum (British Museum of Natural History, London), a young adult male and female (Fig. 2) plus a juvenile. The AMNH individuals are aged, with very heavily worn teeth and some anatomical peculiarities in jaw and cranial shape. Skins, with the typical *flavicauda* yellow proximal tail, are associated with these and the London specimens, so the species identifications are probably correct. However, unlike the AMNH material, the London skulls do not differ much from samples of *lagotricha* in craniodental anatomy. After consulting with Groves (pers. comm.) some years ago regarding the morphology of the AMNH specimens, we believed it would be wise to split *Lagothrix* into two subgenera (see Hartwig et al., 1996). Groves went a step further as a consequence of his parsimony analysis. We can only offer that genus *Lagothrix* may be somewhat variable craniodentally (as is *Ateles,* but neither case is well documented). While this is not a satisfactory status report on research materials or intrageneric variation, we hope it encourages a more comprehensive reinvestigation of the systematics of *Lagothrix* and study of the full sample of cranial material, including the skulls in Lima, Peru (Mittermeier et al., 1977).

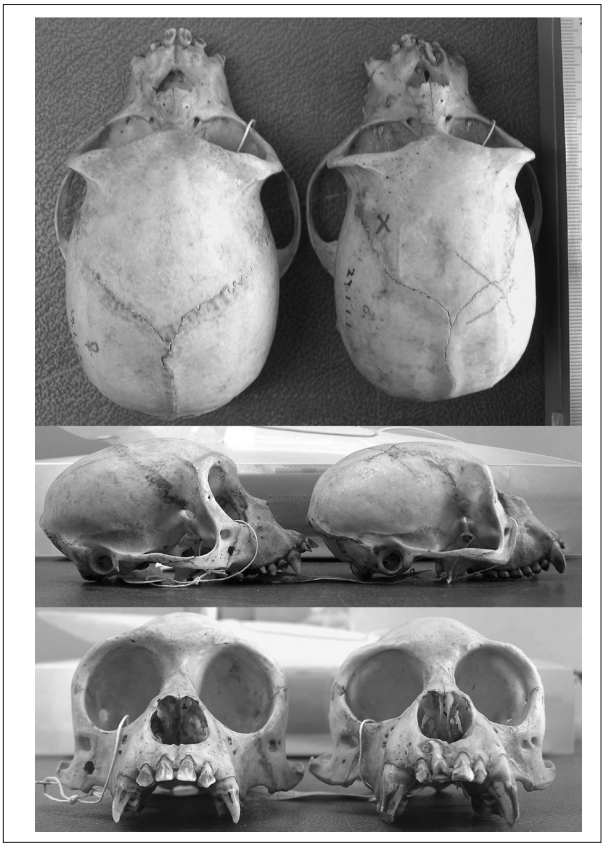

Figure 2. Craniodental morphology of the (right) adult male, the holotype, and (left) female specimen of *Lagothrix flavicauda* in the Natural History Museum (BMNH). The morphology is basically indistinguishable from *L. lagotricha*.

A second point relates to the data Groves (2001) employed. As we discuss to some extent in Matthews and Rosenberger (in press), several of his anatomical characters were problematic, or were coded in ambiguous ways. We tested this by asking three other primate morphologists to score a sample of ateline skulls using Groves' system, and used their determinations in separate PAUP runs. All three produced different cladograms. At another level, some of the features Groves employed, whether or not they are well defined or the characters states easily verified by others, would appear to be low-level population variations that we think would not be reliable as cladistic indicators at the generic level (Matthews and Rosenberger, in press). Finally, we raise a philosophical question. Systematists understand that naming a genus – unlike identifying and naming a species, which has a biological reality – is an artful practice, though it is not without mutually agreed guidelines. We do not believe Groves' (2001) decision to recognize *Oreonax* followed standard practice, irrespective of the difficulties of his parsimony analysis. Conventionally, living primate genera are "defined" by morphology (implicitly or explicitly involving functional/adaptive uniqueness), often with an emphasis on the skull and dentition (even if the taxon is first identified by molecular means and cladistics). Differential diagnoses of ateline genera are not plentiful, as these formalistic descriptions are usually published only as a part of broadly based, synthetic taxonomic revisions. Napier (1976) and Groves (2001), for example, offer such diagnoses and provide at least a brief paragraph of details that allow for identification and diagnosis of each genus by the skull and teeth. Napier (1976) also presents generically distinctive features pertaining to body shape, limbs, hands and feet, and external genitalia. It is worth noting that although she had access to the type series Oldfield Thomas (1927) used in naming *Oreonax flavicauda* when writing her catalogue of primates in the Natural History Museum, Napier retained this species in genus *Lagothrix,* citing the authority of Fooden's (1963) revision.

Groves (2001) also provides apt craniodental and somatic descriptions of *Alouatta*, *Ateles*, *Brachyteles* and *Lagothrix*. However, he offers no similar differentia for *Oreonax,* no anatomical description or list of features that either characterizes *Oreonax* or distinguishes it from any other platyrrhines. In fact, we would argue that the description he gives for his concept of *Lagothrix* perfectly encompasses *flavicauda* as well as *lagotricha*. Instead of an explicit morphological diagnosis, Groves (2001:194) presents the cladistic analysis of traits and concludes:

…the yellow-tailed woolly monkey should be separated generically from *Lagothrix*, because there are no derived character states that appear to unite them; and from all other atelines, because the bootstrap value for the clade uniting it with *Ateles*, its putative closest relative, is not high. Its taxonomic position is isolated.

In other words, Groves' (2001) decision to separate *flavicauda* from *Lagothrix* is based on his inability to establish the monophyly of Woolly monkey species on the basis of his characters and method. However, by the same logic, because his study was so limited in scope, it could also be argued that the one unidentified species of *Ateles* that grouped with *flavicauda* should also thus be a candidate for generic status, either monotypically or grouped with *flavicauda*. Applying Groves' logic to our complimentary multi-species study would suggest that numerous new genera ought to be erected, since in many cases the cladograms (Fig. 1) yielded novel clusters and irresolute branching sequences. Also, the "isolated" status of the *flavicauda* linkage, which Groves evidences by low PAUP bootstrap values, has no biological or phylogenetic meaning. The low numerical value means that the characters analyzed do not consistently link *flavicauda* with *Ateles* sp., more probably because the linkage is wrong or the evidence for it is weak; not because it is sending a biological signal of uniqueness that has classificatory relevance. Essentially, *flavicauda* has been misclassified because a heuristic measure of statistical support has been misconstrued as a biological and phylogenetic characteristic.

The reality is that among all the modern platyrrhines there is no mistaking the dense, woolly brownish coat, stocky body build, thick-looking limbs and tail, and naked helmeted face of a Woolly Monkey from any other platyrrhine. These same characteristics make it hard to tell apart *flavicauda* from *lagotricha* unless one examines the underside of the tail and pubic region, which tends to be a light golden brown in *flavicauda*. It has yet to be proven that *flavicauda* differs in biologically meaningful ways from *lagotricha* that would justify separating it at the genus level. We also wonder if the small allopatric population of Yellow-tailed woolly monkeys can even be shown convincingly to be a different species from its congeners using modern morphological and molecular approaches. We submit that there is no rationale for dividing Woolly monkeys into two genera, *Lagothrix* and *Oreonax*, and the notion should be rejected.

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