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The Making of Platyrrhine Semifolivores: Models for the Evolution of Folivory in Primates

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ABSTRACT

Among living New World monkeys, Howlers and Muriquis are by far the most folivorous. We examine how well the morphology and behavior of *Alouatta* and *Brachyteles* conform to leaf-eating adaptational models derived from other studies. Both genera match these expectations unevenly, which suggests a broader conception of primate folivory is in order. Hence the notion of "semifolivory." While their dentitions prove highly sensitive to selection for leaf-eating, core features relating to body size, brain size, ranging behavior and presumed energy budgets are less predictable corollaries. Leaf-eating in atelines and colobines may have evolved from a preadaptive reliance on seed-eating, which would have necessitated comparable gastric adaptations. Fossils suggest semifolivory in the low-energy Howler lineage may have begun with an increase in body size, a relatively small brain and, possibly, a concomitantly enlarged gut, followed by dental adaptations. It may have advanced via body-size reduction, part of a pioneering adaptation in marginal ecologies on the periphery of rich Amazonian habitats or as a strategy to minimize competition among an abundance of frugivores within the lowland forest—perhaps not as a fallback scheme. In the high-energy Muriqui, semifolivory may have evolved in more intensely seasonal, low-yield forests where frugivores were constrained and rare, a model more consistent with the fallback paradigm. The seed-to-leaves evolutionary pathway hypothesized for anthropoid leaf-eaters may be a widespread phenomenon in primates. We propose it is ultimately rooted in a pre-euprimate reliance on the seeds and seed coats of primitive angiosperms before the latter evolved attractive sugary fruits to coax primates into becoming dispersers of seeds, instead consumers. Anat Rec, 294:2112–2130, 2011. © 2011 Wiley Periodicals, Inc.

Key words: folivory; platyrrhines; dietary adaptation; Howler monkeys; Muriqui; *Alouatta*; *Brachyteles*; primate origins

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INTRODUCTION

Howler monkeys are widespread, ecologically flexible, fruit- and leaf-eating Neotropical monkeys with low-energy budgets. Their predilection for leaves was apparently noted earliest by Rengger (1830) who, according to Carpenter (1934), indicated that their foods were leaves and buds, principally, in addition to fruits and insects. Carpenter was the first to observe and record the wide range of tree species used and parts taken by *Alouatta palliata*, the Howlers on Barro Colorado Island, Panama. He echoed Rengger in saying these monkeys are "...leaf-eaters as well as fruit eaters..." (1934:42). Carpenter was also impressed by the material he found in stomach contents, and how it contrasted with spider monkeys (1934:42):

> Howlers consume large quantities of food which is bulky and fibrous. I have removed as much as three pounds of mash from the stomachs of adult howlers, and relatively large amounts of mash from younger animals. They take many times the amount of bulky, fibrous foods eaten by spider monkeys of a comparable size.

As an indication of overall consumption, though not necessarily pertaining to one day's worth, Carpenter's mash equates to 17%–20% of the average adult body weight (see Ford and Davis, 1992) of *A. palliata*. In contrast, based on the average daily input of food (2200 lbs/year: Pimentel et al., 2008) and average body size measurements provided by the Center for Disease Control (180 lbs: McDowell et al., 2008), adult Americans over the age of 20 consume about 3% of their body weight each day.

By the 1960s and 1970s, Hladik and Hladik (1969), Glander (1978), Milton (1978), Eisenberg (1978), and others had firmly established that Howlers are mixed feeders but not strictly folivorous. Hladik said (1978: 380): "The howler monkey, *Alouatta palliata*, has been described as a folivorous primate in the early literature, owing to superficial observations, but large quantities of fruits are eaten and the leaves can be considered as a complimentary part of the diet." While it was recognized that this dietary flexibility is enabled by dental features widely held to be leaf-eating adaptations, including relatively small incisors and large, intricately crested molars (e.g., Zingeser, 1973; Kay, 1975; Rosenberger and Kinzey, 1976; Kay and Hylander, 1978; Anthony and Kay, 1993), adaptations to digesting leaves in the *Alouatta* gut were known to be modest in contrast with Old World colobines, (e.g., Hladik, 1978; Milton, 1978; Chivers and Hladik, 1984), by then well recognized as highly adapted to folivory (e.g., Bauchop, 1978; Eisenberg, 1978; Hladik, 1978; Kay and Hylander, 1978). Howlers also tended to conspicuously prefer young leaves in addition to copious amounts of fruit when the latter were unavailable. This led Milton (1978:537) to regard Howlers as "behavioral folivores," a view that was consistent with Rosenberger and Kinzey's (1976) emphasis that molar morphology appeared to be a functional compromise between mechanical designs for shearing and crushing/grinding. Since then, however, it has become more clear that *Alouatta* is a highly efficient hindgut (caeco-colic) fermenter (Milton and McBee, 1981), using a different digestive strategy than the colobines, which are foregut (stomach) fermenters (see Chivers, 1994; Lambert, 1998). These alternatives mirror the different systems that evolved among ruminant and nonruminant mammalian herbivores (e.g., Alexander, 1993).

Muriqui are narrowly distributed endemics confined to the Atlantic Coastal Forest of eastern Brazil. They are active monkeys, whose body shape and proportions so resemble the acrobatic Spider monkeys that morphologists long believed there was no need to distinguish *Brachyteles* and *Ateles* at the genus level. The feeding habits of *Brachyteles* only started to be clarified in the 1980s, when it became apparent that leaves make up a substantial portion of the diet, at some sites ranging from 50% to 67% (e.g., Milton, 1984; Strier, 1991; Martins, 2008). This also corresponds with Muriqui dental morphology (see Zingeser, 1973; Rosenberger, 1992; Anthony and Kay, 1993), which involves various features associated with leaf-eating. Less is known about the guts of *Brachyteles* than *Alouatta* but they have strikingly different patterns with respect to locomotion and ranging behavior. The Muriqui's brachiation-like quadrupedalism, which integrates dynamic tail suspension, and their use of space, which may involve day ranges as much as three times larger than those used by Howlers (see DiFiore et al., 2011), suggests *Brachyteles* is not energetically limited in the manner of a Howler, implying it does not employ a similar energy-conserving strategy (e.g., Rosenberger and Strier, 1989).

Field studies of Howlers and Muriqui carried out in a variety of habitats have provided a good picture of what these animals eat but those details only render part of the picture. How much of their morphological and behavioral profiles are adaptive responses that can be related causally to selection for leaf-eating? Answering that question is the principle aim of this study. Fixing the position of *Alouatta* and *Brachyteles* along the frugivore-folivore continuum is a matter of importance in efforts to explain their ecological role and evolutionary history among platyrrhines. More broadly, the mounting morphological and behavioral differences distinguishing *Alouatta* and *Brachyteles*, and between them and colobines, for example, suggests a more expansive notion of primate folivory is overdue. In concurrence with the observations of Milton (1978) and others noted above, who first drew the Howler-colobine contrast and called for a dietary relabeling of *Alouatta*, we prefer to call Howlers and Muriqui "semifolivores" to highlight such alternative adaptive configurations. While trying to establish that "good folivores come in several flavors," we also propose that the parallel shifts to folivory seen in different primate radiations may share a common, preadaptive, seed-to-leaves pathway, which may have been in effect since the origins of primates.

As a point of departure, we adhere to the widely held perception that *Alouatta* is more folivorous than *Brachyteles*, although we admit this is a simplification that poses difficulties and conflicts with our final assessment, that judgments such as these, often tinged by semantics, are unnecessary: each in their own way, *Alouatta* and *Brachyteles* have evolved into full fledged leaf-eaters. We similarly acknowledge that for ease of comparison we adopt the position that colobines are the idealized folivores of the Order Primates while knowing this, too, oversimplifies matters, if only by ignoring the various strepsirhines that are leaf-eaters as well. Furthermore, as discussed below, the evidence is convincing that colobines are adapted to a dietary spectrum focused on leaves *and* seeds. This becomes all the more important to our thesis for it sheds light on the parallel pathways taken by platyrrhine semifolivores and colobine folivores as their dietary specializations evolved.

TAXONOMIC AND PHYLOGENETIC NOTES

The taxonomy employed here generally follows Rosenberger (2002). It differs from an alternative arrangement presented by Rosenberger (2011a) in terms of the ranks used for atelines and pitheciines (there recognized as families instead of subfamilies) to maintain consistency with other work directly relevant to this report (Rosenberger et al., in press). A detailed explanation of the broader interrelationships, adaptations and evolutionary history of platyrrhines, living and extinct, is provided by Rosenberger et al. (2009; see also Rosenberger et al., in press). For the present purposes, Atelidae (atelids) is a family of New World monkeys (NWM) comprised of two subfamilies, Atelinae (atelines) and Pitheciinae (pitheciines). The other family is Cebidae. Atelines are divided into two tribes. One is Alouattini (alouattins), including living *Alouatta* and the extinct genera *Stirtonia*, *Paralouatta, Protopithecus*, and *Solimoea*. *Stirtonia* is known from the middle Miocene site of La Venta, Colombia, approximately 11-13 million years ago. *Solimoea* is known from a younger site in Brazil, dated to about 8 million years. *Paralouatta* and *Protopithecus* are basically Pleistocene-recent subfossils, from Cuba and Brazil, respectively, although the former is also known from a single specimen of early middle Miocene age. The other ateline tribe is Atelini (atelins), including extant *Ateles*, *Brachyteles* and *Lagothrix* and the extinct *Caipora*. The latter comes from one of the same sites that produced *Protopithecus*.

Pithecines are a second subfamily of atelids divided into two tribes as well. Pitheciini (pitheciins) are a large group including about a dozen fossil forms (see Rosenberger, 2002) but only the modern Sakis and Uakaris are of concern here: *Pithecia*, *Chiropotes*, and *Cacajao*. The second tribe (Homunculini) includes living *Aotus* and *Callicebus* and several fossils that are also not of immediate concern. Most of this is not controversial. However, the systematic position of *Aotus* is debatable (see Rosenberger and Tejedor, in press). Molecular studies favor placing *Aotus* among cebids (which coauthor SBC supports), while the morphological evidence points to an affinity with pitheciines.

The specific interrelationships of the semifolivores *Alouatta* and *Brachyteles* are germane (e.g., Rosenberger and Strier, 1989; Schneider and Rosenberger, 1994; Hartwig, 2005; Wildman et al., 2009). There is full agreement that the *Alouatta* lineage was first to diverge from amongst the monophyletic atelines and that the atelins are also monophyletic. The placement of *Brachyteles*, however, is controversial. The molecular evidence favors a link with *Lagothrix* whereas the morphology suggests it is the sister group of *Ateles*. Either way, it appears likely that *Alouatta* and *Brachyteles* evolved their leaf-eating adaptations independently (e.g., Rosenberger et al., in press).

Regarding methods, no special remarks are required here as our analysis is a synthesis of existing published information, whose original sources are referenced throughout.

THE FOLIVORY SYNDROME

Empirical studies of mammals suggest arboreal folivores are characterized by a variety of features in the digestive system that are adaptive evolutionary responses to the chemical and physical properties of leaves. For primates specifically, a variety of summaries dealing with the digestive system are available (e.g., Chivers and Hladik, 1980; Kay and Covert, 1984; Martin, 1990; Lambert, 1998; Kay, 2000; Lucas, 2004). Other contextually pertinent characteristics that have been described involve body size, locomotor behavior, use of space, and metabolism (see Montgomery, 1978; Eisenberg, 1981; McNab, 1986; Martin, 1990; Davies and Oates, 1994). In this section we present as hypotheses several of the major features purported to be adaptations to folivory, and we test the degree to which *Alouatta* and *Brachyteles* conform to predictions. The most recent compilations on the diets of *Alouatta*, *Brachyteles* and other relevant platyrrhines are available in Campbell et al. (2011), summarized in Table 1.

We noted above that our comparisons of the platyrrhine pattern stress the well-studied colobines as the major point of reference, for they are widely held as the primates' (surely the anthropoid's) best operational model of a highly evolved folivorous system. However, studies in the last two decades have altered this notion significantly. As developed in a series of papers in Davies and Oates (1994) covering guts, teeth, feeding behavior, food chemistry, and related topics, it has become clear that the novel colobine diet is not a top-to-bottom adaptation to folivory *per se*; rather, it is an adaptation to leaf- and seed-eating in combination (e.g., Chivers, 1994; Kay and Davies, 1994; Lucas and Teaford, 1994; Oates, 1994). Even when taking habitat and seasonal variations into account, colobines are known to ingest large quantities of seeds in addition to leaves. For the 22 studies of African colobines listed by Fashing (2011) that had a minimum duration of nine months and specifically reported seed-eating as a dietary choice, seeds averaged 17% of the diet. The average amount of seed consumption in the top ten studies was 32%. Thus, no matter how one chooses to interpret the adaptive essence of the colobine diet, as selective responses to the most physically and chemically challenging foods or otherwise, it is clearly a leaf-plus-seed syndrome that defines them.

In contrast, while seeds may also have played an important role in the evolution of platyrrhine semifolivores, the empirical evidence for this does not parallel the colobine situation by its very nature, as will be seen. *Alouatta* and *Brachyteles* dietary choices have not revealed such a conspicuous fraction devoted to seeds, although these data must be interpreted with caution. Seeds have been typically lumped into the "other" food category by field workers (including fruit, leaves, prey, flowers; DiFiore et al., 2011), which amounts to about 3% and 6% of the diets of *Alouatta* and *Brachyteles*, respectively. While it is possible these low values, compiled from many different studies using different methods over several decades, partly reflect a disinclination among early field workers especially to monitor seed-eating carefully—only belatedly did colobine field

TABLE 1. Diets of semifolivores and other atelids

Source		*Aotus*	*Callicebus*	*Pithecia*	*Chiropotes*	*Cacajao*	*Lagothrix*	*Ateles*	*Alouatta*	*Brachyteles*
Norconk, 2011	Fruit %	56, 7	69, 3	28, 3	22, 3	28, 2	71, 7	78, 7	33, 18	22, 3
Fernandez-Duque, 2011	Leaves %	32, 4	13, 3	8, 4	7, 4	4, 2	11.6, 7	11.3, 7	55,18	56, 3
DiFiore et al., 2011	Insects %	17, 3	20, 1	3, 2	NA	4, 2	11.2, 7	1.4, 7	0, 17	0, 3
	Seeds %	NA	22, 1	61, 3	58, 5	60, 20	NA	NA	NA	NA
	Other %	NA	1, 1	6, 5	5, 5	5,1	6.1, 7	5.6, 7	3.2, 16	5.7, 3
	Flowers%	NA	NA	NA	NA	NA	2.4, 7	4.9, 7	5,15	18.7, 3

Data from Fernandez-Duque (2011, *Aotus*), Norconk (2011, *Callicebus*, *Pithecia*, *Chiropotes*, *Cacajao*), and DiFiore et al. (2011, *Lagothrix, Ateles*, *Alouatta, Brachyteles*), which should be consulted for additional information on the original sources, including species, locations and durations of studies, and the varied categorical definitions of food types. Commas separate feeding percentages from the sample sizes, i.e., number of studies from which averages were calculated. NA (not applicable) refers to food categories not employed. Measures presented as <1, for example, were scored as 1; approximated averages were considered actual averages. Note that the "other" category for atelines comprises many foods, including seed pod exudates, bark, soils, and so forth, as well as seeds, which were originally broken out in the other taxa. Data for the nocturnal *Aotus* are considered to be the least reliable. Leaf intake in *Alouatta* and *Brachyteles* is essentially the same, and far exceeds other atelids. The unique seed-eating preferences of *Pithecia*, *Chiropotes* and *Cacajao* is evident. *Callicebus* stands out in utilizing a combined high percentage of hard-to-digest leaves and seeds at a relatively small body size.

workers recognize their importance as well—these figures probably reflect the reality that seed intake among the platyrrhine semifolivores is low by comparison with the elevated level of many colobines. But they may mask the importance of seeds in *Brachyteles*. One recent 12-month study of sympatric *Alouatta* and *Brachyteles* that paid particular attention to seed-eating documented a marked difference between them (Martins, 2008). The feeding breakdown for *Alouatta* was: leaves, 80.7%; flowers, 7.5%; fruit, 8%; seeds, 3.7%. For *Brachyteles*: leaves, 55.3%; flowers, 16.1%; fruit, 12.1%; seeds, 16.5%. Twelve of Fashing's (2011) 22 colobine studies reported seed-eating percentages lower than *Brachyteles*.

Body Size

Mammalian foliage eaters, including primates, are expected to attain a relatively larger body mass than their frugivorous or insectivorous relatives (see Eisenberg, 1978, 1981; Harvey, Clutton-Brock and Mace, 1980; Kay and Covert, 1984; Harvey and Clutton-Brock, 1985; Garber, 1987; Fa and Purvis, 1997; Lambert, 1998). Among primates, the examples of relatively larger-sized indriids, gorillas and siamangs are cases in point. As a group, atelines are larger than other platyrrhines; the smallest species of Howlers are at least 25% heavier than the largest living pitheciine (see Fleagle, 1999). But as Strier (1992) emphasized, there is a wide gap in size between *Alouatta* and *Brachyteles* that is filled by intervening frugivores, *Ateles* and *Lagothrix* (Fig. 1). Furthermore, while *Alouatta* appears to be more specialized as a folivore than *Brachyteles* in a number of ways, it is considerably smaller in body mass. Interspecific comparisons also indicate body size is quite labile among the ecologically flexible, widely distributed *Alouatta*, where local conditions may exert directly selective pressures to maintain an ancestral size, increase, or decrease it. Overall, the body size ranges demonstrated by atelines suggest a more complicated picture of size evolution than one expects based on the folivory model as proposed.

The roughly 5–10 kg weight range exhibited by *Alouatta* and *Brachyteles* is also eclipsed by the largest extinct platyrrhines known thus far. Improved calculations based on a robust sampling of platyrrhines suggest the alouattin *Protopithecus* weighed over 20 kg (Halenar, 2011a). *Caipora*, an atelin, is also in that size class (Cartelle and Hartwig, 1996). Both of these animals have teeth that are clearly nonfolivorous (Rosenberger et al., in press). This, too, highlights the point that the two most typically folivorous platyrrhines are certainly not the largest in body mass. The 5-k weight figure, approximating the lowest body weight for leaf-eating platyrrhines, may also not represent a functional threshold. About one third of the diet of the ~1 kg *Aotus* reportedly includes leaves (Fernandez-Duque, 2011), which is about three times the fraction taken in by *Ateles* and *Lagothrix* (DiFiore et al., 2011).

Relative Brain Size

Mammalian foliage-eaters or grazers have relatively smaller brains than frugivores (e.g., Jerison, 1973; Harvey, Clutton-Brock and Mace, 1980; Eisenberg, 1981; Barton, 1996), or mammals tending to search for foods such as fruits, seeds or vertebrate prey (MacNab and Eisenberg, 1989). As a primary example among primates, leaf-eating colobines have relative brain sizes that are estimated as 35% smaller than the more omnivorous cercopithecines and the apes (Martin, 1984). In their primate wide study, Harvey et al. (1987) noted that none of the 6 of 19 subfamilies they examined that had folivorous species ranked in the top ten groups in measures of brain size. It is well established that *Alouatta* also has a relatively small brain (e.g., Schultz, 1941; Hershkovitz, 1977; Harvey, Clutton-Brock and Mace, 1980; Eisenberg, 1981; Stephan et al., 1981; Harvey et al., 1987), relative to overall skull size and body weight, and particularly among the platyrrhines (Hartwig et al., 2011). Its encephalization quotient is comparable with the values found in leaf-eating colobine monkeys (e.g., Aiello and Wheeler, 1995).

Data on brain volume and body mass of *Brachyteles* are scant (see Hershkovitz, 1977), but it appears that relative brain size in *Brachyteles* is not reduced when endocranial volume is regressed against skull length

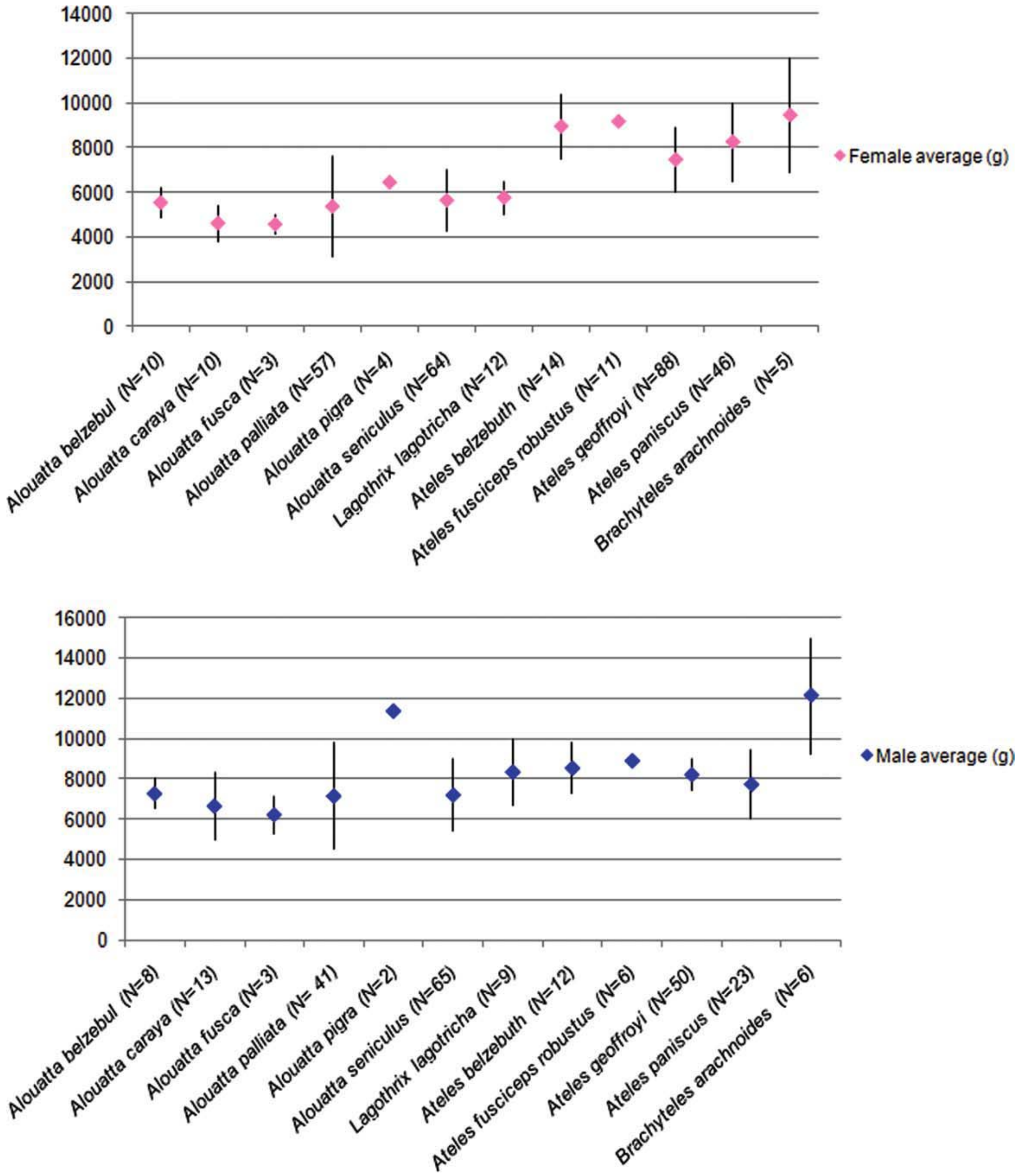

Fig. 1. Male and female body weights for the extant atelines (Ford and Davis, 1992). Data points are averages surrounded by a range bar, where available. The more folivorous genera on either end of the graph, *Alouatta* and *Brachyteles*, are not categorically heavier than the frugivores between them, *Ateles* and *Lagothrix*. *Brachyteles* is heavier than most species of *Alouatta*, despite being arguably less modified in its overall adaptive commitment to a folivorous diet.

which, of course, must also be partially correlated with braincase size. *Brachyteles* falls comfortably among atelins which exhibit an elevated regression line relative to three alouattin genera for whom measurements are available, including the subfossil skulls of *Paralouatta* and *Protopithecus* (Rosenberger et al., in press). This contrast is also evident when regressing endocranial volume against tooth size (the summed area of three lower molars) (Fig. 2). When two- and three-molared callitrichines are included in the analysis, essentially the same picture emerges but the r^2 value rises to 0.87. *Alouatta* and *Brachyteles* are separated convincingly in relative brain size when molars are used as a body size proxy.

Gut Size and Differentiation

Measurements of gut size and differentiation in *Brachyteles* may not exist. Osman Hill (1962) says the shape of the stomach resembles *Ateles*, and he (p. 322) emphasizes that it is “relatively enormous.” In summarizing

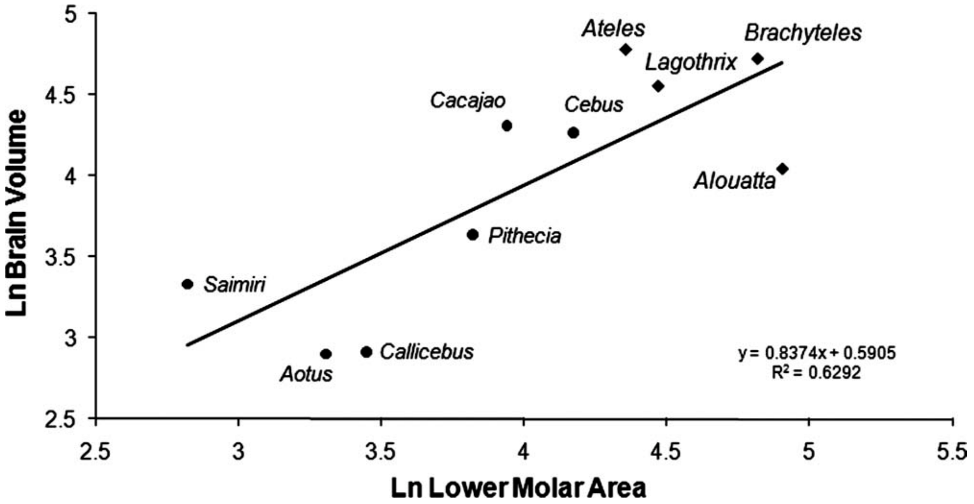

Fig. 2. Logarithmic plot of summed lower molar area and brain volume for the majority of living three-molared platyrrhine genera. Molar area from Rosenberger (1992); brain volume from Hershkovitz 1977. Species included for each genus: *Aotus trivirgatus, Callicebus moloch, Saimiri sciureus, Alouatta palliata, Pithecia monachus, Cacajao rubicundus, Cebus apella, Lagothrix lagothricha, Brachyteles arachnoides, Ateles paniscus*. *Alouatta* falls well below the line along with *Aotus* and *Callicebus*, indicating that they have small brains for their body size (see Discussion). *Brachyteles*, despite its more folivorous diet, falls above the line with the other ateline frugivores, *Ateles* and *Lagothrix*. Regressions using differently configured taxonomic samples, deemphasize the residuals of *Ateles* and *Lagothrix* but consistently find *Alouatta* plotting below the line (Hartwig et al., 2011).

Hill's findings, Bauchop (1978) noted the anatomical evidence merited speculation that *Brachyteles* has gastric modifications for folivory. In addition to stomach size and morphology, he noted an enlarged parotid gland and an extremely large caecum "resembling a second stomach." Muriqui have very large pot bellies, like *Ateles*, which genus also has an enlarged caecum and a sacculated colon (Hill, 1962).

Quantitative studies of the relationship between guts and diet by Chivers and Hladik (1980), however, do not place convincingly *Alouatta* among the folivores, although the evidence is equivocal. In their principle diagnostic ratio relating to the potential for foregut fermentation, the Coefficient of Gut Differentiation (surface area of stomach + caecum + colon/ surface area of small intestine), the *Alouatta* samples differ. *A. seniculus* falls squarely in their frugivore category, in the same bracket as *Ateles* and *Lagothrix*, as well as *Aotus* and *Saguinus*. *A. palliata* has higher values, falling in the bottom tier of their folivore group along with several colobines and cercopithecines. This category also overlaps the frugivorous taxa with more differentiated guts. Using the Chivers and Hladik data and several additional sources to expand the sample of New World monkeys (Fig. 3), plotting the coefficient against body length demonstrates little difference among the atelines, although *A. palliata* is quite distinct. These data confirm the similarity in proportions between *Saguinus*, *Aotus*, and *Alouatta seniculus* and also demonstrate comparably differentiated guts in *Callicebus* and *Pithecia*.

Passage Rates

As reviewed recently by Lambert (1998), the passage rates of digesta are slower in folivores than in frugivores, which allow the former more time to ferment, extract and absorb nutrients from hard-to-process leaves. Here, there is good data on a range of platyrrhine genera (Fig. 4) via projects pioneered by Milton (1984), an effort (done on captive animals) that surely deserves to be replicated to verify and perhaps adjust some measurements that proved difficult due to the physical condition of the individuals at time of testing (see also Edwards and Ullrey, 1999). However, they demonstrate that *Alouatta* have slow passage rates while *Brachyteles* exhibits a more rapid transit time, as does the highly frugivorous *Ateles*. Norconk et al. (2002) confirm that the passage rates of *Pithecia*, also with a well-differentiated gut, are also notably slow in comparison to other NWM.

Dental Morphology

The incisors and molars of primates in general, and platyrrhines in particular, have received much attention in assessments of functional dental morphology and diet (e.g., Hylander, 1975; Kay, 1975; Rosenberger and Kinzey, 1976; Kay and Hylander 1978; Eaglen, 1984; Kay and Covert, 1984; Rosenberger, 1992; Anthony and Kay, 1993; Cooke, 2011). Two of the prominent finds are that folivores have relatively small anterior teeth, presumably because of the unique handling requirements of a flexible, two-dimensional "mat" of material where involvement of the lips may be useful (Lucas, 2004), as well as large shearing molars. This combination is well illustrated by plotting incisor size and shearing length quotients derived from the residuals of bivariate regressions which relate each of the variables to body size proxies (Anthony and Kay, 1993). Among the three-molared platyrrhines, *Alouatta* and *Brachyteles* stand apart, particularly on the *y*-axis which represents upper relative incisor width (Fig. 5). The separation of the semifolivores in molar shearing potential is less marked, as *Alouatta* overlaps with *Aotus*. Cooke (2011) reached a

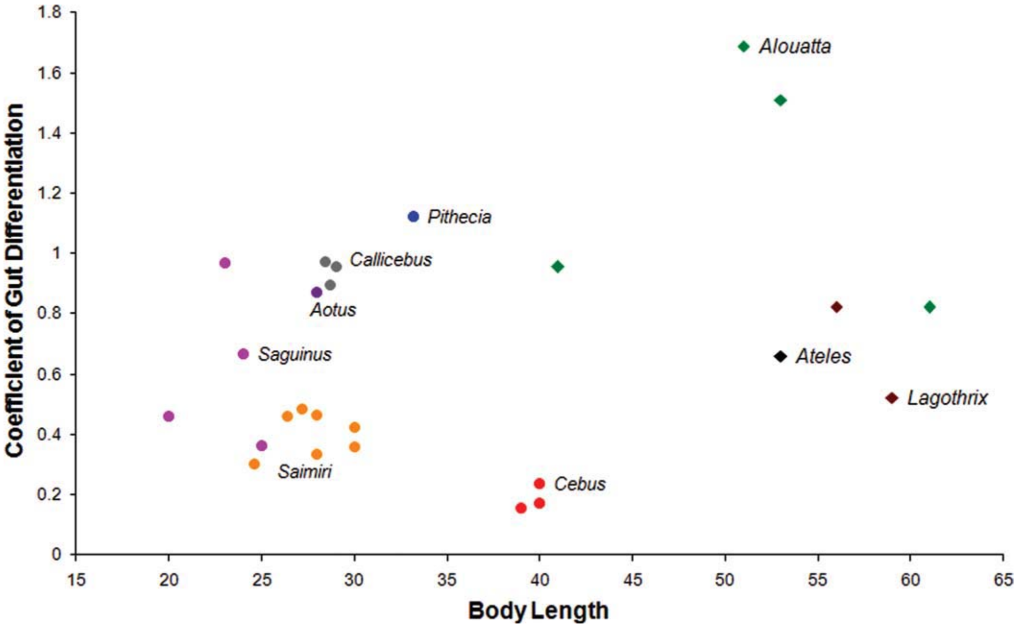

Fig. 3. Coefficient of gut differentiation (CGD) plotted against body length for various platyrrhine taxa (from Chivers and Hladik, 1980; Ferrari and Lopes, 1995). For genera with multiple species: *Saguinus geoffroyi, S. midas; Saimiri oersterdii, S. madeirae; Cebus capucinus, C. griseus; Callicebus calligatus, C. moloch; Alouatta palliata, A. seniculus, A. sp*. *Alouatta palliata* in particular have very high CGD values, as expected based on their folivorous diet. Like *Alouatta*, *Pithecia*, *Callicebus*, and *Aotus* (and one specimen of *Saguinus*, for which measurements seem to be highly variable) appear to have relatively differentiated guts for their body size, although the separation from *Saimiri* and *Cebus* may also be influenced by selection for a short gut in these predatory cebids (Chivers and Hladik, 1980). The proportions of *Pithecia*, *Callicebus*, and *Aotus* may be related to the high percentage of seeds and leaves included in their diets. Being able to digest seed coats, which resemble leaves in their toxicity and secondary compound compliment, may be a preadaptation for folivory (see Discussion).

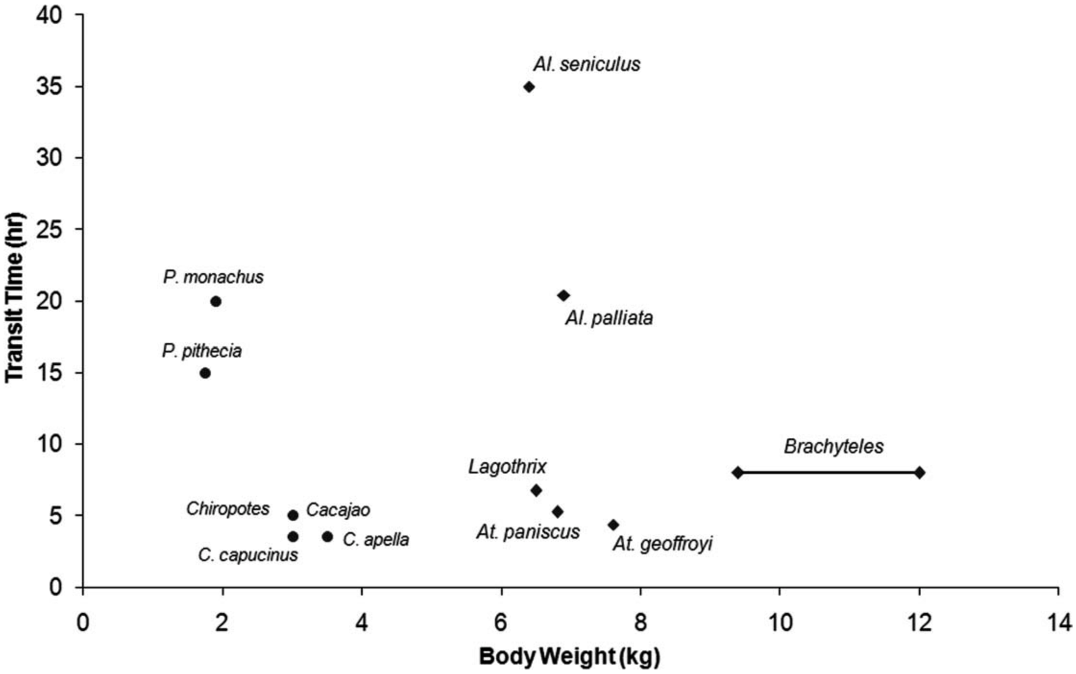

Fig. 4. Transit time plotted against body weight for various platyrrhines (from Lambert, 1998). Paired data points for *Brachyteles* represent the wide range of body size values reported in the literature. The high value is the weight of the individual examined in the original Milton (1984) study; the low value is the average of male and female wild weights reported by de Sa and Glander (1993). Regardless of what figure is used, *Brachyteles* has a much faster transit time than *Alouatta*. As with the CGD data presented above, *Pithecia* is similar to *Alouatta* in transit time but at a much lower body weight. This suggests that a diet of seeds in some pitheciins selects for physiological adaptations comparable with those influenced by a diet of leaves (see Discussion).

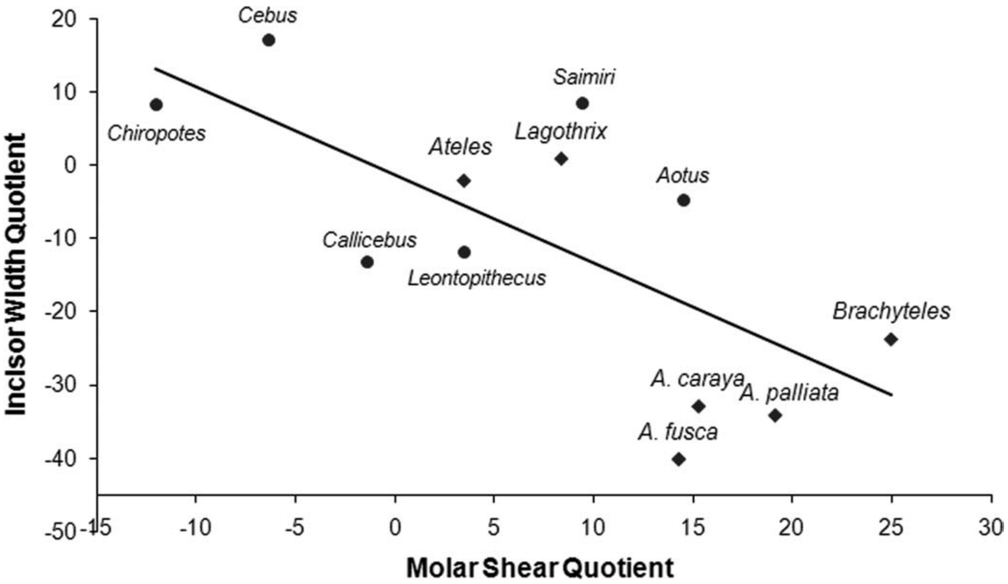

Fig. 5. Bivariate plot of incisor width and molar shear quotient values (from Anthony and Kay, 1993), two "functional" measures thought to be indicative of leaf-eating. The relationship between the variables is inverse in this sample composed of three-molared platyrrhines, but the association is weak ($r^2 = 0.49$). The regression is driven by the special combination of enhanced shearing and reduced incisor size found only in the semifolivores, contrary to the unusually flat, noncrested crowns of *Cebus* and *Chiropotes*. The latter also has a morphologically distinct incisor complex that is not biomechanically equivalent to others in the sample (see Rosenberger, 1992). The opposite, positive association between these variables among semifolivorous species suggests more complexity than would be predicted by this broad intraplatyrrhine taxonomic framework. Across both genera, more molar shearing potential is associated with relatively larger incisors ($r^2 = 0.82$), such that *Brachyteles*, with a lesser overall commitment to leaf-eating, have more shearing potential and larger incisors than any *Alouatta* species in the subsample.

TABLE 2. Activity budgets of ateline primates (from DiFiore et al., 2011)

	Lagothrix	*Ateles*	*Alouatta*	*Brachyteles*
Time spent eating+foraging, %/day	36.1, 3	27, 7	17.7, 14	23.3, 2
Time spent moving, %/day	28.2, 3	25.3, 7	13.2,14	20, 2
Avg (or range) day range (meters)	1925, 9	2142, 7	526, 20	1075, 3
Avg maximum day range (meters)	2565, 9	4297, 7	968, 14	2529, 3

similar finding in assessing the three-dimensional morphology of platyrrhine second molars, wherein some multivariate components associated folivores with the insectivorous-frugivorous *Saimiri*. Among the semifolivorous species measured by Anthony and Kay, there is also a more complicated association between these variables than expected given the biomechanical explanations behind these features. For example, the Muriqui, which appears to be less committed to a leafy diet, exhibits a higher value for molar shearing potential than any of the three Howler species in the sample.

It is not clear if this counterintuitive result stems from a faulty model or actually reflects adaptive compromise. One might argue the latter; *Brachyteles* compensates for having a gut less specialized for chemical processing by evolving a molar battery better designed for shearing. Perhaps feeding experiments can be developed to test this hypothesis. Alternatively, the shearing potential measure may be less robust than desired. It may be a "noisy" measure at low taxonomic levels.

Activity Budgets and Positional Behavior

Minimizing energy expenditure by maintaining a low metabolic rate is logically associated with nutritionally limited food sources. Thus McNab (1978) demonstrated that herbivory or folivory is highly correlated with hypometabolism across mammals. Kurland and Pearson (1986), however, argued that this is not clearly the case for primates, as other nondietary factors may be at play. Later, McNab (1986) noted that the basal metabolic rate of the leaf-eating *Colobus* is not unexpectedly low, perhaps because it exhibits a high level of activity. On the other hand, experienced fieldworkers see it differently: Oates (1994:100) says Black-and-white colobus are "...noted for their inactivity." Either way, reducing energy consumption by any means would be advantageous if energy input is limited. Activity budgets measured indirectly in the wild support this notion. In a broad survey, Milton and May (1976) showed that primate folivores have smaller home ranges than frugivores or omnivores. This is borne out by more closely examining African colobine species (Oates, 1994), where the more folivorous forms (Black, and Black-and-white colobus) tend to have smaller ranges than more eclectic feeders (Red colobus). Among the NWM, there is a marked contrast in use of time and space between *Alouatta* and the frugivorous atelins (Table 2). By far, Howlers spend less time eating/foraging, moving, and traveling each day. In time spent eating/foraging and

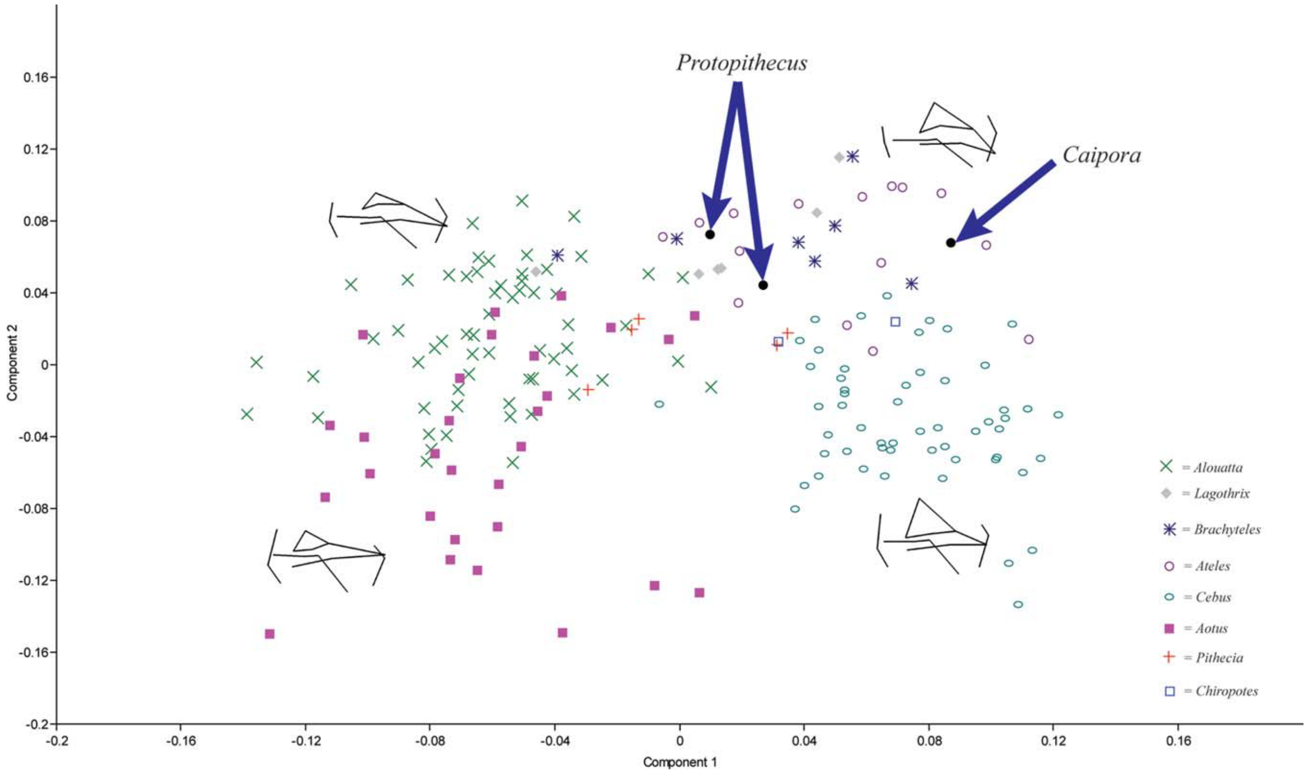

Fig. 6. Results of a principal components analysis of the three-dimensional shape of the distal humerus in various platyrrhines (see Halenar, 2011b). Wireframes represent an anterior view of the right humerus (with posterior aspect superimposed) of the nearest cluster of points/taxa. The shape change along PC1 (representing 23% of the total variance) distinguishes form by the height of the olecranon fossa and the length of the medial epicondyle. PC2 distinguishes based on the height of the lateral epicondyle and orientation of the medial epicondyle. *Alouatta* is clearly separated from the highly agile *Ateles*, which clusters with *Brachyteles*.

moving, *Brachyteles* is intermediate between *Alouatta* and *Lagothrix* and *Ateles*, but the contrast with Howlers is less marked. In measures of day range, *Alouatta* has exceptionally low values as well.

As a corollary to overall activity, summaries of platyrrhine locomotion make it clear that while detailed behavioral information on *Brachyteles* is lacking, field work indicates the Muriqui is a much more agile, speedy, creative, and flexible locomotor than *Alouatta*, a genus notable for its frequently lethargic pace (e.g., Youlatos and Meldrum, 2011). This is borne out by anatomical studies. For example, (Halenar, 2011b) showed that the three-dimensional morphology of the Howler elbow joint was distinguished clearly from *Brachyteles*, which overlapped with Spider monkeys (Fig. 6).

DISCUSSION

Morphology, Behavior, and Platyrrhine Semifolivory

Comparative empirical studies across the primates and other mammals have noted a pattern of anatomical and behavioral features associated with a leafy or herbaceous diet. Core features that can be assessed in leaf-eating platyrrhines include, body size, brain size, incisor size, molar size and morphology, gastrointestinal morphology, and ranging patterns and locomotor profiles which relate to energy expenditure.

Alouatta, long considered the most folivorous platyrrhine, exhibits the expected adaptations in teeth and brain but differs from the most folivorous catarrhines, the colobines, in lacking foregut fermentation. To distinguish the *Alouatta* pattern of leaf-eating, several have characterized Howlers as if they are only partially adapted to folivory, “behavioral folivores” in Milton’s (1978) formulation, requiring the animal’s to be very judicious in selecting leafy foods. To emphasize the more complete picture of the Howler diet and the potential for multiple sources of selection, compound terms have also been used, such as frugivore-folivore (Rosenberger, 1992; Cooke, 2011). Since then, the leaf-eating habits of *Brachyteles* have also become well known. It, too, differs from the colobine model, and both genera appear to have evolved folivory independently. Thus, while following Milton’s lead we prefer to regard these platyrrhines as “semifolivores.” Other terms may be more apt, but the concept of semifolivory may also be widely applicable to include other primates that have evolved only part of the amalgam of characters already generalized as foliage-eating adaptations. One point it is intended to suggest is that primates may benefit ecologically in different ways by evolving a leaf-eating habit. Adaptations to acquire and process food may be paramount, but they do not evolve in a vacuum. A broader notion of folivory may also lead to informative reconstructions of the conditions and pathways under which leaf-eating evolved in different groups, as seen below. The study of primate dietary adaptation has over the years witnessed a similar need to redefine or modify the concept of frugivory, viz. seed-predation and sclerocarpic frugivory (e.g., Kinzey, 1992; Rosenberger, 1992).

The phenotype of platyrrhine semifolivores appears to accord well with the inference that mammalian foliage-eaters tend to be larger than their nearest relatives. However, this generalization only applies when comparing *Alouatta* and *Brachyteles* with modern forms, which is a necessarily skewed sample for it lacks historical context. It also does not fit the pattern of body size distributions among atelines. In fact, within the speciose genus *Alouatta*, there is a large range of sizes. As pointed out by Strier (1992), some forms are considerably smaller than the obligate frugivores *Ateles* and *Lagothrix*. There is a possibility that the morphotype of the *Alouatta-Stirtonia-Paralouatta* clade was reduced in body size from a larger alouattin ancestor. This prospect relates to *Protopithecus*, which is roughly twice the size of other large alouattins while also being the most primitive in both its craniodental and postcranial morphology (Hartwig and Cartelle, 1996; Halenar, 2011b). Indeed, once a balance of adaptations for folivory was established in the *Alouatta* lineage, it might have been beneficial to reduce energy consumption by lowering absolute body size up to a point, so long as the advantages of allometrically large teeth and guts were maintained.

Regarding relative brain size, an equally if not more complex picture emerges when assessing the platyrrhine semifolivores. *Alouatta* meets the expectations of the generalized model in having a relatively small brain, but *Brachyteles* does not. It is fair to attribute the Howler condition to selection for a smaller energy-hungry cerebrum as an accommodation to a nutritionally limiting diet. In this hypothesis, the *Alouatta* brain could be seen as de-encephalized, derivedly reduced in connection with folivory. In its specifics, this is consistent with Aiello and Wheeler's (1995) Expensive Tissue Hypothesis as they point out: there is an inverse relationship between gut size and brain size in primates and Howlers are their prime example wherein guts are derivedly large and brains are correspondingly small.

However, the selective agency of a folivorous diet may be only part of the story. Two additional NWM genera have relatively small brains, *Callicebus* and *Aotus* (see Hartwig et al., 2011). There are several possible explanations for this. As Dunbar has argued most recently (e.g., Harvey et al., 1980; 1998), monogamous primates have relatively smaller brains than species exhibiting larger social groups. But it may also be that diet plays a selective role here as well. For, like Howlers, Titi and Owl monkeys have rather well differentiated guts, suggesting a digestive adaptation to a nonpredaceous diet. As neither *Aotus* nor *Callicebus* have an elevated preference for leaf-eating in the manner of *Alouatta* or *Brachyteles*, another dietary constituent may be involved, perhaps seed coats (testa), which have also been implicated as a source of hard-to-digest secondary compounds among colobine monkeys including lignins, condensed tannins and toxic phenolics, (e.g., Chivers, 1994; Kay and Davies, 1994). Indeed, Waterman and Kool (1994) note that seeds may have higher concentrations of toxins than leaves.

In the context of *Callicebus* and *Aotus*, we cannot discount the possibility that at least a portion of the smallness of *Alouatta's* brain reflects a dietary preadaptation, a retention or predisposition stemming from a prior adaptation to a frugivorous habit that involved seed-eating (see below) or a liberal, facultative mixture of seeds and leaves as staple protein sources. Maisels et al. (1994) have shown that two sympatric species of folivorous *Colobus* in Zaire consume large quantities of both leaves (61%, 50%) and seeds of legumes (33%, 27%), attesting to the likelihood that local preferences reflect satisfactory adaptive trade-offs between these two foods made possible by gut specializations relevant to processing both.

The two clades of atelid NWMs have evolved seed- and leaf-eating specialists within the context of a broadly frugivorous, nonpredaceous framework. Outside the atelines, seeds account for about 60% of the diet of pitheciins, the highly specialized seed-predators (e.g., Kinzey, 1992; Rosenberger, 1992; Norconk, 2011). Thirty-five percent of the diet of the smallest indisputable atelid, *Callicebus*, which is nearly a fifth the body mass of small *Alouatta*, includes seeds and leaves. Even the comparably small, nocturnal *Aotus* is reported to feed on 32% leaves (Fernandez-Duque, 2011), although we caution that the evidence here is seriously limited. This points to a broad capability among the least dentally derived pitheciines to digest seeds and leaves together in combination, much as colobines apparently do. Thus the smallness of *Aotus* and *Callicebus* brains may also be a manifestly primitive character state of atelids, but still linked to diet.

The alouattin fossil record (Rosenberger et al., in press) is consistent with this view and introduces yet another factor to consider. The more primitive alouattins, *Protopithecus* and *Paralouatta*, are both relatively small-brained, and they lack the reduced incisors and shearing molars of *Alouatta* and *Stirtonia*, the fossil most closely related to living Howlers. This means the evolution of relatively small brains preceded the evolution of a highly folivorous dental complex in the clade. The explanation for relatively small brains in these apparently frugivorous monkeys is an open question. The fossil material is insufficient to test for sexual monomorphism, so small group size (e.g., Barton, 1996; Dunbar, 1998) cannot be invoked with credibility. Even if the single skeleton of *Protopithecus* is a large-canined male, as it appears to be, small brains in *Alouatta* are associated with the highest levels of sexual dimorphism exhibited in NWM (e.g., Plavcan and Kay, 1988), and their mating systems center around one-male and multimale groups, depending on the species (e.g., DiFiore et al., 2011). A notable size difference between the two known distal humeri attributed to *Protopithecus* has also been interpreted tentatively as evidence of size disparities within the species (Halenar, 2011a), which could be an effect of sex dimorphism. Equally tenuous, though meriting consideration, is the supposition that small brain size in *Protopithecus* is (developmentally) connected with or constrained by a morphological pattern relating to the evolution of the howling mechanism (see Hartwig et al., 2011), which seems to have been an important factor in their cranial design (Rosenberger et al., in press). Extending the Aiello and Wheeler (1995) model, we also cannot rule out the possibility that one or both of these large-bodied, more basal, bunodont alouattins already had relatively enlarged guts as a precocious, expensive-tissue adaptation to selection for seed-eating, which would benefit from a similar digestive strategy.

Irrespective of these uncertainties, it is clear *Brachyteles* does not have a reduced relative brain size, so de-encephalization is not a prerequisite to evolving or maintaining a semifolivorous feeding regime. And this goes to a larger point. A multiplicity of selective factors must be satisfied when producing either large or small brains, or any shift from the ancestral condition, depending on the particulars of a species' overall ecological strategy. In the case of atelines, Dunbar (1998) may be correct that a relatively large brain is part of the selective package necessary to maintain a large, complex social group in *Brachyteles*, which may involve dozens of individuals (e.g., DiFiore et al., 2011). Barton (1996) has also suggested that brain size is positively correlated with frugivory, while promoting the idea that multiple ecology-based selective factors are involved in selecting for the size of the brain and its components. If so, the status of *Brachyteles* is consistent with a frugivorous ancestry as well as large group size. But absent a comparably powerful social vector in *Alouatta*, where groups tend to be less than one third as large (see DiFiore et al., 2011), there may not have been an overriding selective advantage to increase the size of a primitive, relatively small, relatively inexpensive brain. Thus the particular way in which semifolivory emerges as an adaptive package in any clade is influenced by factors that are not explicitly trophic. The advanced brachiating-like locomotor systems of *Brachyteles*, possibly an extension of a heritage shared with *Ateles* (but see Halenar, 2011b), was evidently maintained by selection even as the lineage was shifting towards more foliage-eating, thus constraining the Muriqui not to evolve a more sedentary, small-group lifestyle resembling *Alouatta*.

Similarly, information on guts and passage rates do not strongly segregate the semifolivores from other platyrrhines, nor does it align them with the colobine pattern. This is an important point, for it suggests a continuity of digestive adaptations may be shared by all atelids, as noted, though exceptionally elaborated in *Alouatta*. This has implications for interpreting ateline history as well as for understanding the process and pattern behind the origins of folivory in other leaf-eating primates. Chivers (1994), Kay and Davies (1994), and Lambert (1998) proposed that seed-eating might be an intermediate step in the evolution of folivory from a frugivorous ancestry. This would be consistent with the findings reported here. While the teeth of the most advanced NWM seed-eaters, pitheciins, are fully the opposite of what one might suppose as morphologic precursors to an *Alouatta* or *Brachyteles* dentition, their guts and passage rates depart from the patterns exhibited by the more insectivorous and predaceous cebids (e.g., Fooden, 1964; Chivers and Hladik, 1980; Lambert, 1998). They suggest special adaptations for hindgut fermentation, as in the semifolivores. The genus *Callicebus* may thus be an important atelid model for a preadaptive, morphotypic feeding pattern, as its feeding preference combines seeds and leaves in larger proportions than in any other atelid—and its dentition falls into neither the seed- nor leaf-eating structural paradigms (see Rosenberger, 1992; Cooke, 2011).

One of the least equivocal morphological findings recognized in this study is that incisor and molar teeth are superbly sensitive to selection for harvesting and masticating leaves. As different as they are in lifestyle and disposition, relative brain size, locomotor behavior, ranging patterns and activity rhythms, *Alouatta* and *Brachyteles* have biomechanically similar teeth. The combination of small incisors and large, crested molars, at a minimum, appear to be a necessary and effective dental predictor of a leaf-eating specialization. Because the gut of *Brachyteles* is insufficiently known, its physiology cannot be securely factored into this equation. However, in light of the role seed-eating appears to play in selecting for gut adaptations, the possible evolutionary linkage between these two strategies, and the evidence that nonfolivorous alouattins had attained very large body size, it is tempting to extend this point by inferring that the digestive system as a whole is also probably highly sensitive to the demands of feeding on leaves and may precede the evolution of other anatomical systems as folivory becomes full blown.

Ecology of Platyrrhine Semifolivory

Alouatta and *Brachyteles* seem to prefer fruits but take leaves when necessary. Some have also stressed shifting frequencies in the uptake of young leaves and fruit at different sites and times (see DiFiore et al., 2011). While this notion might evoke a proximate causal explanation of leaves as a "fallback" food, that is not necessarily the most valuable perspective for investigating the deeper evolutionary reasons. Efficient leaf-eating may simply be an integrated feature of overall dietary and ecological strategies in both forms, possibly for different reasons and expedited in different ways.

Nothing is known about the ecological conditions under which semifolivory evolved in alouattins. Given the enormous geographical range of *Alouatta* and their ecological flexibility, it has been suggested that Howlers evolved as pioneers (e.g., Eisenberg, 1981; Rosenberger et al., 2009), which implies a formative preference for living in marginal neotropical habitats. This also implies that the syndrome arose where there was a limited range of ecological competitors and a persistently low supply of easy-to-eat fruits. However, if the *Stirtonia-Alouatta* lineage, the only segment of the alouattin clade that appears to be fully committed to leaves [although *Stirtonia* appears to have less shearing-enhanced lower molars than two species of Howlers (Cooke, 2011)], arose in a lush lowland habitat, being able to eat the most abundant forest product available would likely minimize ecological overlap and competition with the large, resident frugivore guild of Amazonian platyrrhines, particularly as it requires far less daily travel, which has its own intrinsic energetic benefits. In other words, semifolivory in *Alouatta* may also have evolved partly in response to an abundance of coexisting frugivores. The likelihoods of these two alternative hypotheses may not be distinguishable at this time. But neither seems to require a temporally-based fallback selectional model.

As an Atlantic Coastal Forest (ACF) endemic, it must be assumed that *Brachyteles*, in contrast, evolved its ecological adaptations *in situ* (Rosenberger et al., 2009). This region is less rich biotically than the Amazonian lowlands. Consequently, it now supports a maximum of five to six sympatric primates, including *Alouatta*, that is, half as many species as one finds in many lowland forests. Additionally, the ACF supports two semifolivores living together, unlike Amazonia, where *Alouatta* is not partnered with any other folivorous primate genus. This implies low fruit productivity is a large factor in selecting for folivory in the largest NWMs inhabiting the region, even though *Brachyteles* would appear to be predisposed by heritage and habitus to prefer fruits. It apparently does in primary forest habitats when they are available, eating 59% fruit and 32% leaves (de Carvalho et al., 2004), almost reversing the proportions seen elsewhere (Table 1).

One would have to assume that the presence of *Alouatta* in the ACF is simply a local ecological derivation of its larger geographical situation. *Brachyteles*, on the other hand, is best seen as evolving semifolivory as an overprint upon a highly frugivorous plan that is more comparable to *Ateles* and *Lagothrix* than to *Alouatta*. If its larger incisors, relative to *Alouatta*, are taken as an indicator, they may signal that *Brachyteles* is still more tied to fruits. Thus, given the more intense seasonality of the ACF, semifolivory in *Brachyteles* may be more of a fallback strategy geared to the regularity of intensely lean periods rather than the selective benefits of niche separation among an aggregate of syntopic primate frugivores, which are absent from the ACF. Its ecological separation from *Alouatta* is already made possible by differences in locomotor skills and ranging habits. But the fallback metaphor should not be taken too far. We know too little about the nutritional requirements of large-bodied atelines (see Felton et al., 2009), or the nutritional potential of ACF trees, to presume there is a temporal phenological rhythm that selects for leaf-eating in *Brachyteles*. Ingesting leaves in relatively high proportions may be a fundamental ecological strategy, more related to space than time.

Although it may be appropriate to see the dietary strategies of *Alouatta* and *Brachyteles* as a joint preference for leaves over fruit if and when the latter is unavailable, this does not detract from the notion that *Alouatta* and *Brachyteles* are each specialized leaf-eaters of a certain kind. That *Brachyteles* parallels *Alouatta* only in some important respects while neither exhibits the full complement of colobine-like folivorous adaptations is an indication that there are multiple ways of being folivorous and more than one selective regime behind the phenomenon. In using the term “semifolivore,” we also wish to draw attention to this. Howlers and Muriqui are not distinguished from colobines by an “incomplete,” anatomical commitment to leaf-eating, as if there is a single scale with which folivory is measured and a single adaptive strategy for its evolution in different lineages. The platyrrhines have simply done folivory differently. As we argue, heritage and ecology may have provided alternative historical factors determining or guiding the dietary potentials of both genera in shifting away from their apparently frugivorous ancestors. This raises several issues and questions.

There is some evidence that the fruit yield of tropical forests of Africa and South America (Ganzhorn et al., 2009) are not equivalent in terms of potential nutrients for the arboreal primates. New World fruits may provide a richer source of protein than their Old World counterparts, especially on Madagascar. Ganzhorn et al. propose this as an explanation for the greater taxonomic abundance (and anatomical diversity) of platyrrhine frugivores, which exceeds both catarrhines and strepsirhines. Across the hemisphere in Africa, a lower protein concentration in fruits may also help explain the evolution of two prominent alternate strategies. In the face of enhanced critical resource competition, there may have been: (1) greater selective pressure among arborealists to process leaves in full by evolving elaborate gastric specializations that actually compromise their capacity to digest fleshy fruit (see Kay and Davies, 1994) and (2) a stronger evolutionary impetus to forsake the trees altogether and develop terrestrial lineages within, and ultimately outside, the rain forests. As a corollary to the latter point, platyrrhines may have been less prone to terrestriality if the richness of fruits permitted more extensive resource partitioning within their comparatively smaller body size bracket.

Synthesis: The Making of Platyrrhine Semifolivores

If so, the platyrrhine situation, where semifolivory appears to have evolved twice via parallelism, may be the consequences of a specific shared heritage and a deeper evolutionary explanation. African leaf-eating colobines may be represented by the same number of genera, two (*Colobus* and *Procolobus*), but these are apparently sister-taxa that differentiated through a single speciation event. *Alouatta* and *Brachyteles* represent two genera that evolved semifolivory within different ateline subclades, the alouattins and atelins. Why? How? How is it that this happened twice among platyrrhines?

Perhaps because the atelid clade within which atelines differentiated may be fundamentally preadapted to evolve folivory, whether or not New World forests are capable of supporting a large frugivorous cohort. Atelines and pitheciines may have shared a common ancestor that was adapted to digesting seed coats and leaves, at least facultatively. While the most dentally derived pitheciines are the seed predators *Pithecia*, *Chiropotes*, and *Cacajao* (e.g., Kinzey, 1992; Rosenberger 1992; Norconk, 2011), even the more primitive and basal genus *Callicebus* eats more seeds *and* leaves than any nonpitheciines (see Norconk, 2011) or nonateline (see DiFiore et al., 2011).

Seed coats can have a high lignin content, like leaves, as well as toxins and tannins and other secondary compounds (e.g., Davies and Oates, 1994; Kigel and Galili, 1995; Dixon and Sumner, 2003). Lignin is a chemical compound that is a major constituent of wood, which gives a sense of how indigestible and tough lignified material can be. Thus seeds present some of the same digestive challenges as leaves, in addition to their own unique requirements for harvesting and mastication. Species eating seeds may benefit from comparable digestive adaptations, including guts that are more differentiated than is typical among other frugivores and insectivores, to allow fermentation and detoxification. As noted, this and the high percentage of seed-eating in *Colobus* (see Fashing, 2011), led Kay and Davies (1994), Chivers (1994), and Lambert (1998) to suggest seed-eating as an intermediate dietary step between frugivory and folivory among cercopithecoids. The same may hold true for platyrrhines.

If ancestral atelids were prone to feeding on seeds and evolved guts to accommodate this pattern, atelines would likely have retained this condition in their last common ancestor. This would mean they were originally preadapted for a shift toward leaves, which in turn would have increased the likelihood of parallelism. A seed-eating capacity may, in fact, be more than latent among atelines, as *Lagothrix* and *Ateles* ingest seeds. Although dietary tabulations appear to deemphasize seed-eating in atelins by comparison with pitheciines, *Ateles* and *Lagothrix* are known to be prodigious and effective dispersers of seeds (Stevenson, 2000; Link and DiFiore, 2006). This implies a gut subject to and capable of degrading the inherent secondary compounds of seed coats. Their large pot-bellies, which resemble the distended gut of *Brachyteles* in outward appearance, are evidently capable of retaining a large volume of seeds. And, although the diet of *Ateles* may involve only a fraction of the leaves eaten by an *Alouatta* or *Brachyteles* (e.g., DiFiore et al., 2011), leaf-eating is a regular activity even when fruits are available (8%; Stevenson et al., 2000). This adds to the notion of a continuum between seed- and leaf-eating among the atelids.

A second, hardly separable adaptive feature that might predispose atelines to leaf-eating is sheer body mass. As discussed above, their comparatively large body size corresponds with a volumetrically enlarged gut, and all the trappings associated with that to benefit processing leaves, such as a slower passage rate and more usable space for cultivating microbial symbionts.

There is some cladistic and paleontological evidence supporting this scenario of a seed-to-leaf shift in the differentiation of the *Alouatta* lineage. As noted, there are three fossil genera that offer anatomical information pertaining to phylogeny and adaptation of alouattins (Rosenberger et al., in press); a fourth possible alouattin (*Solimoea*) is a single tooth with consistent but more limited clues. *Stirtonia* is the one most closely related to Howlers. It is comparable to *Alouatta* in body size and its dentition is reasonably well known. The design of its molars conforms closely to Howlers and shearing quotient measures indicate a diet "nearly as folivorous" (Anthony and Kay, 1993:356) as *Alouatta*. Cooke's (2011) geometric morphometric study of lowers molars finds that *Stirtonia* plots just outside the range of two Howler species. Neither *Paralouatta* nor *Protopithecus*, in contrast, have molars designed for shearing and the latter is known to have very wide, large incisors as well, both marks of frugivores. In her classification, Cooke's identifies *Paralaouatta* as a folivore/frugivore, in contrast with the folivores *Alouatta* and *Brachyteles*. *Paralouatta* is roughly the size of a large *Alouatta* and *Protopithecus* is much larger (Halenar, 2011b). As both these genera occupy more basal positions on the alouattin cladogram than *Stirtonia*, in conjunction with the out-group evidence from pitheciines, they indicate the last common ancestor of alouattins was not an obligate folivore. Nor was it a semifolivore in the sense of *Alouatta* or *Brachyteles*, for none of the common dental prerequisites were present. But it may well have been a seed-eating frugivore, possibly even quite capable, facultatively, of digesting leaves in significant proportions because of an allometrically capacious gut.

A Common Scenario: Models For the Evolution of Leaf-Eating in Primates

The evolutionary pathway proposed for the development of semifolivory in platyrrhines presents intriguing parallels with cercopithecoids. As is well known, the two subfamily clades, cercopithecines and colobines, differ fundamentally in diet, as the colobines have evolved chemical and mechanical adaptations appropriate for ingesting leaves (e.g., Davies and Oates, 1994). It is also quite clear that the colobine dental plan is derived (e.g., Szalay and Delson, 1979), that the high-cusped, sharp-crested molar teeth were modified from a blunter design. But underlying this is the cercopithecoid's fundamental dental specialization of bilophodonty, still retained in both groups and requiring only simple modifications to achieve the colobine condition. The biomechanical explanation for bilophodonty has been clarified by modeling and experimentation, and it is evident that this unique morphology is especially favorable to the breakdown of seeds (see Lucas and Teaford, 1994). In other words, seed-eating, or the potential for seed-eating, must have been present as a preadaptation in the colobine morphotype, setting the stage for a dietary shift towards folivory.

Similar dietary transitions may have occurred among the semifolivorous platyrrhines although the hard anatomical evidence is less compelling. There is no manifest dental morphological link between the derived dentition of *Alouatta* and the ateline morphotype, or *Brachyteles* and the atelin morphotype, to suggest biomechanical derivation from a seed-eating complex. Their hypothetical molar morphologies do not present a definitive, diet-specific morphology. The clues here are more circumstantial: prevalence of dedicated seed-eating in close relatives, the possibility that gut specializations to enable seed- and leaf-eating being widespread among atelids, and the relatively large body size of atelines, especially extinct alouattin forms which are probably more primitive dentally than the modern genera. If this scenario proves useful, it would be interesting to test for its generality by considering folivory in strepsirhines as well. Do they also show indications of seed-eating antecedents?

We suggest their evolutionary pathway may have taken a different course. Strepsirhines, including the crown group and its basal members, the adapiforms, may have been folivorous from the start. There are two lines of evidence supporting this supposition. The earliest fossil strepsirhines come from the Eocene epoch (e.g., Szalay and Delson, 1979; Fleagle, 1999; Gebo, 2002), although even at that time they were taxonomically diversified and nothing secure is known of their antecedents, that is, what taxonomic group and morphological bauplan provided their foundation. Generally, these early adapids were medium- to large-bodied primates with large crested molar teeth. Some genera, such as the North American *Notharctus* (e.g., Gebo, 2002) and the African *Afradapis* (Seiffert et al., 2009), show a stunning morphological and functional correspondence with living leaf-eaters such as *Alouatta* (Fig. 7) and the living strepsirhines *Propithecus* and *Indri*. Like living strepsirhines (see Rosenberger and Szalay, 1980; Eaglen, 1986), their anterior teeth also correspond with modern folivores in being relatively small and morphologically

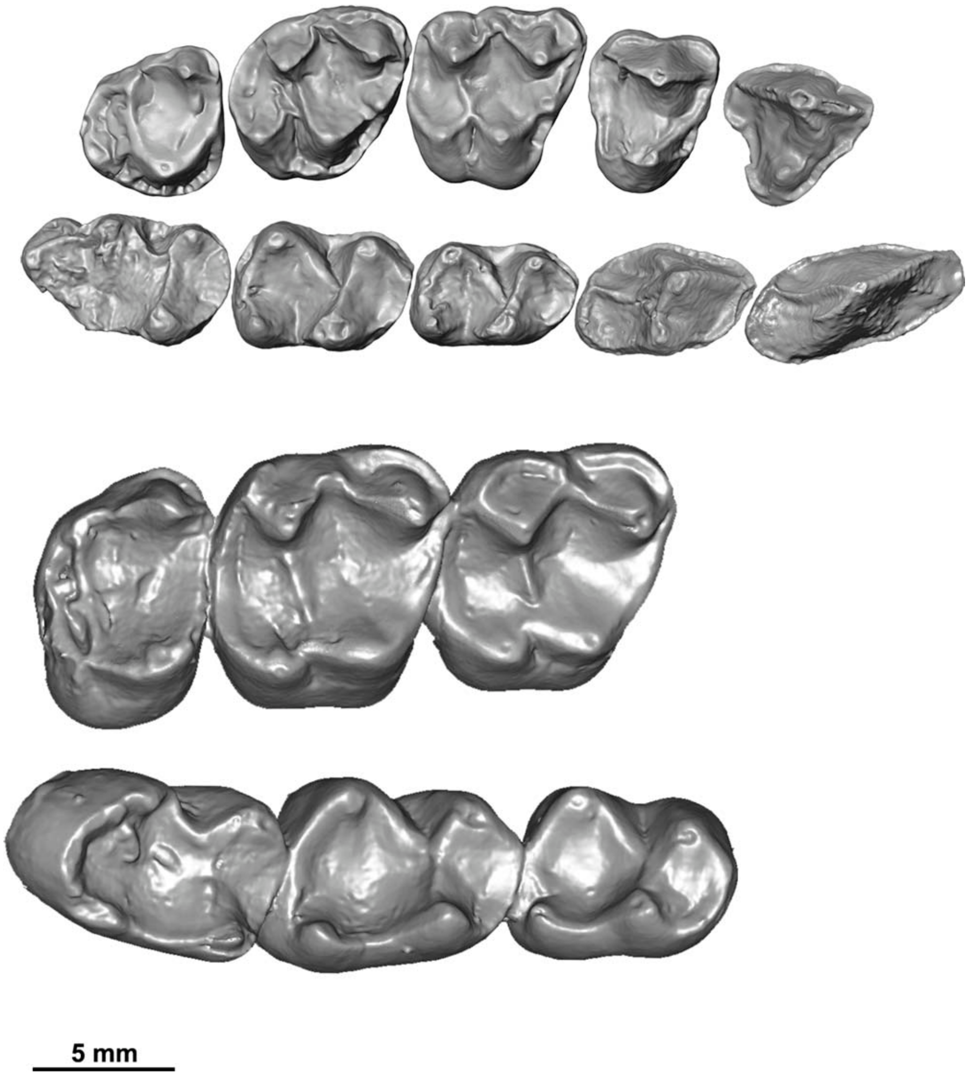

Fig. 7. Comparison of the morphology of *Alouatta* upper and lower molars (bottom two images) with *Afradapis* partial toothrows (top two images; courtesy of Erik Seiffert) illustrating a remarkable convergence of shearing features relating to a folivorous diet.

reduced. In the advanced European adapines, the compact, spatulate incisor-canine battery is shaped like croppers.

The extant strepsirhines are dietarily very diverse (see Fleagle, 1999), but one can argue that they are primitively folivorous. Several lines of evidence can be cited to support this hypothesis. Morphologically, if the lemuriforms, as opposed to the more predatory lorisiforms, are good models of the dental morphotype (e.g., Szalay and Delson, 1979), there is continuity in the morphology of molar teeth shared with adapiforms. There is even continuity in the morphology and inferred functional capability of the upper anterior teeth (e.g., Rosenberger, 2010). Vigorous harvesting roles, as expected in fruit-eaters, do not correspond with the reduced incisor morphology of lemuriforms and lorisiforms, especially when a toothcomb is present in the lower teeth. Additionally, there is evidence that some modern strepsirhines, including both lemuriforms and lorisiforms, are hypometabolic (Kurland and Pearson, 1987), which could reflect a primitively folivorous diet as well, since hypometablism is broadly associated with leafy and herbaceous diets among mammals (e.g., McNab, 1986).

Thus the strepsirhines may have been leaf-eaters from a very early point in their career. If their anterior tooth complex was reduced from a more enlarged battery (Rosenberger and Szalay, 1980), this would imply a dietary shift away from the incisal harvesting of fruits and towards leaves. Fruits would have been a more likely preadaptive, preferred food in the ancestors of strepsirhines than a diet emphasizing insects for it is more difficult to posit a strongly predaceous antecedent, as insectivory is associated with a small, fast gut, the opposite of expectations for folivores (Chivers and Hladik, 1980). An analogous, comparable evolutionary constraint may have been at work among platyrrhines, where the predaceous cebids have apparently not produced any folivores while fruit-eating atelids have done so at least twice. The largest cebid known, *Acrecebus*, was the size of *Lagothrix* (Kay and Cozzuol, 2006), that is, within the range of NWM semifolivores. Although it is known only from a single upper molar, that tooth is shaped much like the highly bunodont, nonfolivorous crown of its close relative, *Cebus*, and shows no signs of a shearing design.

Plesiadapiforms: Early Origins of the Seed-to-Leaf Pathway?

The best fossils available for shedding light on the preadapiform morphology are the controversial plesiadapiforms. The coexisting tarsiiforms (see Szalay, 1976; Gunnell and Rose, 2002), the only other primates pertinent to the time of adapidforms, are not relevant since there is growing evidence many were quite specialized ecologically as vertical clinging and leaping, nocturnal predators occupying a broadly construed "tarsier adaptive zone" (Rosenberger, 2011b). They are the smallest-bodied adaptive radiation of euprimates, generally falling well below 500g in weight (see Fleagle, 1999), and must be regarded as an assemblage occupying the insectivorous-frugivorous spectrum—if they were not nearly as predatory as modern *Tarsius* (e.g., Gursky, 2007). So, what did the taxonomically and anatomically diversified plesiadapiforms eat? This is a difficult matter for which there may be no modern consensus, and a radiation as taxonomically diversified as this is not expected to occupy a single, narrow feeding niche. Insects, fruits, and seeds were likely to have been important in the smaller forms, with their comparatively bunodont molars (Szalay, 1968; Block et al., 2007). Leaves may have been emphasized in the larger forms, including some of the Plesiadapidae (Gingerich, 1976; Bloch et al., 2007; Boyer et al., 2009), which may have been roughly 1–3 kg in body weight (Fleagle, 1999). But the most prominent and puzzling dental characteristics of plesiadapiforms are their moderately large to enormous incisors. The more robust varieties of the plesiadapiform incisor complex would suggest vigorous harvesting behaviors, but gleaning, probing, and picking activities would also have been part of the repertoire where the incisors were proportionately smaller and more delicate and more horizontally oriented (Rosenberger, 2010).

Definition of the plesiadapiforms' preferred food targets depends on clarifying both parts of the organism-environment equation, one dealing with plants and the other with plesiadapiform evolutionary morphology, as well as assumptions derived from current adaptational models. Wing and Tiffney (1987) point out that the consequences of the K/T boundary event would have "destroyed" the existing ecological interactions between angiosperms and herbivores. Nevertheless, angiosperms are assumed to have been the major vegetable food source for plesiadapiforms at the time, even though woody flowering plants were not yet in their heyday during the late Cretaceous and Paleocene. Then, they were producing smaller seeds and fruits without significant fleshy coverings, no larger than 1 mm^3 to 10 mm^3 in size (e.g., Tiffney, 2004; Moles et al., 2005). Many would have been abiotically dispersed dry fruits living in the shrub layer. But there was a large upward shift in seed size from the late Cretaceous to the beginning of the Eocene (Wing and Boucher, 1998), when the coevolutionary relationships with mammalian (and avian) dispersers matured and the angiosperm's developed larger, attractive, fleshy, sugary fruits, and gaudy flowers. Seed size enlarged (Wing and Tiffney, 1987; Tiffney, 2004; Eriksson, 2008), as did the primates. Eriksson et al. (2000) estimates an increase in seed size of 2–3 orders of magnitude by the early Eocene. It therefore stands to reason that the dietary profile of the arboreal plesiadapiforms, as more archaic omnivorous frugivores, would have been invested in the relatively small seeds of the early angiosperm configuration, which the animals would have harvested with their probe-like incisors (Rosenberger, 2010). If some of their targets involved mechanically well-protected seeds, the face-feeding plesiadapiforms would have had to rely quite heavily on incisors for securing food. But without the benefits of large size, we can also assume that the seed coats of pre-Eocene angiosperms would have evolved nonmechanical protectants, allelochemicals that are typically concentrated in seeds and immature fruit (see Kigel and Gali, 1995).

On the plesiadapiform side, since it is evident that folivory was very probably not an option for smaller forms and nutritionally poor wood would have posed even more severe mechanical and chemical disincentives, angiosperm seeds would have been the most abundant edible nonprey material available to them. Morphologically, the essence of this argument is based in the contrasts plesiadapiforms exhibit relative to euprimates in their new Eocene ecological context. The plesiadapiforms were small, nocturnal, smell-oriented, without a fine sense of sight, lacking touch-sensitive nailed fingertips on Rays II–V able to finely discriminate texture, probably wanting the integrated hand-eye coordination that comes with visual acuity and requires high-resolution neural wiring, and lacking the long-limbed, flexible locomotor skeleton that implies limited, finely controlled, free flowing locomotion in the trees (see Bloch et al., 2007).

Collecting small pendant fruits and their seeds would have required no sophisticated handling. The advanced hand-eye coordination and stable arboreal sitting postures that allow dexterous two-handed manipulation and feeding in modern primates—also keys to unlocking large encased seeds like legumes—became efficient only later. As did hands-free, below-branch pedal hanging, which relies on powerful pedal grasping? These capacities may have emerged along with stereoscopy, in concert with the modern euprimate positional behavior system and arboreal balancing mechanisms, all of which would have been associated with the reorganization of the locomotor skeleton of the euprimate morphotype (Dagosto, 1986). This would have coincided with the development of larger seeds and an alteration in vegetation structure, namely the establishment of closed canopy forests in the Eocene (e.g., Eriksson et al., 2000; Tiffney, 2004; Moles et al., 2005). Only then would there be a selective benefit accruing to species able to travel extensively and efficiently through the treetops, foraging for clumped but patchily distributed fruits. If the plesiadapiforms were indeed focused on small seeds, which would have provided lesser nutritional reward per unit and thus require bulky collections, the common occurrence among them of large diastemata behind the incisors may be an indication some also evolved squirrel-like cheek pouches, useful for storing seeds while foraging.

What this speculative scenario implies is that seed-eating—not monolithically, but as a dietetically critical fruit component complimenting insects and in some case leaves—many have been at the root of the primate radiation. If the successful plesiadapiform radiation included consumers of both seeds and leaves, as the dental morphology suggests, it points to an underlying capacity that may have been preadaptive to dietary shifts within a broad zone of digestive tolerance. The original primate digestive system may have adapted early on to the requirements of chemically digesting seeds and nonfleshy fruit, which overlap physiologically with the needs of a leaf-eater. The pathway of seeds-to-leaves may have been set in place early in primate evolution, with the Eocene adapiforms perhaps being the only higher taxon to make a wholesale shift as a basal condition of their adaptive radiation. The anthropoids would later also have been able to make the shift via preadapation but, being diurnal and without much competition in a new adaptive zone, they first moved to broaden their dietary choices by exploiting a new variety of abundant, diversified "low hanging fruit." If the earliest pre-Eocene plesiadapiform primates (and other vertebrates) developed an adaptive preference for small seeds, as argued here, the modern angiosperms may have evolved a counter strategy to enhance their reproductive success by enveloping their now larger seeds in more interesting, energy rich fruit pulps, thus saving their disseminules from destruction while also enhancing their dispersal potential (see Mack, 2005). Later, as seen in the radiations of New and Old World anthropoids, as niche differentiation became a selective priority in ever more complicated ecological webs, this same seed-to-leaf pathway would produce the semifolivorous platyrrhines and the folivorous colobines as upward shifts in body size made seeds—often in balanced combination with leaves—an efficient option for obtaining protein and other nutrients.

CONCLUSIONS

The feeding category "folivory" may understate the importance of nonleafy foods in the diets of leaf-eating platyrrhines and other primates, and thus lead to unsatisfactory or incomplete interpretations of adaptation. The two most folivorous New World monkeys, *Alouatta* and *Brachyteles*, are similar dentally, reflecting expectations of the folivory model. But *Brachyteles* diverges in many ways from the energy-conserving strictures that are also associated with the leaf-eating model, with its costly locomotor pattern, ranging habits, relatively fast digesta passage rate, and unreduced relative brain size. Evidently, taxa evolve different balances with respect to potentially competing selection pressures even when they rely on a diet such as leaves that presents large, complex challenges. In *Brachyteles*, for example, the imperative to maintain a relatively large brain, perhaps because of it advantages in maintaining large, dispersed social groups, outweighs the brain's high metabolic costs and the savings that would be obtained if its was smaller.

The classic adaptational model for primate folivory, based largely on the highly derived colobines, has taken on a different aspect now that their frequently elevated reliance on seed-eating has become well established. Since seed coats can present chemical challenges similar those exhibited by leaves, colobine guts are well suited to process them as well, so leaves cannot be assumed to be the monolithic selective force behind the colobines' digestive adaptations. If one assumes that cercopithecoid bilophodonty evolved in part as architecture suitable for processing seeds, as seems likely, this means that the leaf-eating dentitions and guts of colobines probably arose as an elaboration of a seed-eating preadaptation. Given the wide ecological, behavioral, and morphological gaps (apart from having crested molars) that separate insectivores from folivores, it seems reasonable to expect that a specialization on leaves evolved from somewhere within the spectrum of a fruit-eating diet rather than a predatory one. Seed-eating may have been concentrated in that segment of the spectrum.

A similar seed-to-leaf transition may have occurred among platyrrhines. While *Alouatta* appears to be exceptional in adhering to a more or less seedless diet, there is growing evidence that *Brachyteles* consumes appreciable amounts. Also, platyrrhines much smaller in body mass, *Callicebus* and *Aotus*, are reported to consume relatively high percentages of seeds and/or leaves. Both the latter have incisors and molars that can only be interpreted as being unspecialized for leaf eating, and their lower molars are not easily distinguished from other platyrrhines whose diets fall within the insectivory-frugivory continuum. Thus a precocious gastric adaptation to feeding seeds may explain their ability to eat these items at significant levels as well. Although there are phylogenetic questions that still need to be addressed with respect to these four genera, that is, the position of *Aotus*, it seems reasonable to infer that atelids—including the pitheciin seed-predators—may have evolved from an ancestral stock of frugivores with a tendency to use seeds and/or seed coats where challenging allelochemicals would be sequestered.

The earliest primates lived in an arboreal world where angiosperms had not yet achieved the familiar modern states of the anatomical features making them so attractive as food sources, large seeds and rich pericarp. As the plesiadapiforms must have eaten more primitive fruits, it is likely they would have been exposed to proportionately large amounts of secondary compounds, thus selection to resolve them in the gut. Such chemical deterrents would have been advantageous to the trees before angiosperms evolved the bait-and-switch strategy of offering a pulpy alternative food to protect their seeds from predation while also attracting primates and others as seed dispersers. Thus primates may have early evolved the digestive capacity to handle secondary compounds. If so, the seed-to-leaf pathway that may have been a common feature behind the origins of folivory in various primate radiations, living, and extinct.

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