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Adaptive radiation of the ateline primates

We propose a synthesis of anatomical, behavioral and ecological data in reconstructing the phylogeny and evolution of the ateline primates. The atelines are a monophyletic group divisible into an alouattin lineage, including *Alouatta* and the Miocene fossil *Stirtonia*, and an atelin lineage, including *Lagothrix* and its sister-group, the *Ateles-Brachyteles* clade. Body size increase was important in the origins of atelines and in their subsequent diversification. Larger body size permitted an increased reliance on leaves (probably immature) by comparison with other platyrrhines, even in predominantly frugivorous forms. A novel locomotor pattern involving climbing, some forelimb climbing/hauling and hanging by the prehensile tail, which involved the evolution of many features derived for platyrrhines, was present in the first atelines, perhaps also connected with relatively large body size. The last common ancestor (LCA) of atelines, which morphologically resembled *Lagothrix* more than any other living form, probably lived in fluid multi-male polygynous groups characterized by female dispersal and had a moderate degree of sexual dimorphism.

Alouattins became strongly committed to an energy minimizing adaptive strategy based upon a bulky, nutritionally poor diet composed mainly of leaves. *Alouatta* thus travels relatively little daily, uses a non-acrobatic style of deliberate quadrupedalism, defends resources inexpensively by long distance calling, lives in cohesive polygynous groups that influenced the development of high sexual dimorphism, and has a proportionately small brain size. These are derived characteristics which facilitate their exploitation of a wide variety of habitats, frequently in sympatry with atelins.

Ancestral atelins were probably larger than the LCA. They engaged in more forelimb-dominated climbing and probably ranged widely in fluid, polygynous social groups. The least known modern form, *Lagothrix*, may occupy a hard-fruit feeding niche, in contrast to the soft-fruit specialist *Ateles*. A lithe, brachiating body plan that resembles hylobatids typifies *Ateles* and *Brachyteles*, suggesting a common ancestral foraging strategy involving rapid bursts of energy expenditure. The subsequent evolution of shearing postcanines in *Brachyteles*, which converges on *Alouatta* superficially, is interpretated as a derived adaptive compromise possibly related to the greater seasonality of the Atlantic Coastal Forest of southeastern Brazil, where the genus probably arose, in comparison to inland tropical forests. Energy saving features of *Brachyteles* include contracted home ranges and low intra-group aggression.

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Introduction

The atelines, *Alouatta*, *Lagothrix*, *Ateles* and *Brachyteles*, occupy an important place in the adaptive array of the living New World primates. They are the largest members of a radiation exhibiting a breadth of body sizes ranging from about two to fifteen times the size of the largest members of other platyrrhine lineages. Thus they represent one of the four adaptive modalities that characterize the modern platyrrhine radiation (Rosenberger, 1980), being large-bodied, suspensory oriented in locomotion and subsisting on fruits and leaves. Atelines and the living pitheciines (including *Callicebus*, *Aotus*, *Pithecia*, *Chiropotes* and *Cacajao*) form the Atelidae, one of the two families of New World monkeys recognized here (see Rosenberger, 1979, 1981; Szalay & Delson, 1979); other workers group all these forms with cebines (*Cebus* and *Saimiri*) in a single family, the Cebidae (e.g., Napier, 1976; Hershkovitz, 1977).

Although the species-group taxonomy of this subfamily, like that of most platyrrhines, is

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poorly known, atelines account for as much as 20% of the living New World monkey species and they represent 25% of the currently recognized genera. Geographically widespread in South America, where they inhabit numerous types of forest ecosystems, atelines are also the most widely distributed of the recently evolved Central American primate fauna. Indeed, there are indications that at least one species of *Ateles* (and perhaps an *Alouatta*) reached the Greater Antilles (see Ford, in press) during the Pleistocene.

Major contributions to the behavior and ecology of various atelines, and improvements in our knowledge of their phylogenetic relationships, make it timely to attempt a synthesis of their evolutionary biology. That is the major objective of this paper. We do not strive for an encyclopedic review. Rather, by applying complementary approaches to their analysis, we attempt to integrate data on morphology, behavior, ecology and phylogeny in order to reconstruct the evolutionary history of their adaptive radiation. Our focus arises from our own research interests and from a particular interest in the genera *Alouatta* and *Brachyteles*, two of the better known forms. These forms offer a unique perspective for examining details of the entire ateline radiation, for they share a number of important convergent features that can be teased out from the background traits that reflect their separate phylogenetic histories.

The ateline concept

What is the Atelinae? Who are its members, what do they generally do and look like? Many conventional classifications (e.g., Napier & Napier, 1967; Hershkovitz, 1977) divide the four largest platyrrhine genera into two subfamilies, Alouattinae, reserved for *Alouatta*, and Atelinae, including *Lagothrix, Ateles* and *Brachyteles.* There are a number of reasons for drawing these boundaries (e.g., Rosenberger, 1981), including a long standing debate regarding the phylogenetic position of *Alouatta* and the significance of its unique morphology. This division also reflects a conventional taxonomic approach, wherein the subfamily category has been used to symbolize both morphological divergence and phylogenetic continuity in platyrrhine classifications.

Our interest here, on the other hand, is to create an heuristic framework for evolutionary comparisons. Thus our classification emphasizes the monophyletic relationships of these four genera, following Pocock (1925), Rosenberger (1981), Ford (1986) and others (Szalay & Delson, 1979). We classify the four extant atelines, and their fossil relatives, in a single subfamily, for which the term Atelinae has priority. Since it continues to be useful to differentiate between the *Alouatta* lineage from the collaterally related monophyletic group of *Lagothrix, Ateles* and *Brachyteles* as is classically done, we also recognize the Tribe Alouattini (informally alouattins) for the former and the Tribe Atelini (atelins) for the latter.

Atelines, therefore, are a morphologically and behaviorally heterogeneous group. Perhaps their most noteworthy shared derived characteristics are large body size, ca. 5–10 kg, a prehensile tail which bears a long, hairless, grasping surface ventrally, and the frequent use of suspensory positional behaviors; atelines often hang by tail or feet, in various combinations, when they feed. Atelins, especially *Ateles* and *Brachyteles*, are also highly agile, even acrobatic, when locomoting through the canopy, abetted by their very long forelimbs and flexible shoulders. At the opposite end of the ateline locomotor spectrum is the even-limbed, robust *Alouatta*, the group's most deliberately moving quadruped. They move cautiously in a forward-crouch attitude, forelimbs flexed, elbows bent outwards, head pitched below the hip, and they rarely use forelimb suspension or cross gaps in the canopy by leaping (Schön Ybarra & Schön, 1987).

Alouatta and *Ateles* are both remarkably distinctive primates. The former presents a most unusual skull for an anthropoid. It has a very large head, an elongate, massive muzzle and a peculiar head carriage that reflects a posterodorsal, as opposed to a ventral, articulation of the skull with the vertebral column. The raucous calls of *Alouatta*, the Howler Monkey, are produced through a highly specialized apparatus involving an enlarged hyoid bone situated high in the neck. This is generally thought to have had a marked influence upon the evolution of the skull (e.g., Biegert, 1963). *Ateles*, the Spider Monkey, is known for its long, slender, spidery limbs, small head and face, and long hands, which have little more than a nubbin for a thumb. *Lagothrix* is a robustly built animal with a large head and moderately prognathic muzzle. Its stockiness is exaggerated by a dense coat; hence they are called Woolly Monkeys. *Brachyteles*, the Woolly Spider Monkey, combines the roundish head, muscularity and dense coat of a *Lagothrix* with the long-limbed body build of an *Ateles*. It is the largest species of the group in body mass.

The species-level taxonomy and geographical distribution of atelines is still poorly known in detail. The regional distributions of some forms, however, pose interesting biogeographical questions that have some relevance to the history of the subfamily as discussed herein. Napier (1976) and Groves & Ramirez-Pulido (1982) recognized six species of *Alouatta*, which is the most widespread of all platyrrhine genera. They range from southern Mexico and Guatemala to northern Argentina in a ubiquitous pattern across several different ecosystems, frequently in sympatry with an atelin. For example, *A. seniculus* has a huge distribution in the lush northern and west-central parts of South America; *A. caraya* is associated with savannah-like *cerrado* vegetation in Brazil, Paraguay and Argentina; *A. fusca* is endemic to the seasonal, semi-deciduous Atlantic Coastal Forest of eastern Brazil.

The species-level taxonomy of *Ateles* is also controversial, with four species according to Napier (1976) and three according to Groves & Ramirez-Pulido (1982). Their more restricted continental distribution occurs in the northern and western reaches of South America, probably corresponding with more tropical and montane forest, but *Ateles geoffroyi* also ranges northward as far as southern Mexico. *Lagothrix* includes two species in the middle and upper Amazon basin, *L. lagothricha* and *L. flavicauda*. *Brachyteles* is monotypic, with *B. arachnoides* disjunctly isolated from other atelins in Brazil's Atlantic Coastal Forest along with *A. fusca*.

The precarious conservation status of all the atelines cannot be overly stressed (Mittermeier *et al.*, 1989). Due to their large body size, atelines have been an abusively exploited food source for humans during the past century. Recent surveys demonstrate that *Brachyteles* is one of the most highly threatened of all primate species. *L. flavicauda* and *A. fusca* are also officially recognized as endangered species, and as many as seven other subspecies of *Alouatta* and *Ateles* may be endangered.

Little is known of the fossil record of atelines. Two species from the middle Miocene of La Venta (Colombia), approximately 15 million years old (MacFadden, in press), *Stirtonia tatacoensis* and *S. victoriae*, closely resembly *Alouatta* dentally (e.g., Delson & Rosenberger, 1984; Kay *et al.*, 1987). There is no doubt that these fossils are closely related to *Alouatta*. Although occasional, older references often suggest an affinity between the Argentinian early Miocene *Homunculus* and modern *Alouatta*, it is most likely that the former is related to pitheciines (e.g., Rosenberger, 1984). Thus a pre-middle Miocene differentiation of atelines from pitheciines, which are also represented in the La Venta as well as in earlier sites in Argentina (e.g., Kay, in press; Rosenberger *et al.*, in press), is likely and there is no reason to suspect that the radiation of atelins was not well under way by La Venta times (Rosenberger, 1984).

Morphology and systematics

As indicated above, there is a growing consensus that the atelines are the monophyletic descendants of a single common ancestor. This view was developing during the 19th century, as workers such as Spix (1823) and Gray (1870) seized upon the prehensile tail as a diagnostic character of the group, albeit without recognizing its importance for phylogenetic or adaptive interpretations. During this century, Pocock (1925) and Gregory (1922), both espousing a strongly phylogenetic orientation, laid the groundwork for more current, confirming cladistic arguments (e.g., Rosenberger, 1976, 1981; Falk, 1979; Dunlap *et al.*, 1985; Ford, 1986; Kay *et al.*, 1987). These are basically corroborated by immunological and karyological studies (e.g., Cronin & Sarich, 1975; Baba *et al.*, 1979; de Boer, 1974).

The interrelationships within the atelines are not resolved to everyone's satisfaction (Figure 1), nor are they highly obscure. There is broad agreement that the alouattin lineage was first to differentiate and that atelins are probably monophyletic. Nevertheless, Dunlap *et al.* (1985), based upon a quantitative phyletics study of forelimb myology that did not include the rare *Brachyteles*, concluded that *Alouatta* and *Lagothrix* were sister-taxa. Among those accepting the notion of a monophyletic Atelini, opinions differ on genealogical details. The crux of this debate is the systematic position of *Brachyteles* which, on the one hand, has been noted to share important dental resemblances with *Alouatta* and, on the other, shares a large suite of postcranial resemblances with *Ateles*.

Zingeser (1973) regarded *Brachyteles* as an offshoot of a primitive ateline ancestral stock that simultaneously gave rise to an alouattin branch. He argued that there was a close "affinity" between *Brachyteles* and *Alouatta*. This emerged from his view that they shared

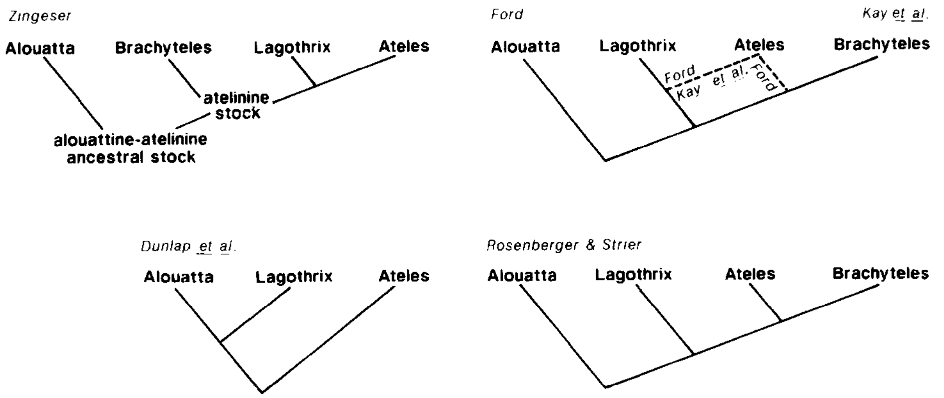


Figure 1. Some current views on the interrelationships of modern atelines. The terms appearing at the nodes in the Zingeser (1973) scheme are his own; his hypotheses are diagrammatically shown here in cladistic format. The two alternatives of Ford (1986) are indicated by dotted lines, as is the preferred cladogram of Kay *et al.* (1987). *Brachyteles* was not included in the analysis of Dunlap *et al.* (1985). See text for further discussion.

primitive ateline characteristics. However, since shared primitive features cannot demonstrate genealogical affinity, Zingeser's discussion perhaps should not be misconstrued as advocating a collateral relationship between *Brachyteles* and *Alouatta*. On the other hand, Zingeser discussed *Ateles* and *Lagothrix* more clearly as the sister-taxa of a third ateline branch, which included *Brachyteles* as its basal twig.

Also working exclusively with dental morphology but using a quantitative phyletics approach, Kay *et al.* (1987) found that *Brachyteles* and *Alouatta* shared derived traits, while *Ateles* and *Lagothrix* formed another sister-taxon. They noted, however, that the evidence was not highly convincing and conflicted with the postcranial information. Hence they proposed a pair of alternatives that appeared equally plausible: (1) *Brachyteles* as the sister-taxon of *Ateles* + *Lagothrix*; or (2) *Brachyteles* as the sister-taxon to all the other atelines. Kay *et al.* selected the first of these alternatives as the most likely one. Ford's (1986) methodologically similar study of the shoulder, elbow, knee and lower ankle joints favored an *Ateles-Lagothrix* linkage that placed *Brachyteles* as the sister-group of this pair. But in evaluating all of the available anatomical evidence, she concluded that there was an equal probability of *Brachyteles* or *Lagothrix* being the nearest living relative of *Ateles*. Her data strongly confirmed the monophyletic unity of atelins.

Dunlap *et al.* (1985) also demonstrated the monophyly of atelines in their cladistic analysis of platyrrhine forelimb myology, although their dissections did not include *Brachyteles*. In their two favored cladistic arrangements, *Lagothrix* and *Alouatta* appear as sister-taxa, linked by a presumably derived clavicular insertion of pectoralis major. However, as they explained, the taxonomic distribution of the several anatomical patterns of this muscle makes solid polarity inferences difficult.

Working hypotheses and approach

In our view, the full range of available information as outline below, from morphology, behavior and ecology, indicates very strongly that *Brachyteles* and *Ateles* are sister-taxa (e.g., Rosenberger, 1979, 1981; Rosenberger & Correa, 1983). Thus the cladistic model that we prefer (Figure 1) involves a sister-taxon linkage between *Ateles* and *Brachyteles*. This idea dates to the very first description of *Brachyteles* by E. Geoffroy in 1806, and many authorities (most recently Fiedler, 1956) have included *Brachyteles* in the genus *Ateles*.

The conceptual basis for our genealogical interpretation developed out of a platyrrhine-wide character analysis (Rosenberger, 1977) that relied upon in-group and out-group taxonomic distributions to infer the morphocline polarity of anatomical features. Following the commonality principle (e.g., Eldredge & Cracraft, 1980), character states broadly distributed within the platyrrhines were compared with phenetically similar and presumably homologous states found in other primates, when possible. Joint occurrence was taken to mean that those traits were primitive for New World monkeys. Derived features were used to recognize and link up monophyletic groups. The methods of that early study were broadly similar to the approaches taken in other cladistic works relevant here (i.e., Ford, 1986; Dunlap *et al.*, 1985; Kay *et al.*, 1987), except that in those applications parsimony-based algorithms were employed to identify primitive conditions by reference to out-groups, without making *a priori* decisions about homologies.

Our procedures have subsequently been modified to rely less upon out-group distributions and more upon functional analysis of characters and behavioral information (e.g., Rosenberger, 1979), in a "transformational" approach to character analysis (e.g., Szalay, 1981). In-group and out-group comparisons are used as a way of finding the cross-taxonomic covariation of characterers, which we regard as evidence for their functional or phylogenetic (homologous) linkage. Morphotypes are therefore reconstructed as individual features as well as patterns. Polarity determinations are reinforced by hypotheses regarding the most likely directions in which specific characters and patterns may have evolved, given their functions, possible biological roles, relationships to other anatomical/behavioral systems and implications for understanding ateline evolution overall. Our current thinking on ateline cladistics, even with these alterations in procedure, has not changed from prior studies (e.g., Rosenberger, 1977, 1979; Rosenberger & Correa, 1983). Thus, the characters we present here as features of the ancestral ateline morphotype represent an extension of previous studies made in a broader taxonomic context (e.g., Rosenberger, 1976, 1979; Rosenberger & Correa, 1983); they are not based upon evaluating atelines alone, or by selecting a species as an archetype.

Our point of departure in this paper is the working-hypothesis cladogram (Figure 1). We add more data to it here and flesh out its strengths by reworking some of the original data upon which it was based. One of our principal goals will be to integrate features into character complexes, which we believe have more inherent value for phylogeny reconstruction than isolated traits. We also stress the importance of functional morphology for distinguishing between homology and analogy, and for falsifying phylogenetic interpretations based upon mistaken homologies.

Since our general conclusions are almost predicated upon our confidence in the *Ateles-Brachyteles* linkage, we point out that our notion of cladistic "parsimony" is often based upon an *a priori* assessment of the high phyletic weight of character patterns and complexes. Examples of patterns which we discuss include the combinations of traits which form the shearing architecture in *Alouatta* molars or the brachiating body plan of *Ateles*. This may be contrasted with the view that parismony is a tool, driven by the commonality principle and motivated by an attempt to avoid *a priori* inferences, which finds the greatest number of individual character states that will generate a cladogram having the smallest possible number of character transformations and the fewest number of nodes (e.g., Ford, 1986; Kay *et al.*, 1987). In each of those studies, a character-by-character approach to parsimony yielded first order results that were regarded unsatisfactory. We contend that there is no reason why high weights cannot be ascribed *a priori* if the characters are so similar that homology is not doubted. Likewise, we place emphasis on particular features or patterns that seem to be parts of functional complexes. In this case, it is the postcranial morphology, reflecting unique locomotor behaviors among certain atelines, that we consider the most convincing phylogenetic evidence; we give it the most weight in deciphering key points in ateline phylogeny. Consequently, a major theme of our discussion is directed at showing how the postcranium proves to be quite robust, and that the dental resemblances alleged as evidence of an *Alouatta-Brachyteles* linkage are demonstrably nonhomologous.

Our interpretation of the phylogenetic significance of the postcranium is consistent with a number of resemblances in disparate systems. Some of these resemblances are striking phenetic patterns of ambiguous homology (e.g., an unusual diploid chromosome number of 2n = 34 in *Ateles* and *Brachyteles*; de Boer, 1974) while others are more readily interpretable, derived homologies shared in certain lineages. For example, in the *Ateles-Brachyteles* clade there is also a rudimentary or absent external thumb (Figure 2); a pervasive functional similarity in the anatomy of the axial and appendicular skeleton

Figure 2. A left hand of *Brachyteles arachnoides*, demonstrating the vestigial thumb found also in *Ateles* (Erikson, 1963).

related to suspensory climbing and rapid brachiation (Erikson, 1963); a hypertrophy of the labia and clitoris in the female (Pocock, 1925); special aspects of social behavior and vocalization, such as a stereotypic pattern of play involving joint tail-hanging and a grappling embrace, accompanied by a distinctive chuckling call. Thus we find the hypothesis of a sister-group relationship of *Ateles* and *Brachyteles* compelling.

The objectives of the following sections are: (1) to present data on the morphological and behavioral diversity of atelines; (2) to attempt to determine how these features functionally and adaptively co-vary; (3) on this basis, and with reference to well-supported phylogenetic hypotheses and information on other platyrrhines, to infer the main characteristics of the last common ancestors (LCAs), or morphotypes, at each of the major divergence points of the most likely ateline cladogram; and (4) to develop an ecological hypothesis that describes the history of the ateline adaptive radiation.

Analysis

Size and sexual dimorphism

Accurate estimates of body size and the degree of sexual dimorphism in atelines are becoming more available, but the information is still quite sparse. Data for the rare *Brachyteles* are very few. Adult, sexed specimens in the British Museum (Natural History) yield an average head and body length of 595 mm for two males and 573 mm for four females (Napier, 1976), confirming reports of recent observers that *B. arachnoides* is the largest Neotropical primate (Table 1). Body weight for *Brachyteles* is even less reliably known. The value of 12–15 kg comes from Aguirre (1971), while Milton (1984*b*) gave a weight of 12 kg for a captive female held in the São Paulo Zoo. Thus, although experienced field workers familiar with the animal and with other atelines endorse these estimates, a definitive weight for *Brachyteles* is still wanting.

To compare the expression of sexual dimorphism, we have compiled quantitative observations on body size measurements (Table 1) and canine size (Table 3; see also Kay *et al.*, 1988). We note that there is a degree of intrageneric variability in canine sexual dimorphism that has not been adequately documented, such as the differences in canine

Table 1 **Adult body size and sexual dimorphism in ateline primates, showing species ranges (top row), means, sample sizes and percentage dimorphism (f/m = mean female/mean male × 100)**

	Head and Body (mm)			Weight (g)			
	Male	Female	f/m	Male	Female	f/m	Average
			Alouatta				
belzebul	540–560 550 (8)	374–540 493 (10)	88%	6540–8000 7376 (8)	4850–6200 5474 (10)	74%	6425
caraya	500–550 527 (3)	480–490 483 (3)	92%	5000–7300 6533 (3)	4600–5400 4933 (3)	76%	5733
fusca	520–535 528 (8)	460–520 497 (3)	94%	5300–7150 6217 (3)	4100–5000 4533 (3)	73%	5375
palliata	440–560 494 (10)	377–560 449 (10)	91%	5600–8626 7164 (10)	4600–6600 5598 (10)	78%	6318
seniculus	434–640 533 (10)	488–616 535 (10)	100%	5400–8172 6922 (10)	4300–7000 5300 (10)	77%	6111
			Lagothrix				
lagothricha	414–568 491 (58)	390–580 492 (51)	100%	8000–10,000 8767 (3)	5000–6500 5740 (5)	66%	6875
			Ateles				
belzebuth	421–550 498 (10)	421–544 484 (10)	97%	7264–9800 8194 (10)	7491–10,400 8466 (10)	103%	8330
			Brachyteles				
arachnoides	580,610 595	565,600 573	98%	estimated	12,000–15,000	??	??

Data for *Alouatta* and *Ateles* from United States National Museum specimens; *Brachyteles* from British Museum (Natural History). *Lagothrix* lengths from Napier & Napier (1967), weights from Fooden (1963).

crown height, and we do not consider intersexual difference in the pelage, genitalia, hyolaryngeal development, etc. among the species. Kay *et al.* (1988) have also shown that diameter measurements at the base of canine crowns have complex intraspecific distributions. Nonetheless, some generalizations are possible, such as the tendency for atelines to be more sexually dimorphic in body weight than in body length and canine size, indicating that weight is often under independent selective pressure. For example, *Alouatta* is consistently the most highly dimorphic in body weight and canine diameters across all species (Kay *et al.*, 1988), but is only moderately dimorphic in head and body length (*A. belzebul* and *A. fusca* females at 88% and 94% the size of males) even in the most extreme cases of weight dimorphism (74% and 73%, respectively).

Brachyteles, at the opposite extreme, is essentially monomorphic in body length; weight differences are not established. In our sample of field-sexed individuals, upper canine mesiodistal length (Table 3) is essentially monomorphic, with a 5% difference between the sexes, a result that is consistent with the upper canine measurements of Kay *et al.* (1988). Kay *et al.* also show that *Brachyteles* lower canines, and a multivariate measure of male : female canine ratios, present a small degree of overall canine dimorphism (their value of 1·158, with 1·00 representing absolute monomorphism). Our measurements of basicranial length in the same sample of adult *Brachyteles* skulls (*N* = 12 males, x = 68·7 mm; *N* = 12 females, x = 67·8 mm; f/m = 98%) indicate a lack of dimorphism as well, whereas measurements of unworn C^1 crown height in a smaller sample exhibit more intersexual variability (*N* = 4 males, x = 9·68 mm; *N* = 5 females, x = 8·34 mm; f/m =

86%). What is most critical regarding *Brachyteles* canine dimorphism, however, is that the canine is essentially nonprojecting in males and females (see below).

More information is required for *Ateles*, although it appears that males and females are roughly equal in body length and weight in at least some species; upper canine length dimorphism is more variable but males are only slightly larger than females, and far less than in *Lagothrix lagothricha* (see Kay *et al.*, 1988). For *L. lagothricha*, we speculate that weight dimorphism is less extreme than Fooden's (1963) sample implies (65%), which would be more consistent with their moderate (84%) to strongly (Kay *et al.*, 1988) dimorphic canines. Regarding head and body length in *L. lagothrica*, the values presented by Napier & Napier (1967) give a 99% dimorphism ratio, and recalculation of Fooden's (1963) data for maximum cranial length in his sample of Colombian *L. lagothricha* yields a 95% difference between the sexes. *L. flavicauda* appears to be monomorphic in canine size (Kay *et al.*, 1987). Thus we regard *Lagothrix* as monomorphic in body length, moderately dimorphic in weight and no more than moderately in canine size.

Alouatta is thus overall the most highly dimorphic ateline, and its fossil relatives appear to have been as well (Kay *et al.*, 1987). The situation among atelins is less clear. As a genus, *Lagothrix* is probably dimorphic as well, but *Ateles* and *Brachyteles* are more nearly monomorphic. Canine length dimorphism varies interspecifically in *Ateles* but at levels below *L. lagothricha.* Dimorphism may be statistically demonstrated to occur at low levels in *Brachyteles* (Kay *et al.*, 1988), but its biological expression is so distinctive in this genus because of the reduced canine crown height. We thus regard *Brachyteles* as essentially monomorphic in canine size.

This taxonomic pattern makes historical reconstructions tenuous, in part because it is difficult to ascribe homological significance to numerical values. In *Ateles*, *Lagothrix* and *Alouatta*, the canines tend to be large in males and females whereas in *Brachyteles* they are absolutely and relatively small in both sexes, and essentially non-projecting. This pattern is definitely a uniquely derived condition among platyrrhines (*contra* Rosenberger, 1977). Morphologically, it is also quite unlike the anatomical pattern found in the other platyrrhine with relatively non-projecting, monomorphic canines, *Callicebus.* Thus ancestral atelines may have had at least moderately enlarged and no more than moderately dimorphic canines, perhaps partly because they were relatively large in body size (Kay *et al.*, 1988). These features were exaggerated in the *Alouatta* lineage, in concert with other secondary sexual characters having display value (vocal apparatus, facial beards, pendulous scrotum, etc.), and in forms like *Lagothrix lagothrichia.* It is difficult to determine whether among atelins there was a derived reduction in canine dimorphism in the morphotype, although it is possible that monomorphism in weight and canine size evolved together in the LCA of *Ateles* and *Brachyteles*, contrary to the tendency for these two parameters to scale up as body size increases among platyrrhines. Lest it be thought that *Brachyteles* is entirely monomorphic, it should be noted that the geneitalia strongly differ, and males are characterized by a very large scrotum. This is a unique feature of the genus and another dimension of the dimorphism problem that we consider briefly below.

Craniodental morphology

Skull. Each of the four atelines present entirely distinctive cranial and dental morphologies (Figure 3). Thus, in contrast to the taxonomic distributions of postcranial traits (Table 4), craniodental features cannot be easily arranged into morphoclines (Table 3). Here we ignore many of the small scale variations of craniodental features (e.g., details of cingula,

Table 2 **Taxonomic distributions, morphotypes and polarities of craniodental traits, arranged into functional complexes. Derived combinations of traits are emphasized. Descriptive terms introduced in columns represent states interpreted as derived relative to the ateline or atelin morphotype conditions. See symbols below and text**

Ateline morphotype	*Alouatta*	*Lagothrix*	*Ateles*	*Brachyteles*
	I. Craniofacial design/proportions			
a. Face mod. large	Huge	P	Reduced	P
b. Braincase spherical	Cylindrical	P	P	P
c. Braincase mod. large	Small @	P	P	P
d. Occipital plane convex	Small, flat @	P	P	P
e. Foramen magnum basal	Posterior @	P	P	P
f. Glabella flat	P	P/convex	Convex	Convex
g. Orbital tori lateral	P	Medial @	D	D
	II. Basicranium			
a. Basicranium flexed	Kyphotic	P	P	P
b. Basicranium short	Long @	P	P	P
	III. Masticatory system			
a. Temporal fossa moderate	Huge @	P/small	Small	D/DD
b. Postglenoid process mod.	Huge @	P	Reduced @	P
c. Lat. pteryg. plate mod.	Huge @	P	Reduced @	Large
d. Angular region large	Huge @	P	Reduced	P
e. Ascend. ramus mod. tall	Elevated @	P	Reduced @	P
f. Corpus mod. deep	Very deep @	P	Reduced @	P
g. Temporal lines mod./weak	Strong @	P/weak	Reduced @	D/DD
h. Mandib. cond. elliptical	Complex @	P	P	P
i. Orbital floor open	Often sutured	P	P	P
	IV. Dentition/occlusion			
a. Postcanine relief mod.	High	P	Reduced	High
b. Postcanines unenlarged	Huge	P	Reduced @	P/large
c. Lingual notch absent	P	P	P	Present @
d. Cristid obliqua moderate	Long	P	Short	DD (?)
e. M_{1-3} subequally long	Lengthen post. @	P	P	P
f. P^3–M^2 buccal styles and cingulum mod.	Hypertrophied @	P/reduced	P/reduced	D
g. M^2 metacone unreduced	Enlarged @	P	P/reduced	Reduced
h. I^2 unenlarged	P	P	Large	P
i. $I_{1,2}$ reduced	P	Large	Large(?) @	Small

Symbols: (?), trait presence, coding or polarity questionable; (/), divides an alternative coding of a (variable) trait; (P), primitive ateline condition retained; (D), derived in the atelin morphotype; derived state occurs; (DD), derived and unique to *Ateles* and *Brachyteles*; (@), correlated with prior trait(s).

Abbreviations: mod., moderate; ascend., ascending; lat., lateral; cond., condyle; ptery., pterygoid; post., posteriorly; mandib., mandibular.

cuspules, crest connections; see Rosenberger, 1979; Ford, 1986; Kay *et al.*, 1987 for analyses) that may contribute to deciphering ateline phylogeny at certain levels. Instead, we concentrate on more general patterns in an effort to develop transformational hypotheses. We begin with the premise that highly crested, large postcanines are adapted to folivory while the more bulbous cusps, blunted crests and relatively smaller cheek teeth are suitable for frugivory, especially involving ripe, fleshy fruits (e.g., Kay, 1975; Rosenberger & Kinzey, 1976). Mention will also be made of the digestive system, where correlative structures and features can contribute to a reconstruction of the evolution of dietary adaptations in atelines.

The functional divisions we identify (Table 2; Figure 3) are partly descriptive and not based upon mutually exclusive categories. Obviously, many features categorized as masticatory correlates, for example, are integrated with others, such as the subbasal space (see Biegert, 1963), or are elements of general cranial design. Nevertheless, no matter how one organizes them or compares ateline cranial morphology, what emerges is a long list of unique features and combinations that describe the *Alouatta* skull. We interpret many of these as primary (e.g., strong temporal lines) or secondary aspects (e.g., small braincase reflecting the relatively small brain) relating to two adaptive themes, folivory, most prominent in the development of the masticatory system, and vocal communication, which conditions the design of the basicranium in response to the unusual hyolaryngeal mechanism, which also relates to social organization and feeding strategies (see below). There is little doubt that this morphological "package" is derived for atelines, and essentially all of the traits of the craniodental categories I–III that are not primitive in *Alouatta* are unique specializations, autapomorphies.

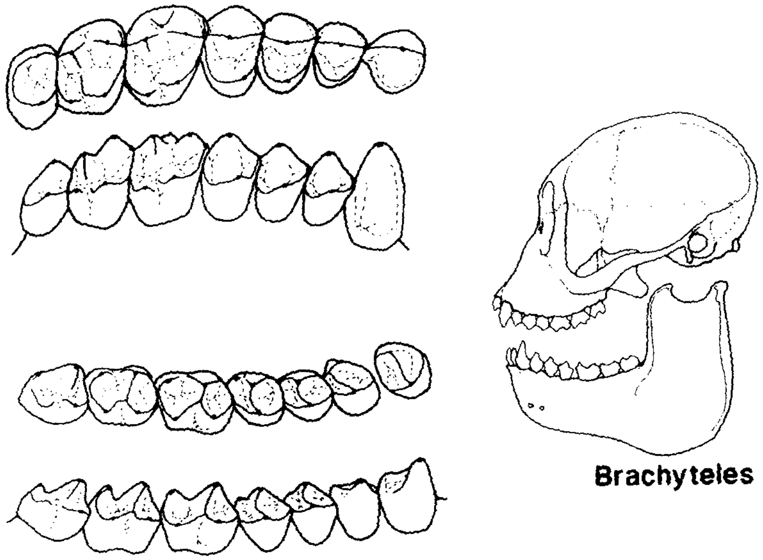
The remaining features are shared in common by the atelins. They are also broadly similar to the characteristics of other platyrrhines, which suggests they represent a pattern. Thus the common atelin cranial design, with a generally rounded neurocranium and occiput, moderately developed circumorbital tori and a short, flexed basicranial axis, etc., is likely to represent the ateline cranial morphotype as well. We also postulate that the relatively large face and large mandibles shared by *Lagothrix* and *Brachyteles*, reflect the ancestral pattern, as opposed to the very small face and reduced mandible of *Ateles*, which are clearly related to the latter's unique, reduced dentition. From among those traits listed, only a few are potentially derived atelin character states, including several in the orbital region (convex glabella and a tendency to differentiate the circumorbital margin to form a torus medially; possibly a reduced temporal fossa) and fewer still potentially characterize the *Ateles-Brachyteles* common ancestor (further reduced temporal fossa; strongly convex glabella; weak temporal lines; see Table 2).

Postcanine teeth. Extending this argument to the dentition, and again emphasizing our position that each of the four living atelines has its own highly distinctive dental pattern (Figure 3; Table 2), we propose that the moderate relief of the cheek teeth in *Lagothrix*, a widespread platyrrhine feature, is ancestral, whereas the reduction in relief, morphological detail and relative size of the postcanines in *Ateles* (Table 2) is derived.

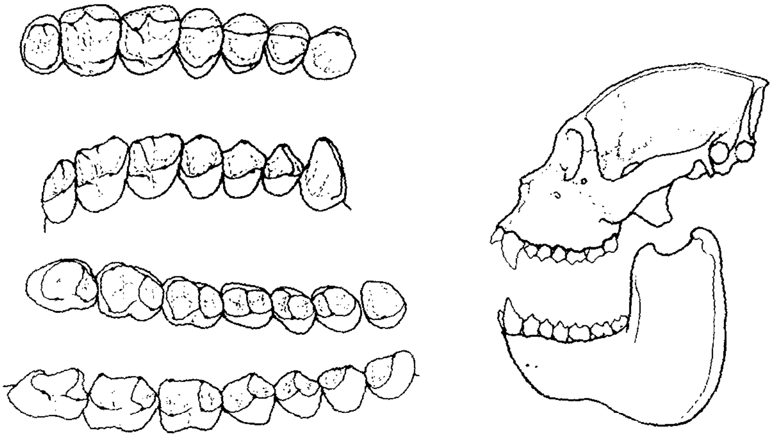
This raises the issue of alleged special resemblances shared by *Alouatta* and *Brachyteles*. Each genus presents postcanine teeth of high-relief which some (e.g., Zingeser, 1973) regard as ancestral for atelines. Conversely, the most parsimonious cladogram of Kay *et al.* (1987) also linked *Brachyteles* with alouattins on the basis of two presumed derived conditions. If that alternative is rejected, as was done by Kay *et al.*, it remains to be determined whether the *Alouatta-Brachyteles* resemblances are primitive ateline homologies or convergently evolved similarities.

We suggest that the resemblances of *Alouatta* and *Brachyteles* are not homologous and thus not indicative of the ateline LCA, but reflect a convergence in folivorous adaptations. In fact, the only decisive resemblance they share, apart from general ateline similarities that also occur in *Lagothrix* and *Ateles*, is a high-relief cusp pattern, the functional basis of a shearing crown design. That their shearing characteristics have evolved independently is shown by the contrasting occlusal patterns of their crowns.

As is well known (e.g., Rosenberger & Kinzey, 1976), shearing in *Alouatta* is



Brachyteles



Alouatta

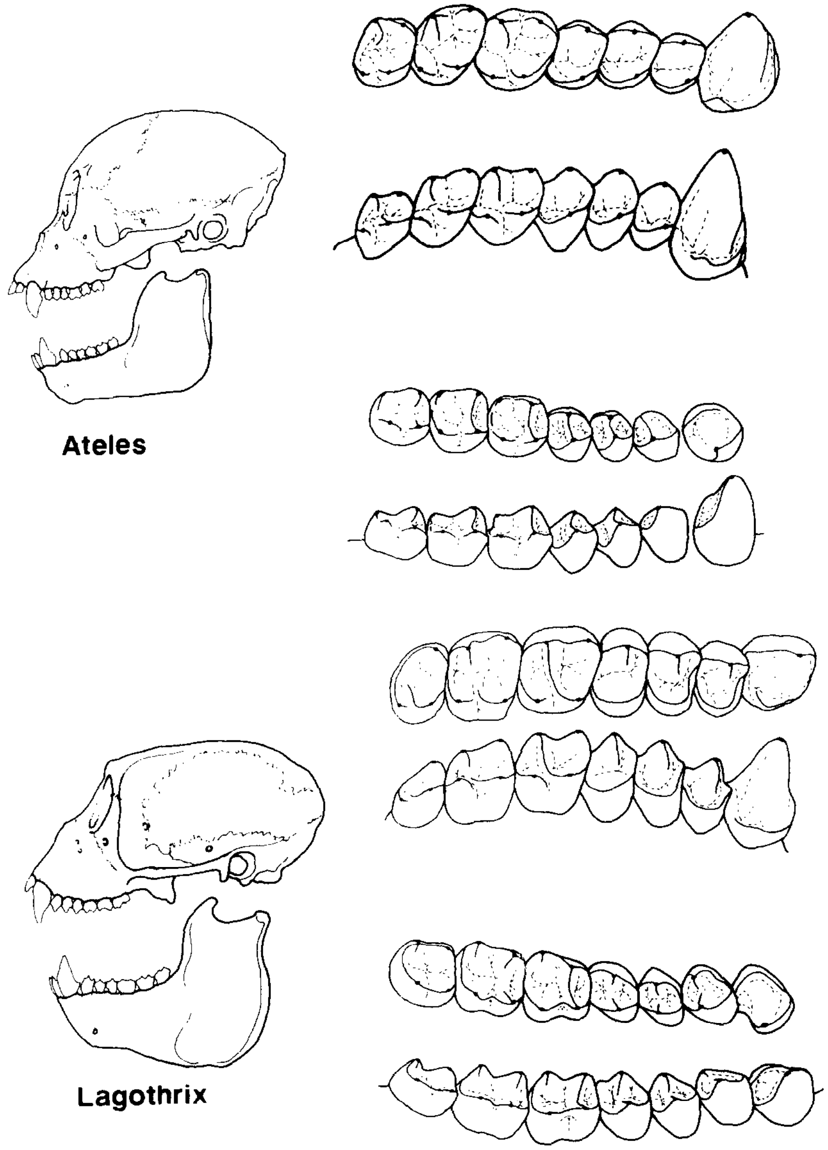


Figure 3. Comparative craniodental anatomy of *Brachyteles*, *Ateles*, *Lagothrix* and *Alouatta*. Skulls drawn to approximately same maximum cranial length. Maxillary (occlusal and 3/4 lingual views) and mandibular (occlusal and 3/4 buccal views) dentitions each drawn to approximately same length.

Table 3 **Mean upper canine length, canine sexual dimorphism (female/male in percent) and postcanine tooth area (length × breadth) in atelines. Sexes separated for canines, pooled for cheek teeth. Sample sizes in parentheses**

Canines (mm)	Postcanines (mm^2)						Summed
Male, female	P2	P3	P4	M1	M2	M3	P2–M3 area
			Alouatta seniculus				
7·3(8),6·8(6)	31·4	33·0	32·7	53·9	59·8	41·4	252(9,18)
f/m = 93%							
			Lagothrix lagothricha				
6·8(5),5·7(4)	19·6	22·9	22·9	33·2	33·2	24·5	132(4,5)
f/m = 84%							
			Ateles belzebuth				
7·3(4),6·2(6)	19·4	20·6	21·1	27·6	25·3	15·2	129(5,14)
f/m = 85%							
			Brachyteles arachnoides				
6·3(9),6·0(9)	27·4	34·6	37·7	52·3	50·6	32·5	235(7,17)
f/m = 95%							

L. lagothricha data from Orlosky (1973). Minimum and maximum sample sizes for postcanines appear in last column.

concentrated along the buccal aspect of the tooth, where the paracone and especially metacone are large and the ectoloph is prominent, with strongly developed styles and cingula to support and elongate the shearing crest. Lower molars have correspondingly elongate talonids, a particularly long cristid obliqua and a bowed postcristid, making the basin fairly broad and rounded distally. Thus the essence of *Alouatta* (and *Stirtonia*) occlusion is buccal shear.

Brachyteles, on the other hand, is dominated by lingual shear. The paracone and metacone are much smaller than the protocone, for example; both cusps are reduced drastically on M^2, the ectoloph is unimpressive, styles and cingula only occur as remnants, with low frequency (Kinzey, 1973), and they are not mechanically integrated into the crown's crest system to play a significant role in shearing. In the lowers as well, the cristid obliqua is not long relative to the mesiodistal axis of the crown and the talonid basically reduces in relative length posteriorly. However, the lingual aspect of the molar crowns in *Brachyteles* presents a large protocone and prominent interdental embrasures between the protocone and hypocone. Into this gap occludes a very tall, acute metaconid, while an unusually acute entoconid shears into the sharp notch between protocone and hypocone. The differentiation of the entoconid is related to the appearance of a strong lingual notch (Table 2) between the metaconid and entoconid in *Brachyteles*, not seen elsewhere among atelines.

The marked differences in relative postcanine size among atelines (Table 3) reinforces this morphological contrast. *Alouatta* clearly has relatively very large cheek teeth, following the usual folivorous pattern (e.g., Kay, 1975). *A. seniculus*, one of the largest species, has about twice as much crude postcanine area as *Lagothrix lagothricha* or *Ateles belzebuth*, which weigh about 18%–35% more on average. *Brachyteles*, on the other hand, which is considerably heavier than all of the other atelines, has cheek teeth absolutely smaller than

Alouatta, but much larger than *Lagothrix* and *Ateles*. Finally, *Ateles* and *Lagothrix* have similar postcanine areas while the latter is estimated to be about 15% heavier. By comparison, therefore, *Ateles* has relatively small postcanine teeth.

In summary then, the often cited resemblances of *Alouatta* and *Brachyteles* are rather superficial. If one assumes that shearing features (and other occlusal details) and relative tooth size evolve in concert in a folivorous lineage, it seems highly unlikely that a putative ancestral ateline pattern of *Alouatta*-like design, with massive postcanine teeth and uniquely hypertrophied buccal features, would have become transformed into a *Brachyteles*-like pattern. On the other hand, the *Brachyteles* pattern is also unique among platyrrhines, with a lingual shearing mechanism and reduction in potential shearing function posteriorly. This makes a transformation in the opposite direction equally unlikely, given the same selective constraints. Therefore, we consider it highly probable that these two derived folivorous adaptations are convergent and unlikely to represent the primitive ateline pattern. For obvious reasons, each is also a poor model for the antecedents of the *Lagothrix* or *Ateles* dentitions. Since the reduced, soft-fruit-adapted postcanines of *Ateles* (correlated with a derivedly reduced, shallow face and mandible) are also unique, it is most reasonable to reconstruct the ateline morphotype as resembling *Lagothrix*, with its moderate-relief molar pattern (and more robust gnathic morphology). One notion that needs to be further tested is the possibility that the distinctive occlusal morphology of *Brachyteles* arose from a dentition of reduced relative size inherited from the *Ateles-Brachyteles* common ancestor (e.g., Rosenberger, 1979), as might be implied by the several dental traits (Table 2) that may be uniquely shared by them.

Of relevance to the distinctive dental morphologies exhibited by atelines is the morphology and physiology of their digestive tracts. In reviewing the available data, Chivers & Hladik (1980) noted that *Ateles* and *Alouatta* each exhibit morphological specializations. The large J-shaped stomach of *Ateles* they associated with extreme frugivory. This may be related to a very rapid passage rate which contrasts with the slow passage time of *Alouatta* (Milton, 1984*b*). *Alouatta* presents a large globular stomach sac, a tubular pylorus guarded by strong pillars and rugae radiating from the cardia and running longitudinally within the body (Chivers & Hladik, 1980: 340). These features relate to the great bulk, mixing and transport of digesta down the gut. Although Chivers & Hladik classify *Alouatta* as a frugivore in their mammal-wide survey, they noted that the stomach of *Alouatta* ". . . shows the greatest complexity." Measurements of stomach size are similar in *Ateles* and *Alouatta* and indices of foregut : hindgut differentiation, related to the fermentation capacity of the stomach and/or large intestine, are also similar in *Ateles*, *Alouatta* and *Lagothrix* (with only *A. palliata* falling into the range of colobines). The relative size of the caecum, compared to the stomach, in *Ateles* and *Lagothrix* also falls within the range of *Alouatta*. The morphology of *Brachyteles* is not well known. However, the outward appearance of its voluminous, pot-bellied abdomen resembles that of other atelins, particularly *Ateles*, suggesting similarities in shape and suspension. Furthermore, the reported passage time for *Brachyteles* appears to be 2·5 times faster than *Alouatta*, but similar to *Ateles* and *Lagothrix* (Milton, 1984*b*).

These data, together with dietary information on wild populations (see below), suggest that the relatively large-bodied, ancestral atelines had guts suitable for digesting some, perhaps young, leaves. Only in *Alouatta* has this capacity developed into an adaptive specialization. Furthermore, if the rapid *Brachyteles* passage rate observed in the only experiment performed accurately reflects its digestive strategy (Milton, 1984*b*), then

Brachyteles starkly contrasts the slow-digesting specialist *Alouatta*, where selection mosaically combined the derived occlusal adaptations of a folivore with the rapid digestive tract of a soft-fruit, *Ateles*-like frugivore. At the very least, this strongly argues against the notion of *Alouatta* and *Brachyteles* sharing either ancestral or homologously derived adaptations to folivory, and favors the idea that those folivorous features which they do share in common evolved convergently.

Incisors. The proportions of the upper incisors probably represent a derived pattern distinguishing atelines from other platyrrhines. Eaglen (1984), using bi-incisal breadth as a measure of overall size, showed that the incisors of platyrrhines are negatively allometric with respect to body mass, especially so among atelines. Thus the larger atelines have relatively small incisors, with *Brachyteles* smallest of all. This implies either selection for incisor reduction, as occurs among catarrhine folivores (Hylander, 1975), or that ancestral atelines were selectively neutral to incisal size increase, which has been linked with increased incisivation, as one might expect in some frugivores. In either case, it appears that this is a derived pattern.

It is also of interest that the lower incisors of *Brachyteles* are far smaller relative to body mass than those of *Alouatta*, while *Lagothrix* has larger lowers than some *Ateles* (see Eaglen, 1984, Figures 1, 2). This may signal independent adaptive responses to folivory in *Brachyteles* and *Alouatta*, following the arguments laid out above. (A pleiotropic effect of canine reduction cannot be ruled out for *Brachyteles*, however.) Unlike most other platyrrhines where I^1 is not excessively broader than I^2, which is the case for *Aotus*, *Ateles* does exhibit this condition (Table 2). We intepret their large median upper incisors as an autapomorphic adaptation reflecting a strong commitment to frugivory: the uppers probably serve to stabilise a relatively large food object, like a whole fruit, against the pressure exerted by the lowers. The contrast shown by Eaglen between *Ateles* and *Lagothrix*, with the latter having broader lower incisors, may reflect sampling error, but it is also possible that separate enlargement of lowers in the latter is indicated, perhaps related to ingesting relatively harder fruits. In Milton's (1984*b*) feeding trials, *Lagothrix*, like *Cebus* but unlike *Ateles* and *Alouatta*, would immediately bite into commercial walnuts, apparently using the anteriormost premolars and canine to crack them open. She suggests this behavioral response indicated which species included hard fruits within their foraging search images. Thus, the different incisor proportions of *Ateles* and *Lagothrix* may relate to different fruit preferences.

Summary of skull and dentitions. The LCA of the atelines was structurally like atelins, and more specifically *Lagothrix*-like, in the skull and postcanine dentition (e.g., moderately large face; well defined circumorbital rings; convex glabella; flexed basicranial axis; relatively rounded occiput; simple temporomandibular joint; moderately large postglenoid process; deep, robust jaw; moderate-relief postcanines, unenlarged molars), but it probably had reduced incisors and a moderately large, slightly to moderately dimorphic canines. Many of the cranial features were retained in *Brachyteles* as well as *Lagothrix*, and they typify the atelin morphotype. Once *Ateles* and *Brachyteles* split from their common ancestor, the *Brachyteles* group evolved more shearing features, causing it to superficially resemble *Alouatta*, and probably further reduced incisor proportions as it achieved its comparatively very large body size. The *Ateles* lineage, in adapting to relatively soft fruits, enlarged the incisors for harvesting but reduced the masticatory correlates of heavy chewing in the face, lower jaw (i.e., its musculature and bony resistance to large force production and transmission) and the postcanine teeth, which also lost some of their complexity. *Lagothrix* apparently retained much of the ancestral atelin pattern but enlarged its incisor teeth, and perhaps evolved more bunodont molar crowns to accommodate relatively hard fruits. At the other extreme, *Alouatta* evolved a highly modified skull and dentition, together reflecting its huge, folivorous cheek teeth and hypertrophic hyolaryngeal apparatus.

Postcranial morphology

Limbs. To evaluate the phylogenetic and evolutionary implications of the limb skeleton, which has been adequately discussed in only a handful of studies (e.g., Erikson, 1963; Schön Ybarra & Conroy, 1978; Schön Ybarra & Schön, 1987; see also Ford, 1986), we have concentrated on the evidence of the forelimb presented by Erikson (1963), reworking it into a modern perspective (Table 4). However, our treatment does not comprehensively summarize his data, for it is meant to serve as an example only. As above, we develop the morphological and behavioral data together in an attempt to explain anatomical diversity in light of the different locomotor styles and positional behaviors evident among the atelines.

Table 4 Taxonomic distributions of postcranial traits in atelines, mostly following Erikson (1963), arranged into functional complexes and emphasizing character correlations. Symbols and abbreviations as in Table 2 with some additions (below)

Ateline morphotype	*Alouatta*	*Lagothrix*	*Ateles*	*Brachyteles*
	I. Prehensile tail			
a. Mod. elongate (*)	P	Longer D	Longer DD	DD
	II. Forelimb complex			
Hand				
a. Thumb unreduced	P	P	Vestigial DD	DD
b. Zygodactylous grip	P	P	Midcarpal DD @	DD
c. Metacarpals simple	P	P	Long, curved DD	DD
Shoulder and elbow joints				
d. (>) Spine slightly oblique (*?)	P	Mod. oblique D	Highly DD	DD
e. (>) Acromion unred.	P	?	Reduced DD @	DD
f. (>) Mod. dorsad (*)	P	More D	Fully DD @	DD
g. (>) Glenoid lateral	P	P/cranial D ?	Cranial DD @	DD
h. (>) Head large (*?)	P	Larger D (?)	Larger DD @	DD
i. (>) Head posterior	P	P/cranial D(?)	Medial	D
j. (#) Trochlea spool-like	P	P/cylin. D	Cylin. DD	DD
k. (>) Lateral epicondyle unreduced	P	Reduced D	Small DD @	DD
l. (>) Medial epicondyle unenlarged	P	Large	Prominent DD @	DD
m. ($) Olecranon process unreduced	Large	Moderate	Reduced DD	DD
Proportions				
n. (>) Forelimb not elongate	Short (?)	Mod. long D	Elongate DD	DD
F/H	98 (92–105)	98 (93–99)	105 (99–109)	105 (102–110)
F/VC	91 (85–97)	109 (105–115)	150 (135–166)	140 (137–147)
R/Hu	92 (84–96)	89 (85–92)	102 (96–108)	94 (89–102)

Symbols: (*), derived in ateline morphotype; (>), denotes morphoclines and/or data [mean, ranges] from Erikson (1963); (#), from Ford (1986); ($), from Schön Ybarra & Conroy (1978) and Erikson (1963).

Abbreviations: cylin., cylindrical; F, forelimb; H, hindlimb; VC, vertebral column; R, radius; Hu, humerus.

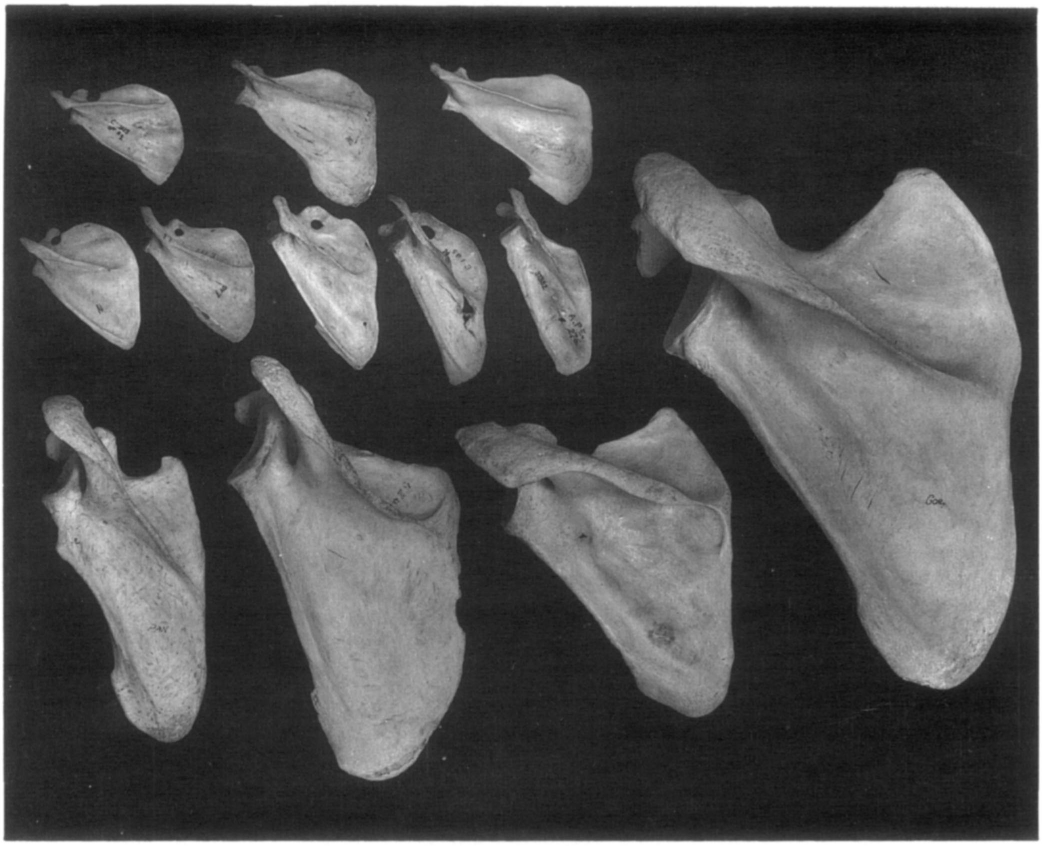


Figure 4. Left scapulae of (left ro right): *Cebus*, *Colobus*, *Macaca*, (top row); *Alouatta*, *Lagothrix*, *Brachyteles*, *Ateles*, *Hylobates*, (middle row); *Pan*, *Pongo*, *Homo*, *Gorilla*, (bottom row). Note strongly diagonalized shape of *Ateles* and *Hylobates*; relatively large size and strong development of fossae and processes in *Alouatta*, contrasting *Lagothrix* and *Cebus*. *Brachyteles* closely resembles, but is not identical to *Ateles* (Erikson, 1963).

Erikson (1963) presented most of his observations on the taxonomic distribution of characters as a gradient, or cline, presumed to reflect a spectrum of locomotor styles ranging from quadrupedalism to brachiation (Table 4). The cline ranges from *Alouatta* to *Lagothrix*, then to *Ateles* and *Brachyteles*, both being regarded as fully advanced brachiators. While there is little question that the derived extreme of this distribution is at the *Ateles-Brachyteles* pole, we propose that the morphocline should be more specifically confined to atelins, without assuming that all the states found in *Alouatta* are consistently ancestral for the subfamily. Rather, we suggest that some of the features of *Alouatta* are related to a methodical, deliberate form of quadrupedalism that is novel to this genus. Their movements contrast with the more agile, fluid quadrupedal style of *Cebus*, for example. *Alouatta*-like quadrupedalism, well described by Schön Ybarra & Schön (1987), is not seen in other atelines, and is thus not a good model for the more general pattern of the ateline LCA (but see Schön Ybarra & Schön, 1987). Many of the distinctive features of the genus are also overlaid upon more flexible climbing adaptations (Schön, 1968; Schön Ybarra, 1984). Thus the ateline morphotype is better reconstructed as an agile quadruped

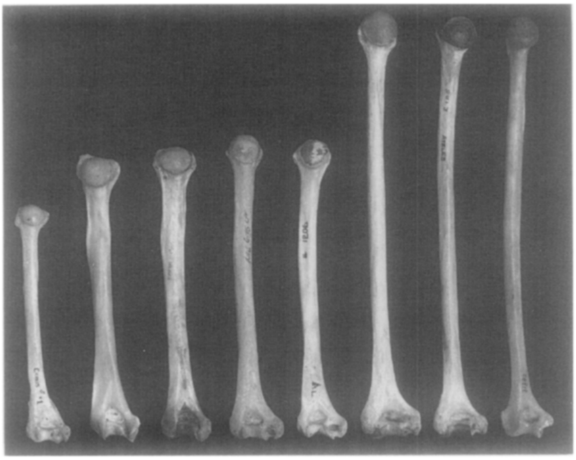


Figure 5. Left humeri of (left to right) *Cebus*, *Macaca*, *Colobus*, *Lagothrix*, *Alouatta*, *Brachyteles*, *Ateles* and *Hylobates* (Erikson, 1963). Note for *Ateles* and *Brachyteles*: extreme relative elongation of shaft, large head, enlargement of distal articular surfaces.

that climbed to a significant degree. Atelins would have retained this more general pattern and enhanced it by evolving a variety of postcranial adaptations specifically relating to forelimb-dominated climbing.

The forelimb data (Table 4) are arranged into four categories. There is little doubt that the elongate metacarpals, vestigial thumb and consequent midcarpal grasping pattern of *Ateles* and *Brachyteles* (Figure 2) are derived features, very probably connected with their extensive suspensory behaviors. Additionally, the scapular and humeral features at the *Ateles* + *Brachyteles* end of the morphocline are also derived resemblances shared with hylobatids (Figures 4, 5), related to powerful circumduction of a highly mobile forelimb. Their further resemblances in the elbow (Figure 5), such as the enlargement of the medial epicondyle, reflecting powerful manual flexors and forelimb pronators, and the spool-like humeral trochlea which enhances joint stability (e.g., Jenkins, 1973), are also advantageous in brachiators, as are their highly elongate forelimbs. The morphologically intermediate position of *Lagothrix*, in many of these features, suggests a less advanced commitment to suspensory locomotion, and a pattern that is probably typified by forelimb-dominated climbing habits as opposed to "simple" quadrupedalism. On the other hand, the enlarged olecranon process of *Alouatta* (see also Schön Ybarra & Conroy, 1978) and features such as the strongly developed supraspinous fossa, scapular spine and acromion process of the scapula (Figure 4), do not especially resemble non-ateline platyrrhines and are not necessarily associated biomechanically with climbing or suspensory locomotion. They may reflect an alternative set of adaptations relating the deliberate quadrupedalism (see Schön Ybarra & Schön, 1987).

Although there is insufficient data for standardizing the limb proportion information (Table 4), it is also likely that atelins are derived in having relatively long limbs in general, with *Ateles* and *Brachyteles* developing extremely long forelimbs (Figures 5, 6). *Lagothrix*, *Ateles* and *Brachyteles* present similar ratios of hindlimb relative to trunk length (174, 177, 183, respectively: Erikson's calculations) and *Alouatta* has quite the shortest leg ratio (151), falling roughly between *Aotus* (143) and *Cebus* (162), animals that are much smaller in body size. This fact does not support the notion that *Alouatta* is simply at the primitive end of an ateline morphocline. Rather, like other details of the skeleton, these features probably reflect a unique alouattin adaptation to quadrupedalism.

Prehensile tail. The evolution of the grasping tail is an intriguing problem central to the adaptive radiation of the atelines but its ecological significance is barely understood. The atelines have a fully prehensile tail, including a dermatoglyphically coated feeler pad to enhance friction. This contrasts with the semi-prehensile tail of *Cebus*, which lacks a friction skin. The morphological distinctions between these types of tails extends to other characters and systems (Rosenberger, 1983), implying that they evolved in parallel in the LCA of atelines and in the *Cebus* lineage.

Within atelines, a number of different allometric scaling models consistently indicate that the *Alouatta* tail, in each of the four species studied, is relatively the shortest, followed by a slight increase in relative size in *Lagothrix*. *Brachyteles* is slightly longer still, followed by some species of *Ateles*. The most reasonable interpretation (Table 4) is that the moderate length of *Alouatta*, perhaps only slightly longer than the norm for a platyrrhine of its size, is primitive for the group, and that both the atelin and *Brachyteles-Ateles* common ancestors each evolved slightly more elongation as body size and/or a commitment to climbing and suspensory locomotion increased.

Why the prehensile tail evolved in atelines, and the nature of its parallelism with the *Cebus* condition, is another matter. Scattered observations (Rosenberger, personal observation; Strier, personal observation) suggest that the semi-prehensive tail of *Cebus* and the ateline prehensile tails serve different biological roles. *Cebus* commonly uses its tail as a brace in tripod stances, tensing it against gravity and two grasping feet as it arches its body away from the substrate, manipulating objects with the hands. During quadrupedal locomotion it carries the tail curled behind the rump, rarely making contact with a support. *Cebus* uses the tail as a brake in halting descents on large vertical supports, but rarely hangs freely from it in postural behaviors. In contrast, in the most advanced atelines, *Ateles* and *Brachyteles*, the tail is used fluidly, to grasp branches at various angles and distances from the body, or to join with the hand to produce a two point pendulum as the animal swings below supports with the trunk twisting at the tail base, bent upwards upon it or dropped vertically below it. In *Alouatta*, such dynamism is probably very rare and strenuous, but the tail is commonly used as the only supporting member in hanging postures.

The more extensive grasping abilities of *Ateles* and *Brachyteles* tails are evidenced not only in a greater reliance on their tails in locomotion, but in the more frequent use of tail-hanging in postural behaviors. Comparisons between sympatric *Ateles* and *Alouatta* (Mittermeier & van Roosmalen, 1981) and *Brachyteles* and *Alouatta* (Strier, unpublished data) indicate that tail suspension is employed more often by the atelins than by *Alouatta*.

Postcranial summary. The locomotor behavior and post-cranial anatomy further support the idea that *Brachyteles*, despite its comparatively large body size and folivorous feeding habits, shares greater adaptive resemblances with *Ateles* and *Lagothrix* than with *Alouatta*. The most detailed functional resemblances are with *Ateles*, however, including such features as: the stiff, craniocaudally reduced sacrum (Ankel, 1962); shortened lumbar length (Erikson, 1963); vestigial thumb (Figure 2); bowed metacarpals and phalanges (Erikson, 1963; Figure 2); mobile shoulder joint (e.g., strongly oblique scapular spine, cranial glenoid, large humeral head; Figure 5) and the comparatively long humerus (Figure 5) and forelimb (Figure 6; see also Table 4). The postcranial features support the notion that atelines and atelins are also monophyletic (see Ford, 1986). Regarding the behavior of the ateline LCA, Ford noted that the long posterior talocalcaneal joint of all atelines was an important climbing adaptation. Gebo (1989) has also recently identified an ateline-wide pattern in the foot that converges upon hominoids and is functionally related to a highly mobile, climbing pattern. It includes a shallow talar body, deep calcaneo-cuboid pivot joint, relatively wide anterior calcaneus, a plantar tubercle and a relatively large first metatarsal.

Given the initial possession of the ateline prehensile tail in combination with a climbing foot, there is little question that quadrupedal climbing and tail-hanging were important, if not critical, behavioral modes in the earliest atelines. Functionally, suspensory feeding positions permit the large-bodied atelines to exploit food from terminal branches and understory vegetation that would otherwise provide insufficient structural support (e.g., Grand, 1972; Fleagle & Mittermeier, 1980). Access to such vegetation may be particularly important for the atelines because new leaves, which are easier to digest and generally lower in tannin and secondary compound content, are more abundant in these areas.

Within atelines, if the atelins and the *Ateles-Brachyteles* lineages each represent successive derived states of tail elongation, their greater locomotor agility and flexibility continued to evolve, perhaps in concert with body size increase and/or a reliance on particular feeding strategies or sites. The elongate limbs of atelins imply that more forelimb-dominated climbing was prevalent in their LCA than in the ateline morphotype. The full brachiation-like locomotor style evolved exclusively in the *Ateles-Brachyteles* lineage, which added features such as extreme forelimb elongation, while at the opposite end of the spectrum, the alouattins possibly modified their quadrupedal pattern by intensifying their cautious sort of quadrupedalism while still retaining the primitive pedal climbing and tail-hanging abilities.

Behavioral ecology

Diet and activity budgets

Dietary data for the atelines have generally been calculated from the proportion of feeding time devoted to different food types, with researchers drawing the most significant distinctions between the relative importance of fruit and leaves in their diets. There are obvious limitations to such generalizations (e.g., van Roosmalen, 1985; Ayres, 1989), including their failure to take into account the importance of seasonal or annual variations in diet. From an evolutionary perspective, ecologically stressful periods are likely to play a highly significant role in selecting for morphological specializations. Yet pronounced seasonal shifts in diet, known to occur in all atelines, are often masked by or confused with feeding preferences observed over the course of annual cycles. One consequence is that inferences about diet generated from morphology may be inconsistent with direct observations of feeding behavior (Rosenberger & Kinzey, 1976).

A second limitation of distinguishing primate diets by whether they tend to be more frugivorous or more folivorous is that such categories may be misleading when they are associated with divergent behavioral strategies. For example, frugivores generally rest less and travel longer distances than more folivorous primates, presumably because fruit is both higher in energy and more patchy in distribution than leaves. Frugivores appear to follow a strategy of maximizing energy intake that contrasts directly with the folivorous strategy of minimizing energetic expenditure (see Milton, 1980). While the relationships

Table 5 **Dietary preferences and seasonality in ateline primates. Annual means and seasonal ranges (in parentheses) are presented for the major categories of food items eaten. The annual rainfall and duration of each study period are also given**

	% Fruit	% Leaves	% Flowers	Rainfall (mm)	Study (mos)	References
			Alouatta			
palliata	42 (10–65)	48 (26–85)	10 (0–22)	2730	14	Milton, 1980
	13 (9–15)	64 (59–67)	18 (17–20)	1431	14	Glander, 1978
	51 (0–80)	49 (3–92)	1	4500	12	Estrada, 1984
	29 (0–55)	49 (0–95)	22 (0–50)	900–2400	24	Chapman, 1987
fusca	16 (1–30)	71 (64–78)	9 (6–11)	1186	13	Mendes, 1985
seniculus	42	53	5	1942	10	Gaulin & Gaulin, 1982
			Lagothrix			
lagothricha	69–79		Not provided			Soini, 1987
			Ateles			
belzebuth	83 (78–100)	7 (3–22)	1	??	15	Klein & Klein, 1977
geoffroyi	78 (15–100)	11 (0–90)	10 (0–30)	900–2400	24	Chapman, 1987
paniscus	83 (58–96)	8 (1–23)	6 (1–28)	2000–2400	26	van Roosmalen, 1980
	75 (55–99)	16 (1–38)	4 (0–20)	1971	21	Symington, 1988*a*
			Brachyteles			
arachnoides	32 (13–66)	51 (28–78)	11 (0–33)	1186	14	Strier, 1986
	21 (4–59)	67 (41–93)	12 (0–34)	1263	11	Milton, 1984*a*
	19 (12–44)	51 (35–78)	28 (0–44)	??	7	da Sa, 1988

between diet and behavioral strategies appear to be consistent in some cases, in other cases, such as that of *Brachyteles*, they are not so clear.

While *Ateles* and *Lagothrix* are undisputedly more frugivorous than *Alouatta*, there is a substantial overlap between the relative proportions of fruit and leaves that comprise ateline diets (Table 5). Within the atelins, *Ateles* and *Lagothrix* are more frugivorous than *Brachyteles*, with fruit, and in particular ripe fruit, accounting for 69–90% of their annual feeding time (see references in Table 5). However, *Ateles* may devote as much as 38% of its feeding time to leaves during certain months when ripe fruit is scarce (Symington, 1988*a*, *b*), and *Brachyteles* may spend up to 66% of its feeding time on fruits during particularly abundant periods (Strier, 1986). Fruit accounts for an average of 21–32% of feeding time in *Brachyteles* and 13–60% in *Alouatta*. *Brachyteles* and *Alouatta* rely more heavily on leaves than the other atelines, with annual ranges of 50–67% feeding time devoted to leaves in *Brachyteles* and 40–71% in *Alouatta*. Data are lacking for *Lagothrix*. All three genera for which data are available show strong preferences for flush leaves and all four consume some flowers.

In view of the fact that adult female *Brachyteles* are considerably larger than other female atelins, it is not surprising that *Brachyteles* also shows stronger tendencies for folivory. Body size energetics (e.g., Gaulin, 1979) predict that larger primates can rely upon more abundant but energy-poor foods, such as leaves, than smaller primates. Indeed, the larger body size observed in *Brachyteles* may reflect their historical expansion and subsequent evolution in the more seasonal Atlantic Coastal forest where a capacity to tolerate seasonal food shortages and store energy would have been selectively advantageous (Linstedt & Boyce, 1985).

The relationship between body size and diet is confounded, however, when *Brachyteles* and *Alouatta* are compared. Although *Brachyteles* females are up to twice as large as *Alouatta* females, they do not consume more leaves. Indeed, at the only Atlantic forest site where the two genera have been studied sympatrically, *Brachyteles* devoted less of their annual feeding time to leaves, on average (50%: Strier, 1986) than *Alouatta* (71%: Mendes, 1985).

One interpretation of these findings is that the feeding strategy employed by *Brachyteles* is distinct from that of *Alouatta*. From this perspective, *Brachyteles* may be as much a "frugivore" in its foraging strategy as *Lagothrix* and *Ateles*, only larger and morphologically better equipped to survive in the more seasonal Atlantic forest. As argued above, the moderate (relatively small by *Alouatta* standards) and fairly restricted shearing adaptations of *Brachyteles*, in particular, support this interpretation (but see Kay *et al.*, 1987). Possessing derived shearing adaptations at the level in which they are manifest need not imply that leaves are a preferred food type or major dietary component year-round for *Brachyteles*. Similarly, while their large size and seasonal habitat may require *Brachyteles* to consume more leaves than the other atelins, morphological adaptations do not necessarily predict behavioral preferences. The diet of *Brachyteles* is more folivorous than that of other atelins and within the range of folivory for *Alouatta*. However, its overall behavioral strategy resembles those of the other atelins in its emphasis on maximizing energy intake and differs from the energy minimization of *Alouatta*. Sympatric comparisons of *Brachyteles* and *Alouatta* show that *Brachyteles* is more frugivorous than *Alouatta*, despite its larger size, when ecological variables such as food availability are constant (Strier, in preparation). Although it is more folivorous than the smaller atelins, *Brachyteles* is more frugivorous than sympatric *Alouatta*.

If *Brachyteles* is behaviorally continuous with the other atelins, as a "frugivore," then the question remains whether *Alouatta* is as divergent from the common ateline ancestor in its diet as it undoubtedly is in its morphology. The morphological similarities of *Brachyteles* and *Alouatta* dentitions are superficial, and *Alouatta* possess a number of elaborate folivorous features derived since the atelin-alouattin LCA. Therefore, the higher degree of folivory observed in *Alouatta* should be considered an intrinsic adaptive specialization of its lineage rather than a response to local ecological conditions affecting food availability. We propose that folivory in *Alouatta* emerged either as a result of competition with the more frugivorous atelin genera throughout their geographic distribution or in response to selection pressures imposed on *Alouatta* as a "colonizing" species in more marginal habitats (Eisenberg, 1979).

That *Alouatta* stands out as behaviorally distinct from the atelins is further supported by a comparison of activity budgets (Table 6). While activity budgets exhibit both inter- and intrageneric variability among the three genera for which data are available, the ranges of variation conform to a bimodal pattern. *Alouatta* devotes from 66–78% of its time to resting, whereas *Ateles* and *Brachyteles* rest between 45–63% and 49–62% of their time, respectively. At the one site where *Brachyteles* and *Alouatta* have been studied sympatrically, *Brachyteles* devoted far less time to resting (49% *vs.* 72%) and more time to travelling (29% *vs.* 11%). The general inactivity observed in *Alouatta*, associated with its greater reliance on low-quality leaves, supports the classification of *Alouatta* as an energy minimizer (e.g., Milton, 1980). Sympatric *Brachyteles*, along with *Ateles*, and perhaps *Lagothrix*, may thus be characterized as energy maximizers. This dichotomy between energy minimization and energy maximization is consistent with their contrasting locomotor patterns: deliberate quadrupedalism in *Alouatta*; more climbing in *Lagothrix*; and frequent brachiation in

Table 6 Annual mean and seasonal ranges (in parentheses) of activity budgets of ateline primates

	% Resting	% Travel	% Feeding	References
		Alouatta		
palliata	66 (60–68)	10 (9–12)	15 (15–22)	Milton, 1980
fusca	72	11 (8–14)	17 (15–20)	Mendes, 1985
seniculus	78	6	13	Gaulin & Gaulin, 1982
		Lagothrix No data available		
		Ateles		
belzebuth	63 (50–65)	15 (5–20)	22 (15–25)	Klein & Klein, 1977
geoffroyi	??	19–26	27–29	Chapman, 1988
paniscus	45 (30–60)	26 (18–35)	29 (20–50)	Symington, 1988*b*
		Brachyteles		
arachnoides	49 (36–54)	29 (24–35)	19 (13–27)	Strier, 1987*d*
	61 (53–66)	10 (7–13)	28 (24–36)	Milton, 1984*a*
	62 (56–68)	15 (11–24)	18 (9–23)	de Sa, 1988

Brachyteles and *Ateles*. It would be interesting to directly compare the digestive abilities of *Brachyteles* with *Alouatta* along the lines pioneered by Milton (e.g., 1980).

Ranging patterns and behavior

Ranging behavior is related to the distribution of food resources and is an integral part of any foraging adaptation. In general, more frugivorous primates tend to have larger home ranges and longer day ranges than folivores (Milton & May, 1976; Clutton-Brock & Harvey, 1977) because fruits are generally less evenly distributed than leaves. The atelines conform to this expected relationship, with the more frugivorous *Ateles* and *Lagothrix* ranging more widely than *Brachyteles*, and all three atelins ranging more widely than *Alouatta* (Table 7). *Alouatta* home ranges are considerably smaller (8–60 ha) than those of the atelins, which vary from 70–740 ha. While *Alouatta* day ranges average between 123 and 706 m, the atelins generally travel much farther. *Ateles* may travel as little as 500 m on any particular day, but they have been reported to travel up to 5000 m, farther than any of the other genera (van Roosmalen, 1980). The most detailed ranging data on *Ateles* show an average daily path length of 1977 m (Symington, 1988*b*). Estimates of *Lagothrix* day ranges vary from 100 to 3000 m (Soini, 1987; Defler, 1987), while *Brachyteles* average between 630 m (Milton, 1984*a*) and 1283 m (Strier, 1987*a*). Such a large difference in the day ranges reported for *Brachyteles* may reflect differences in the availability and distribution of their food resources. Indeed, *Brachyteles* travelled further and exploited a larger home range at the site where they were most frugivorous (Strier, 1986).

Despite extensive variation within the atelines, it is clear that *Alouatta* is distinct from the atelins in both its reduced travel and restricted range use. Minimized ranging parameters and vocally-mediated resource defense are consistent with an overall strategy of energy conservation. Indeed the evolution of the hyolaryngeal apparatus, utilized in *Alouatta* spacing calls, suggests strong selection favoring energetic efficiency (Sekulic, 1982).

In addition to food distribution, differences in the ranging behavior of the atelins and *Alouatta* may also be associated with their respective modes of locomotion. All of the atelins travel by means of climbing and various degrees of suspensory locomotion, whereas

Table 7 Annual means (ranges in parentheses) for home & daily range and group size in atelines

	Daily range (m)	Home range (ha)	Group size	References
		Alouatta		
palliata	443 (326–550)	40	17–19	Milton, 1980
	596 (207–1261)	99	17	Glander, 1978
	123 (11–503)	60	9	Estrada, 1984
fusca	523 (197–1–010)	8	6	Mendes, 1985
seniculus	706	22	9	Gaulin & Gaulin, 1982
		Lagothrix		
lagothricha	3000	740	20–23	Delfer, 1987
	100–950	350	3–13	Soini, 1987
	?	350/450	13/45	Nishimura, 1987
		Ateles		
belzebuth	500–4000	259–389	18	Klein & Klein, 1977
geoffroyi	900	280	?	Cant, 1977
paniscus	500–5000	220	18	van Roosmalen, 1980
	1977 (465–4070)	153/231	40/37	Symington, 1988*b*
		Brachyteles		
arachnoides	1283 (465–4070)	168	26	Strier, 1987*a*
	630 (314–814)	70	7	Milton, 1984*a*
	840 (350–14,125)	40	15–18	da Sa, 1988

Alouatta is strictly quadrupedal. There is some evidence that suspensory locomotion is more energetically expensive than quadrupedalism (Parsons & Taylor, 1977), and Cant (1977) has proposed that these costs may be outweighed in primates such as *Ateles* by the benefits of minimizing travel time when the distances between widely-dispersed, energy-rich fruit sources are great. Locomotor adaptations among the atelines may therefore be linked, at least secondarily, with feeding and ranging patterns.

The variance in ranging behavior among the atelines can be attributed, in part, to differences in group size. Across the primates, larger, heavier groups utilize larger supply areas and travel further each day than smaller groups (Clutton-Brock & Harvey, 1977). Indeed, comparisons of ranging in the three *Brachyteles* groups for which systematic data are available are consistent with these predictions (Table 7). Similarly, the larger home ranges of *Ateles* and *Lagothrix* are consistent with their larger groups. However, comparisons between these atelins and *Alouatta* are complex because although both *Ateles* and *Lagothrix* associate in groups of up to 40 individuals, they generally divide into smaller subgroups to avoid feeding competition. These foraging "parties" resemble the size of *Alouatta* social groups more closely than their overall group sizes suggest. Thus, for an approximately equal number of individuals (and biomass), *Alouatta* ranging parameters are relatively small and those of these atelins much larger, providing further support for the divergent behavioral adaptations of these atelines.

Group size and social structure

The four genera exhibit a high degree of variation in group size and social structure (Table 7). *Alouatta* groups average between 6 and 19 individuals, and are usually cohesive associations composed of females and immatures and varying numbers of adult males (see Crockett & Eisenberg, 1987). All *Ateles* populations presently known are comprised of fluid, heterosexual communities ranging in size from 15 to 42 individuals. Entire communities are rarely found together; rather, they split up into smaller subgroups or feeding parties. Subgroup sizes correlate closely with the size of food patches (Klein & Klein, 1977; Symington, 1988*a*). Data from ongoing field studies of *Lagothrix* indicate groups consisting of from 3–45 individuals (Defler, 1987; Soini, 1987; Nishimura, 1987). All three observers report fluid groups, due to either subgrouping (Defler, 1987) or flexible associations between groups (Soini, 1987; Nishimura, 1987).

Brachyteles presents the greatest intraspecific discrepancies, with the three populations that have been studied to date showing remarkably different group sizes and social structures. At Barreiro Rico, a group of seven individuals comprised of three adult females and four immatures routinely split into smaller foraging units. Males travelled together, and interacted with females only when a female was sexually receptive (Milton, 1984*a*). In contrast, *Brachyteles* at Montes Claros (Strier, 1986) and Fazenda Esmerelda (de Sa, 1988) occur in more cohesive, heterosexual groups of 34 and 16 individuals respectively. The study group followed at Montes Claros since 1982 has grown from 22 to 34 individuals due to births and immigrations (Strier, 1987*b*), yet until quite recently the group travelled as a cohesive unit.

It is difficult to explain such pronounced differences in the grouping patterns of *Brachyteles*. Preliminary evidence suggests that the greater availability of large food patches at Montes Claros may permit the formation of larger, more cohesive associations than are possible at Barreiro Rico (Strier, 1986, in press *a*). The tendency toward fragmentation seen in the Montes Claros group has increased and may reflect the limits of patch size on cohesive groups at this site as well (Strier, in press *a*). At another level, the temporal and spatial distribution of large fruit patches may also explain the differences between the fluid groups observed in *Ateles* and *Lagothrix*, and the cohesive groups of the more folivorous *Alouatta*.

One striking characteristic shared by all the atelines is the occurrence of female dispersal. Longterm field studies have documented female dispersal in *Ateles* (Symington, 1988*b*), *Lagothrix* (Nishimura, 1987), *Brachyteles* (Strier, 1986, 1987*b*, in press *b*), and *Alouatta* (Crockett, 1984). While male atelins appear to remain in their natal groups, in *Alouatta* they also disperse (Crockett, 1984). Female dispersal is thus probably the primitive ateline condition which has been retained in all four genera. The addition of male dispersal in *Alouatta* may be a derived condition that is associated with their more cohesive social system.

Mating systems and sexual dimorphism

The degree of sexual dimorphism is generally a good indicator of the strength of male–male competition and thus mating systems (Alexander *et al.*, 1979; Kay *et al.*, 1988). In primates, single-male polygynous mating systems lead to the most pronounced examples of sexual dimorphism. Sexual dimorphism is also evident in the majority of multi-male polygynous species, particularly when males are unrelated and therefore highly competitive (Clutton-Brock & Harvey, 1978).

The relationships between mating systems and sexual dimorphism in the atelines, however, are not clear cut. Although the most extreme cases of sexual dimorphism are seen in *Alouatta*, sexual dimorphism among the three atelins appears to be inversely related to body size (Table 2). Thus, *Lagothrix* is highly dimorphic in body weight, variably dimorphic in canine size, but monomorphic in body length; *Ateles* is moderate to only slightly dimorphic in canine size but monomorphic in body weight and, in some species, body length; and *Brachyteles* is relatively monomorphic in all three variables. This distribution, as discussed above, suggests that atelines were probably primitively monomorphic in body length, slightly to moderately dimorphic in canine size, and no more than moderately dimorphic in body weight, similar to the modern condition of *Lagothrix*. Body weight monomorphism is probably shared derived in *Ateles* and *Brachyteles*, whereas canine crown length and height reduction (coupled with monomorphism) is further derived in *Brachyteles*.

It is possible that sexual dimorphism in body weight was constrained by ecological pressures as body size increased in the *Ateles-Brachyteles* lineage. If natural selection favored rapid long distance travel to exploit widely-dispersed fruit resources (cf. Cant, 1977) or to monitor independently foraging females (cf. Rodman, 1984), locomotor constraints may have overridden sexual selection for a differential increase in male body size in these large, arboreal primates (Strier, in press *a*). That there are constraints which limit size increase among atelines is suggested by the fact that all are so similar in head and body length while weight varies broadly interspecifically and, within *Alouatta*, intraspecifically.

The derived canine reduction observed in *Brachyteles* may be a consequence of female choice (Milton, 1985*b*). Female choice or male–male competition may also account for the remarkably large testes of male *Brachyteles*, particularly if males compete at the level of fertilization rather than copulation, and with sperm rather than through overt aggression (Milton, 1985*a*). Despite their divergent social structures, both *Brachyteles* populations for which data exist are quite similar in the absence of male–male competition for access to receptive females. At Barreiro Rico, males copulated with a receptive female in close succession (Milton, 1985*a*); at Monte Claros, copulations by individual males were never harassed or threatened by other males (Strier, 1986, 1987*c*). This highly unusual degree of tolerance between males has been explained as an alternative to the high energetic costs of aggressive competition (Milton, 1984*a*, 1985*a*). An extension of this hypothesis integrates the consequences of sexual monomorphism and female choice, wherein males are unable to monopolize sexually receptive females through overt aggression (Strier, 1986, in press *c*). The large testis size of *Brachyteles* may be a derived condition resulting from the limits on aggressive competition in these large bodied, sexually monomorphic primates living in a seasonally energy-poor habitat (Milton, 1985*b*; Strier, in press *c*).

Discussion

The taxonomic distributions of derived craniodental and postcranial characters supporting our interpretation of ateline cladistics (Tables 2 and 4) are diagrammatically shown in Figure 6. Our more general hypotheses describing the adaptive transformations and ecological divergence within the ateline primates are depicted in Figure 7. One of the weaknesses of our analysis is that we have generalized genus-level adaptations in some cases where we thought it appropriate, even when interspecific (and intraspecific) variability is not well known. Furthermore, although we may understand some of the biological associations or implications of patterns such as the suspended feeding postures that employ the prehensile tail, or the primitively climbing feet of an ateline, it is frequently unclear why such features were advantageous in the first place. Hanging by the tail is evidently a comfortable feeding posture, but did it originally benefit leaf eating or fruit eating, locomotor descents in travelling, interpersonal interactions, etc.? Simply summing

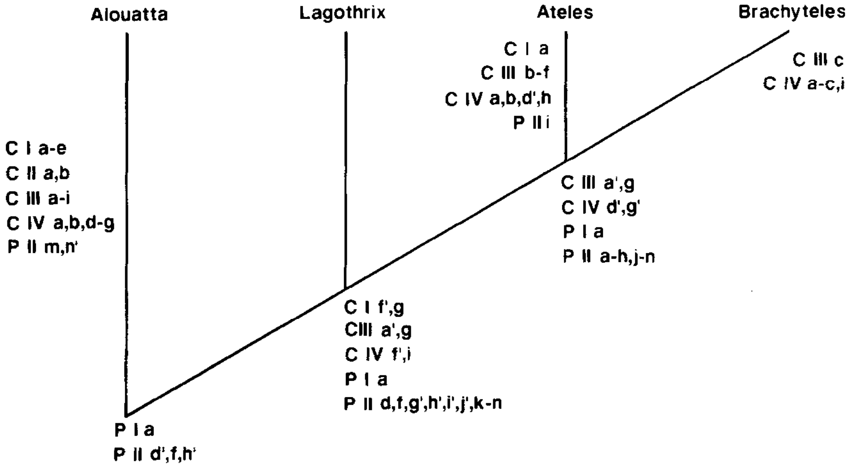


Figure 6. Distribution of selected derived craniodental (C) and postcranial (P) characteristics among modern atelines. Roman numerals (I–IV) and letters refer to functional complexes and their underlying anatomical characters, respectively, as in Tables 2 and 4. Refer to the tables to identify the individual character *states* for each taxon (letter codes are synonymous in some case). The prime (') symbol indicates questionable distributions and/or polarities.

up the frequencies with which these and other behaviors occur across the ateline taxa will not lead toward a resolution of these questions. Additional work is needed to identify the current and evolutionary interactions of such patterns with others to place them in a more informative context.

In general, we propose that the original ateline divergence from an LCA shared with pitheciines involved their exploitation of a new protein resource, leaves, which is unavailable as a bulk food to smaller platyrrhines. A minimal date for this separation can be inferred from the fossil record. Alouattin atelines are represented by two species of *Stirtonia* in the Miocene deposits of La Venta (Colombia), each showing strongly folivorous adaptations. Pitheciines, the sister-group to atelines (e.g., Rosenberger, 1981), are represented by *Soriacebus* (Fleagle *et al.*, 1987; see Rosenberger *et al.*, in press), *Homunculus* and *Tremacebus* (Fleagle & Rosenberger, 1983) during the earlier Santacrucian and Colhuehuapian land mammal-ages in Argentina. Thus we infer a La Ventan or pre-La Ventan separation of alouattins from atelins and a Santacrucian or pre-Santacrucian origin for the ateline subfamily (see Rosenberger, 1984). As has been generally assumed, the most likely place of origin for the group was somewhere in South America, rather than Central America. The intriguing lack of atelines in the small but growing primate fossil faunas of Patagonia, which thus far has produced only pitheciines and cebines (*Dolichocebus*), may suggest a community/habitat difference in the south that was not conducive to ateline occupation. However, as implied above, that should not deter an alouattin, with inherently good colonizing abilities. Their absence may be due to poor sampling, or it may indicate that the group, if already evolutionarily distinct, had not yet reached Patagonia from a more northerly source area.

We reconstruct the first atelines as an animal much like *Lagothrix*, but probably somewhat smaller in body size, perhaps the size of a small *Alouatta*, about 5·5 kg. This represents a derived, upward shift in body size that we regard as a primary adaptation to

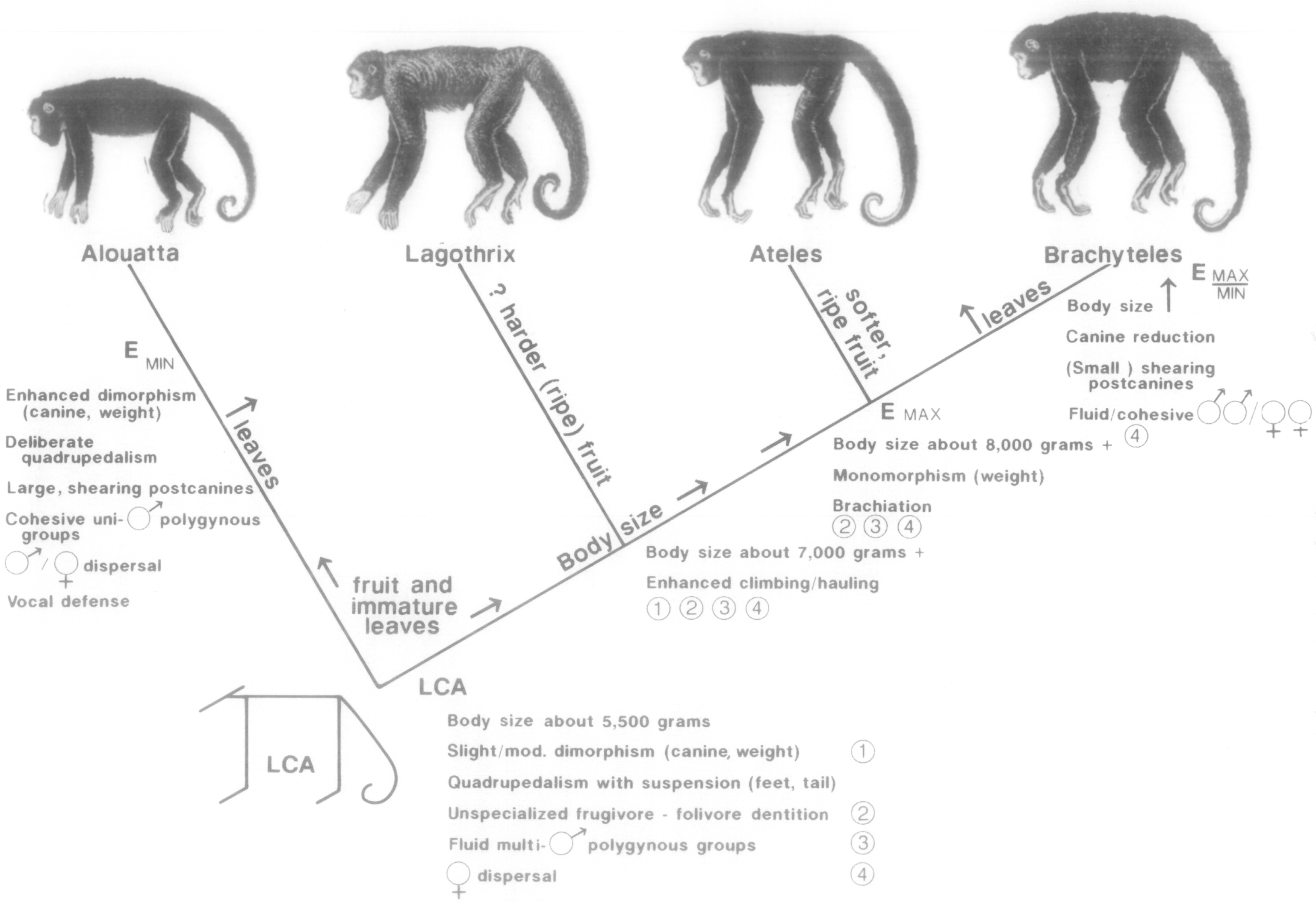


Figure 7. Adaptive radiation of the ateline primates, emphasizing ecological and behavioral patterns of the hypothetical last common ancestor (LCA) and their evolution. Circled numbers are keyed to four characteristics of the LCA: *arrows indicate increase in labelled characteristic.* Energetic paradigms (E min; E max; $E\frac{\max}{\min}$) are indicated. Specializations of the *Alouatta* and *Brachyteles* lineages are

permit an increase in the amount of leaves eaten. A postulated size shift is consistent with the idea that there is a size threshold associated with a folivorous habit in mammals, at about 4 kg (Kay, 1973; see also Chivers & Hladik, 1980).

Since the postcanine dentition of the ancestral ateline was not characterized by relatively large size or highly developed shearing features, nor was the digestive system derived for folivory as in *Alouatta*, it is very likely that the ateline LCA concentrated on immature rather than mature leaves, but was nonetheless predominantly frugivorous. The relatively small incisors (or narrow, but without high crowns as in pitheciines) that are expected in the ancestral morphotype also indicate that leaves would have been an important part of the diet, and that there were no functional specializations related to husking tough fruits, as seen in pitheciines, for example, with their tall, stylate lower incisors.

Postcranial specializations, such as the prehensile tail and the climbing feet, were also connected with the origin of atelines, but how closely these characters related to potentially novel ways of feeding on fruits and/or leaves remains to be determined (cf. Kinzey, 1986); a connection with large size is possible. Locomotion would have included hang-feeding, perhaps some forelimb suspension and a generalized form of quadrupedalism, not the cautious quadrupedal style that typifies *Alouatta*. Males and females were probably of similar body lengths but differed somewhat in weight. Sexual dimorphism in canines would also have been only slightly to moderately expressed. Social organization was not monogamous, nor was it as cohesive as in modern *Alouatta*; their preferred diet involved dispersed food sources, and ranging parameters were large.

From this basis, the atelin and alouattin stems diverged along dichotomous paths, which reflect strategies of minimizing energy expenditure and maximizing energy intake. Folivory became a dominant adaptive theme for alouattins, the Energy Minimizers, built upon a broad framework of uniquely derived features. Mature leaves became a viable dietary staple as the postcanines enlarged and developed strong buccal shearing blades. The highly deliberate form of quadrupedalism also minimizes energy expenditure. An inexpensive mode of resource defense, by howling vocalization, evolved as home ranges contracted and long distance foraging for dispersed fruits became relatively expensive energetically. Social groups became more cohesive and an enhanced sexual dimorphism emerged via sexual selection. Males thus tended to monopolize females and their food sources. Relative brain size was reduced in conjunction with a ubiquitous, energy-poor diet, perhaps as an energy conserving measure or as a response to slow energy uptake by mother, fetus and/or neonate (e.g., Eisenberg, 1981).

It is possible that this adaptive package was selected for as alouattins occupied increasingly seasonal or marginal habitats, where fruits may have been less abundant. Or, it may be associated with intra-ateline feeding competition, for atelins tend to be sympatric with *Alouatta* in all but the most extreme habitats throughout South and Central America. While appearing morphologically "specialized" for a primate of frugivorous ancestry, folivory in alouattins is actually ecologically "generalized". It enables *Alouatta* to invade a wide variety of habitats, perhaps playing the role of a primate colonizer (Eisenberg, 1979).

During their differentiation, atelins maintained a balance of fruits and immature leaves as their main food sources, but probably increased their body size further. Climbing and suspensory locomotion probably became a more important component of their repertoire. Other features of the ateline LCA were retained in this *Lagothrix*-like animal. As the atelins later differentiated into the two final lineages, probably in South American lowland rain forests, feeding and locomotor differences may have begun to separate the *Lagothrix* stock from the *Ateles-Brachyteles* clade. The former may have shifted its preference to fruits with a tougher skin, as well as harder mesocarp and/or seeds, whereas the *Ateles-Brachyteles* branch evolved its unique locomotor system.

The speciation process involved in the *Ateles-Brachyteles* split had a significant geographical effect that somehow left *Brachyteles* isolated in the Atlantic Coastal Forest of eastern Brazil. Although it is possible that *Brachyteles* dispersed across what is now savannah-like *cerrado* in central Brazil, it is more likely that they were passively isolated in Atlantic forests during a dry climatic cycle. This ancestral form, which was morphologically quite unlike *Alouatta*, was probably not as adept as a colonizer. Proto-*Brachyteles*, with its brachiating skeleton, unenlarged postcanines and energetically expensive lifestyle, evolved new folivorous adaptations in a habitat which we believe was more seasonal and less rich in fruit availability. These features included a much larger body size and a lingual molar shearing complex. This compromise of folivory superimposed upon a heritage of strong frugivory may have influenced the evolution of a new mating system, based upon the inexpensive approach of sperm competition.

Ateles, feeding upon ripe fruits as a specialty, and regularly locomoting across large home ranges, oftentimes in acrobatic fashion, is the extreme example of an Energy Maximizer. Its unique anatomical features, particularly the reduced postcanines and jaws, and the enlarged incisors, are associated with soft-fruit frugivory. The lithe body plan and long limbs are connected with rapid, agile travel. The fission–fusion social system is related to their clumped, widely dispersed food sources. This overall foraging strategy easily permits ecological separation *vis à vis* sympatric *Alouatta* and *Lagothrix*, although *Ateles* tends to be limited to quality forests where high levels of energy intake can be sustained.

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