# ON ATELINES

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Looks can be deceiving. Although they are the largest and most easily recognizable New World monkeys, atelines are neither the most studied nor the best understood. Important aspects of their behavioral ecology and evolutionary history have yet to be researched in the field or collected from the fossil record, which increases the likelihood of making significant discoveries. For example, it has long been taken for granted that living atelines are the largest New World monkeys, but we have just found out that the surviving species are far from the largest. Their taxonomy has also been neglected; surprises may await, insight is inevitable. The most comprehensive systematic treatment of howler monkeys is over 60 years old (Lawrence, 1933); Froehlich's (1991) study of spider monkeys is the first assessment since the Kellogg and Goldman's revision of WWII vintage (1944); woolly monkeys haven't been looked at since the Kennedy administration (Fooden, 1963). The wisdom of our overall research strategies, which we usually associate with lengthy gestation if not maturation, is also suspect: the woolly spider monkey reached the very brink of extinction before rigorous field studies began (Aguirre, 1971; Valle et al., 1984; Milton, 1984; Strier, 1986).

Living atelines represent one of the obvious clades in primate systematics, characterized most prominently by a suite of derived postcranial adaptations to climbing locomotion. A growing number of molecular studies complement modern morphological interpretations. We argue strongly that the living atelines are a monophyletic group (Table 1; Schneider and Rosenberger, this volume), negating the once routine placement of

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**Table 1.** Genus level classification of Atelines

- Family Atelidae
  - Subfamily Atelinae
    - Tribe Alouattini
      - _Alouatta_ - Howler monkeys
      - *_Stirtonia_ - Middle Miocene, Colombia
      - *_Protopithecus_ - ? Pleistocene/Recent, Brazil
      - *_Paralouatta_ - Pleistocene, Cuba
    - Tribe Atelini
      - Subtribe Atelina
        - _Ateles_ - Spider monkeys
        - *_Caipora_ - Pleistocene, Brazil
        - _Brachyteles_ - Woolly spider monkeys
      - Subtribe Lagotrichina
        - _Lagothrix_ (_Lagothrix_) _lagotricha_ - Woolly monkeys
        - ?_Lagothrix (Oreonax) flavicauda_ - Yellow-tailed woolly monkeys

*Extinct genus. See Schneider and Rosenberger (this volume) and Rosenberger (1988) for references and discussion. "Other atelines" include fossils whose relationships _within_ Atelinae are uncertain

*Alouatta* into a separate subfamily. The four extant genera, *Alouatta*, *Lagothrix*, *Ateles* and *Brachyteles*, neatly form a tight cluster in the panorama of New World monkey phylogeny, a quite distinct adaptive radiation within the platyrrhines (Rosenberger and Strier, 1989).

All atelines occupy a swathe of niche-space in the canopy of neotropical forests. Their basic diet shows relatively little variation among species, except in the proportion of fruits and leaves (see Strier, 1992). Locomotor behavior is dichotomous, ranging from a gradation of climbing and acrobatic suspension (*Ateles*, *Brachyteles*, *Lagothrix*) along one phylogenetic axis to climbing and deliberate quadrupedalism (*Alouatta*) along the other. Regarding social organization, the hallmark *Ateles* pattern - daily foraging parties that are flexible in size and composition - also characterizes *Brachyteles* and *Lagothrix* (e.g. Milton,1984; Strier, 1992; Peres, 1994, this volume; Defler and Defler, 1996). Group composition appears to be more stable on a day-to-day basis for *Alouatta* (Strier, 1992; Crockett, this volume). Thus atelines also exhibit differences in social behavior and locomotion despite basic similarities in habitat use and diet, and these correspond with the phylogenetic structure of the subfamily.

Phylogenetically, the interrelationships of the subfamily are still problematic. Cladograms based on morphology and molecules do not agree (Schneider and Rosenberger, this volume), and new fossil material adds another dimension. A difficulty in deciphering relationships exclusively from the living species is that the four genera are confounded by extreme deviations in the anatomy of howlers, coupled with primitive retentions in the limbs of non-howlers. Thus our sense of the evolutionary history of atelines is somewhat bipolar. However, it cannot be taken on faith that this taxonomic quartet is the truest foundation for ateline systematics. Lessons from higher phylogeny have had little reciprocal impact on issues of alpha and beta taxonomy, the impetus for which has been lost in the wake of Philip Hershkovitz's (see 1977, et seq.) aborted attempt to revise the entire platyrrhine infraorder. As with the genus *Callithrix*, which may include some species more closely related to the pygmy marmoset, *Cebuella pygmaea* (Barroso et al., in press), there may be a taxonomic problem with the genus *Lagothrix*, a point that Colin Groves brought to our attention.

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Two species have been broadly accepted since Fooden's revision (1963), *L. lagotricha* and *L. flauvicauda*. The latter has received scant attention. It is a relict population, thought for a long time to have been extinct (Ruiz and Mittermeier, 1979), and it remains poorly represented in museum collections. Fooden, and Ruiz and Mittermeier, summarized what little was known of the species, but there has never been a detailed systematic analysis, certainly none that places *flauvicauda* in the context of atelin systematics. Cranial characters, usually the key referent for generic distinction, are suggestively different from *Lagothrix lagotricha*. The pattern of *L. flavicauda* includes a deeper, more inflated posterior mandible; more projecting and narrower snout; less inflated braincase; stronger postorbital constriction; more rounded nuchal plane; and, an assortment of basicranial features involving foramina, petrosal and ectotympanic shape, pterygoids, sphenoid, etc. Incisor proportions may differ and the molar cusp pattern is distinct; for example, the hypocone and talon region is less enlarged. In many respects, these characters resemble *Brachyteles* from eastern Brazil. Interestingly, Ruiz and Mittermeier (1979) note that the thumb of live, adult *flauvicauda* is markedly shorter than the second digit, which is a possible point of derived similarity shared with *Brachyteles* and *Ateles*.

We are left with no firm conclusions. Additional study, taking into account not only the other atelines but also *Alouatta* and the new Brazilian fossils discussed below is required. For the moment, we propose to keep open the questions: To whom is *flavicauda* most closely related, and how is it best classified? Thus we resurrect, with a query, the taxonomy presented when the animal first became well established in the literature (Thomas, 1927): *?Lagothrix* (*Oreonax*) *flauvicauda*. The hypotheses we plan to test are that *Oreonax* is a "good" genus, perhaps more closely related to the *Ateles-Brachyteles* branch, perhaps a geographical relict of an Amazonian rather than Andean community, and perhaps with deeper implications for early ateline evolution than *L. lagotricha* and other living atelins.

Discoveries made more than 150 years apart are dramatic proof that fossil evidence - always painfully elusive - will be the ultimate arbiter in our rethinking of ateline evolution. The specimens are still rare (Rosenberger and Hartwig, in press) but they add richness to the artificially narrow frame of reference depicted by the surviving living forms. They show that atelines were even more widespread in the past than the present: that atelines are an old part of the platyrrhine fauna; that archaic forms may have persisted for long stretches of geological time; that our contemporary slice of the radiation, if not depauperate taxonomically, is certainly not archetypical in an adaptive sense. One fossil genus is known from the middle Miocene deposits of Colombia, *Stirtonia*. Another comes from the far flung Pleistocene or Quarternary of Cuba, *Paralouatta*. Both of these are howler-like forms, judging from craniodental parts, and they fit comfortably in the prevailing phylogenetic-adaptive evolutionary model of Rosenberger and Strier (1989). However, we now have evidence for atelines of types we could only barely imagine scientifically.

The third and fourth fossil genera are more revealing but also more difficult to interpret. Each is represented by a nearly complete skeleton from the Pleistocene, reported in 1993 by Dr. Castor Cartelle, a paleomammalogist working in cave deposits in eastern Brazil. One skeleton is a large juvenile (>20kg) that very closely resembles living spider monkeys cranially (Cartelle and Hartwig, 1996), *Caipora bambuiorum*. The other is an even larger adult (approximately 25 kg) that postcranially resembles the spider and woolly spider monkeys, but resembles howler monkeys cranially (Hartwig and Cartelle, 1996). The latter is referred to *Protopithecus brasiliensis*, first named by Peter Wilhelm Lund in 1838 for a partial femur and humerus he found in the Brazilian state of Minas Gerais (Hartwig, 1996).

With bodies complete, there is little doubt about the manifest mosaic: Heads looking like the two derived polar opposites of the ateline radiation (*Alouatta* vs. *Ateles*) but skeletons looking much alike, akin to the climbing-suspensory system of *Ateles*. Finding this combination in a howler relative, *Protopithecus*, was not predictable based on the four living genera. The new data make quite clear the need to document better the morphology of each genus in systematic detail, and reformulate the outlines of ateline evolution. It also reminds us there is limited resolution to studies which exclude fossil evidence and, by corollary, that informative fossils can provide a powerful test of detailed cladistic hypotheses.

Whereas the howler monkey axis was even recently considered so uniformly derived that it could shed little light on atelines broadly (see Rosenberger and Strier, 1989), these advances draw our attention to *Alouatta* as another focus in our rethinking of ateline evolution - keeping in mind that phylogenetic analysis of adaptive radiations is a process of historical triangulation. Clearly, *Protopithecus* is a closely related genus of relatively great size in which the signature cranial features of howlers - less the dental morphology - is combined with essential postcranial characters formerly associated only with the atelin lineage, which are related to climbing. Previously, we had inferred (Rosenberger and Strier, 1989) that the common ancestor of atelines was more of a quadruped than an acrobatic climber or brachiator, although climbing was indeed indicated by the behavioral repertoire and morphology of living howlers. We further argued that the deliberate quadrupedalism of howlers was somehow linked with a strategy to minimize energy expenditure, as befits a folivore (Strier, 1992). The evidence of *Protopithecus* suggests the following: 1) A confirmation that the alouattin lineage at its base was a climbing stock, with functional adaptations in fore- and hindlimb. 2) Adaptive anatomical specializations relating to vocal communication - not to diet - shaped the howler skull early on and was fundamental to the origins of the lineage. 3) Changes in stance and movement, which may be correlated with unique limb proportions, elbow joint morphology, shoulder and probably the rib cage anatomy - anatomical areas that are uniquely derived in *Alouatta* - may also be related primarily to the *production and delivery* of sound rather than foraging behavior or locomotor travel.

Primatology is not short of theoretical models for New World monkey evolution, in general (Rosenberger 1992) or ateline evolution, in particular (Rosenberger and Strier 1989). As we rethink atelines in light of a multidisciplinary front of advances, we must remember that a wealth of information has yet to be obtained from the animals themselves, whether from nature or the museum drawer.

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