

Diet and Dental Topography in Pitheciine Seed Predators

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KEY WORDS *Pithecia*; *Chiropotes*; *Cacajao*; teeth; dietary adaptation

ABSTRACT Pitheciines (*Pithecia*, *Chiropotes*, and *Cacajao*) are a specialized clade of Neotropical seed predators that exhibit postcanine teeth with low and rounded cusps and highly crenulated occlusal surface enamel. Data on feeding ecology show that *Pithecia* consumes proportionally more leaves than other pitheciine species, and comparative studies demonstrate its greater molar relief and relative shearing potential. However, data on pitheciine food mechanics show that *Pithecia* masticates seeds with greater crushing resistance than those preferred by *Chiropotes*. This variation predicts an opposing morphology characterized by low and more rounded occlusal surfaces in *Pithecia*. We build on previous research using new methods for molar surface shape quantification by examining pitheciine second molar shearing crest length, occlusal relief, surface complexity, and surface curvature relative to nonseed specializing platyrrhines and within the context of the observed

interspecific variation in pitheciine feeding ecology. Consistent with the previous analyses, our findings demonstrate that pitheciine molars exhibit low shearing, relief, and curvature compared with nonseed predators, independent of phylogeny. Pitheciines also exhibit highly “complex” occlusal topography that promotes the efficient breakdown of tough seed tissues. Overall, *Pithecia*, *Chiropotes*, and *Cacajao* share a similar topographic pattern, suggesting adaptation to foods with similar structural and/or mechanical properties. However, *Cacajao* differs in surface complexity, which reflects some variation in its feeding ecology. Contrary to the predictions, *Pithecia* and *Chiropotes* do not differ in any of the topographic variables examined. The range of demands imposed on the postcanine teeth of *Pithecia* might therefore select for an average topography, one that converges on that of *Chiropotes*. *Am J Phys Anthropol* 150:107–121, 2013. © 2012 Wiley Periodicals, Inc.

Diet and dental morphology are inextricably linked. Decades of research support the hypothesis that primate dental shape is adapted to cope with variation in the structural and/or mechanical properties of food (Kay, 1975, 1978; Kay and Covert, 1984; Kinzey, 1992; Anthony and Kay, 1993; Bunn and Ungar, 2009). This association provides the opportunity to closely examine the relationship between dental form and function in living taxa, thus allowing researchers to infer diet from dental morphology in extinct forms for which direct data on dietary ecology are unavailable (Strait, 1991; Meldrum and Kay, 1997; Ungar, 2004; Boyer et al., 2010).

Dietary needs appear to be an important selective pressure that influence the evolution of many primate clades, including humans (Vallender and Lahn, 2004). Fossil primates, including australopiths and adapiforms, have been hypothesized to possess dental adaptations for feeding on resistant foods (Robinson, 1960; Ungar, 2004; Perry et al., 2010). However, a broad and detailed understanding of dietary adaptations in tooth bearing vertebrates is necessary to understand the evolution of such adaptations in extinct taxa (Kay and Cartmill, 1977). Here, we evaluate the association between diet and molar occlusal variation in the Pitheciinae, a clade of extant primates that consume resistant foods but that vary in morphology and feeding ecology.

Pitheciine monkeys (the sakis and uakaris) are a monophyletic subfamily of Neotropical seed predators

from northern and central South America that represent a model organism for testing hypotheses related to dietary adaptation. Pitheciine monophyly has been well established by both molecular (Schneider and Rosenberger, 1996; Finotelo et al., 2010) and morphological (Ford, 1986; Kay, 1990) studies, with *Pithecia* (the sakis) being the sister taxon to a clade including *Chiropotes* (the bearded sakis) and *Cacajao* (the uakaris). These genera exhibit a suite of cranial, mandibular, and dental morphologies hypothesized to be adaptations for feeding on mechanically challenging unripe fruits and seeds, yet

Additional Supporting Information may be found in the online version of this article.

Grant sponsor: 2009 American Society of Mammalogists, Leakey Foundation, 2010 AAPA Professional Development, Evolving Earth Foundation, NSF grant (NSF BCS-1157295).

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Received 16 April 2012; accepted 28 September 2012

DOI 10.1002/ajpa.22181

Published online 5 December 2012 in Wiley Online Library (wileyonlinelibrary.com).

this clade is known to exhibit enough variation in feeding ecology to associate differences in dental form with differences in diet (Kinzey, 1992). Recent molecular phylogenies further support the inclusion of *Callicebus* as the most basal member of the pitheciine clade (von Dornum and Ruvolo, 1999). However, we reserve the subfamily Callicebinae for this taxon.

Pitheciines are almost exclusively frugivorous, and they show a preference for unripe fruits (Mittermeier and van Roosmalen, 1981; van Roosmalen et al., 1988; Ayres, 1989; Kinzey and Norconk, 1993). Sclerocarpic harvesting (Kinzey and Norconk, 1990), uncommon among primates, may reduce dietary stresses and competition with sympatric taxa during periods of preferred-food scarcity by providing early access to fruits and seeds (Norconk, 1996; Norconk et al., 2009). The seeds of unripe fruit appear to represent a novel means of acquiring necessary nutrients (Kinzey and Norconk, 1993). Young seeds are a particularly good source of lipids, proteins, and carbohydrates, but as fruit ripens and becomes softer, the seeds harden, and develop higher levels of toxic secondary compounds (Norconk and Conklin-Brittain, 2004).

Many primate taxa are known to ingest and masticate seeds (e.g., Terborgh, 1983; Waser, 1984; Maisels et al., 1994; Bowler and Bodmer, 2011). However, seeds exhibit a certain degree of variation in their structural and/or mechanical properties, a product of both phylogeny and phenology. Young seeds of many fruit-bearing plant species can be described as being soft and tough, whereas mature seeds are often hard and brittle. Mechanically, a “tough” food item is resistant to crack propagation, a “hard” food is resistant to indentation, and a “brittle” food is one that exhibits the absence of toughness (Lucas, 2004). Terms such as “resistant” or “mechanically challenging” can be used when additional information on fracture properties is unavailable.

Hard and brittle seeds and nuts are those that absorb energy, resist crack initiation, and experience low deformation while being loaded by the dentition. When subjected to sufficient stress, cracks initiate and are propagated with considerably less muscular effort than required by tough materials. Hard and brittle foods can withstand large loads without being permanently deformed but shatter when yield strength is met (Lucas, 2004). Crack growth is greater in these materials, and cracks will often propagate in front of the applied loading point (i.e., in front of the cusp tip). Such foods are described as being highly stress-limited (Agrawal et al., 1997). Postcanine teeth with low and bulbous cusps are inferred to be efficient at fracturing stress-limited foods, including seeds and nuts, because they are thought to fracture such foods with lower occlusal force than required by teeth with sharp cusps (Lucas, 2004; Ungar, 2004). Additionally, as the fracture strength of a tooth cusp is inversely related to its curvature (Lawn and Lee, 2009), blunt cusps might reduce the risk of tooth crown fracture during high-magnitude biting of stress-limited food items (Lawn and Lee, 2009; Berthaume et al., 2010).

In contrast to the high stress-limitations characterizing the diets of some “hard” object-feeding taxa (e.g., *Cercocebus*; Waser, 1984), seeds masticated by saki monkeys (*Pithecia* and *Chiropotes*) are described as being elastic (Kinzey, 1992) and highly fibrous (Norconk and Conklin-Brittain, 2004); yet, they exhibit high crushing resistance (Ayres, 1989; Kinzey and Norconk, 1990,



Fig. 1. Skull of *Ch. satanas* (AMNH 94128). Note the large and robust canines, and procumbent incisors. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

1993; Norconk and Veres, 2011). That is, they are both tough and hard, and require considerable bite force and chewing effort to be efficiently processed.

Large canines and procumbent incisors allow pitheciines to extract nutrient-rich seeds from inside unripe fruits before being processed by the postcanine dentition (Fig. 1). Pitheciine premolars are molarized, a characteristic of “hard” object-feeding primate taxa (Kay, 1990). Both the molars and the premolars have low and expanded occlusal surfaces for efficient trituration of unripe seed tissues (Kinzey, 1992; Rosenberger, 1992). These teeth can be described as exhibiting virtually no cresting and have low, rounded cusps relative to New World taxa that do not prey upon seeds (Rosenberger and Kinzey, 1976; Kinzey, 1992). As unripe seeds masticated by pitheciines are tough and lack brittleness, the low occlusal topography in pitheciine molars can be viewed as a grinding adaptation that prevents the interlocking of steep molar cusps rather than an adaptation for countering highly stress-limited tissues (cf. Kay, 1975). This grinding of tough seed tissues is further promoted by an expanded occlusal surface, and crenulated occlusal enamel (Kinzey, 1992). Crenulations facilitate secondary breakdown of seed particles (Lucas and Luke, 1984; Kinzey, 1992), and might also help position seeds along the postcanine tooth row during mastication (Lucas and Teaford, 1994). Skinner et al. (2010) demonstrate that enamel crenulations and occlusal complexity in *Chiropotes* differs from that of nonpitheciine taxa in being solely due to surface enamel deposition rather than being present also at the enamel–dentine junction. Further, although pitheciines have relatively thin enamel, they exhibit extensive molar enamel prism decussation and Hunter–Schreger bands, both of which structurally defend enamel against crack propagation during forceful biting (Martin et al., 2003).

Pitheciines supplement their diet with leaves and occasionally small proportions of other foods, including

TABLE 1. Diet composition of pitheciine taxa, *Aotus* spp., and *Callicebus* spp.^a

| Species | % Seeds | % Pericarp | % Flowers | % Leaves | % Insects | Reference |
|----------------------------|-------------|------------|-----------|---------------------|-----------|--|
| <i>A. azarae</i> | – | 16 | 33 | 40 | – | Wright (1986) |
| <i>A. azarae</i> | – | 45 | 14 | 41 | – | Arditi (1992) |
| <i>A. azarae</i> | – | 66 | 1 | 15 | – | Giménez and Fernandez-Duque (2003) |
| <i>A. nigriceps</i> | – | 60 | – | – | – | Solano (1995) |
| <i>Cal. brunneus</i> | – | – | – | (23–66) | – | Wright (1986) |
| <i>Cal. personatus</i> | 21.9 | 54.7 | – | 17.2 | – | Müller (1996) |
| <i>Cal. personatus</i> | – | 81 | 1 | 18 | – | Kinzey and Becker (1983) |
| <i>Cal. torquatus</i> | – | 71 | – | 4 | 20 | Kinzey (1981) |
| <i>Cal. torquatus</i> | 26.9 | 59.4 | 3.9 | 6.4 | 3.4 | Palacios et al. (1997) |
| <i>P. albicans</i> | 46.2 | 28.6 | 6.5 | 9.5 | 0.4 | Peres (1993) |
| <i>P. monachus</i> | 38 | 55 | 3 | 4 | – | Soini (1986) |
| <i>P. monachus</i> | 18 | 53 | 13 | 16 | – | Happel (1982) |
| <i>P. pithecia</i> | (26–31) | – | 15.9 | (4–18.4) | – | Setz (1993) |
| <i>P. pithecia</i> | 53.3 | 31 | 2 | 10.4 | 3.7 | Homburg (1997) |
| <i>P. pithecia</i> | 60.6 | 27.8 | 2.2 | 7.1 | 2.3 | Kinzey and Norconk (1993); Norconk (1996) |
| <i>Ch. albinus</i> | 35.9 | 53.9 | 3 | 7.2 | – | Ayres (1981, 1989) |
| <i>Ch. satanas</i> | 63.3 | 9.3 | 11.4 | [16.1] ^b | – | Ayres (1981) |
| <i>Ch. satanas</i> | 66.4 | 27.6 | 4.6 | – | – | van Roosmalen et al. (1981) |
| <i>Ch. satanas</i> | 50.7 (4–60) | (0–52) | (0–8.1) | (0–1.5) | (1–21) | Peetz (2001) |
| <i>Ch. satanas</i> | 74.8 | 21.6 | 0.4 | 0.2 | 0.5 | Kinzey and Norconk (1993); Norconk (1996) |
| <i>Cac. calvus</i> | 66.9 | 18.4 | – | 3.3 | 5.2 | Ayres (1989) |
| <i>Cac. calvus</i> | 46 | 50 | – | – | – | Aquino and Encarnacion (1999) |
| <i>Cac. melanocephalus</i> | 67 | 28.8 | 5 | 4 | 2 | Boubli (1999) |

^a With the exception of Palacios et al. (1997) and Happel (1982), all dietary data have been previously referenced by Fernandez-Duque (2007) and Norconk (2007). Spaces left blank do not always indicate that the food is absent from the diet. In many studies, fruit pericarp and seeds were not considered separately. Furthermore, some dietary categories lack quantitative data. This is especially true for insectivory in the two nonpitheciine taxa. It should be noted that some studies (e.g., Setz, 1993) report ranges that reflect the annual diet, whereas others focused only on the periods of resource scarcity (e.g., Palacios et al., 1997).

^b This value also includes bark and stems (Ayres, 1981).

faunal prey (e.g., Ayres, 1989; Norconk, 1996; Boubli, 1999). Although extant pitheciines are among the most frugivorous of all New World monkeys, data suggest that the diet of *Pithecia* is composed of a higher proportion of leaves compared with *Chiropotes* though this difference is minor for some species (Table 1). Nonetheless, *Pithecia* spp. are regarded as being proportionally more folivorous than *Chiropotes*, and this finding has been linked to apparent differences in their molar occlusal morphology (Kinzey, 1992). *Cacajao* species rarely feed on leaves, but they may become more important during dry seasons (Ayres, 1989; Barnett and Brandon-Jones, 1997; Boubli, 1999; Barnett and de Castilho, 2000).

Cacajao spp. are often found among seasonally flooded forests where they rarely overlap with other pitheciine taxa (Ayres, 1989; Barnett et al., 2005), whereas *Chiropotes* and *Pithecia* inhabit nonflooded forests and are often sympatric (Norconk, 2007). Interspecific competition over dietary resources may lead to nonrandom patterns of species distribution within a primate community, particularly among frugivorous taxa (Kamilar and Ledogar, 2011). However, sakis and bearded sakis are thought to reduce direct competition in sympatry by exploiting fruits and seeds at different stages of maturity. Norconk and colleagues (Kinzey and Norconk, 1990, 1993; Norconk and Veres, 2011) demonstrate that ingested fruit pericarps preferred by *Chiropotes* are at an earlier stage of development and have greater puncture resistance than fruits breached by *Pithecia*. However, the more mature fruits exploited by *Pithecia* contain seeds with significantly greater crushing resistance.

Based on seed structural property data, *Pithecia* is expected to exhibit dental features, reflecting their tendency to masticate seeds of greater crushing resistance

than those in the diet of *Chiropotes*. Indeed, Spencer (2003) demonstrates that *Pithecia* has greater molar tooth root surface area relative to *Chiropotes*, suggesting that these teeth experience heavy and/or repetitive loads during mastication. Additionally, Teaford and Runestad (1992) show that *Pithecia* and *Chiropotes* differ in their molar microwear signature, with *Pithecia* exhibiting a higher incidence of large pits consistent with their preference for seeds with higher crushing resistance. However, other work reports greater molar occlusal relief in *Pithecia* relative to *Chiropotes* and *Cacajao*, a finding linked to their proportionately higher leaf intake (Kinzey, 1992). Further, by quantifying the shearing quotient (Kay, 1978) in a broad sample of platyrrhine taxa, Anthony and Kay (1993) report greater molar shearing potential in *Pithecia monachus* compared with *Chiropotes satanas*. The postcanine occlusal surface is also broader in *Pithecia*, which might reflect their more highly folivorous dietary intake compared with *Chiropotes* and *Cacajao* (Kinzey, 1992; Anapol and Lee, 1994; Norconk et al., 2009). Thus, there is some inconsistency between the dietary ecology and the dental adaptations of pitheciine monkeys.

Relatively little research has focused on the diet of the reclusive *Cacajao*, although there have been a number of recent studies (Barnett and Brandon-Jones, 1997; Aquino and Encarnacion, 1999; Boubli, 1997, 1999; Barnett and de Castilho, 2000; Bowler and Bodmer, 2011), confirming earlier work by Ayres (1981, 1986, 1989). These studies indicate a near full commitment to frugivory, which suggests likely differences in the mechanical signature of its diet compared with sympatric *Pithecia* and *Chiropotes*.

This study examines the relationship between intergeneric dietary variation and variation in second

mandibular molar topography within this specialized clade of seed predators. Pitheciine molar form is interpreted relative to two Neotropical primate frugivores that do not occupy a specialized seed-feeding niche: *Callicebus* and *Aotus*. Recent molecular phylogenies identify *Callicebus* as the sister taxon to the Pitheciinae; the position of *Aotus* is less well resolved, but most recent analyses place it as closely related to, or embedded within, a clade including the Callitrichinae, *Saimiri* and *Cebus* (Schneider and Rosenberger, 1996; Schneider et al., 2001; Fabre et al., 2009; Wildman et al., 2009). The use of two “outgroup” taxa, only one of which is closely related to the pitheciines (or possibly its most basal member; von Dorum and Ruvolo, 1999), could indicate that differences in dental morphology are likely due to the specialized use of the postcanine dentition for seed predation in saki and uakari evolution rather than to their close evolutionary relationship, particularly if the teeth of *Aotus* and *Callicebus* are found to be relatively similar.

Table 1 provides an overview of dietary ecology in *Aotus* spp., *Callicebus* spp., *Pithecia* spp., *Chiropotes* spp., and *Cacajao* spp. Fleshy fruit makes up the largest component in the diets of both *Callicebus* (Kinzey, 1981; Kinzey and Becker, 1983; Müller, 1996) and *Aotus* (Wright, 1986; Puertas et al., 1992; Giménez and Fernandez-Duque, 2003). For both taxa, fruits are supplemented by leaves and insects, and these resources can become quite important during periods of low fruit abundance (Kinzey, 1981; Wright, 1986; Solano, 1995; Giménez and Fernandez-Duque, 2003).

We build on previous research by examining molar morphology using new methods for surface shape quantification. Specifically, we quantify the shearing ratio (SRA), relief index (RFI), Dirichlet normal surface energy (DNE), and orientation patch count rotated (OPCR) in *Pithecia*, *Chiropotes*, and *Cacajao*, as well as in *Callicebus* and *Aotus*. These methods have been recently reviewed by Bunn et al. (2011), and are described in more detail below. Briefly, SRA is the summed length of molar shearing crests divided by the associated square root of two-dimensional (2D) molar area (Strait, 1991). It is therefore a measure of relative shearing crest length. Studies show that folivorous and insectivorous primates can be morphologically distinguished from frugivorous primates by the relative length of their molar shearing crests (e.g., Kay, 1975, 1978, 1984; Kay and Hylander, 1978; Kay and Covert, 1984; Covert, 1986; Strait, 1993).

The RFI is computed as the ratio between the three-dimensional (3D) area of a tooth’s functional surface and a 2D projection of its occlusal area (Ungar and Williamson, 2000). It is a measure of relative occlusal surface area or crown height. The RFI has been shown to distinguish folivorous from frugivorous hominoids (M’Kirera and Ungar, 2003) and cercopithecoids (Ulhaas et al., 2004; Ungar and Bunn, 2008; Bunn and Ungar, 2009). Additionally, Boyer (2008) demonstrates that RFI distinguishes both insectivores and folivores from frugivores in his sample composed of strepsirrhine primates and euarchontan mammals.

The recently introduced dental topographic variables DNE and OPCR incorporate novel approaches to quantify dental form (Fig. 2). DNE is calculated as the change in normal vectors over the 3D surface of a tooth. This metric characterizes a tooth’s overall degree of surface curvature, and is greatest among insectivorous and folivorous taxa (Bunn et al., 2011). OPCR describes dental “complexity” by calculating the number of surface patches with distinct orientations on an occlusal surface map (Evans and Jernvall, 2009). Taxa that routinely masticate vegetation or

other tough foods have been shown to exhibit more “complex” tooth surfaces relative to those that focus on foods that are less tough (Evans et al., 2007).

Dental topographic variables such as those examined here detect similar adaptations to diet and can therefore covary to some degree, particularly DNE and RFI (Bunn et al., 2011). However, although DNE and RFI may correlate, there is evidence that they are metrically decoupled and can be modified in uncorrelated ways through the evolutionary process. For example, Boyer et al. (2011) find that DNE exhibits much greater variance than RFI between *Ateles* and *Alouatta*. Further, these metrics capture different aspects of molar surface shape, which allows researchers to gain a greater level of dietary resolution; for example, RFI captures tooth height by comparing the total surface area of a crown to the area of the occlusal outline, whereas DNE quantifies the curvature of the surface. It is possible that a hypsodont tooth with a relatively flat occlusal surface would have a high RFI value, but low DNE, as may be the case for *Ateles* among platyrrhines (Boyer et al., 2011).

We test the hypothesis (Hypothesis 1) that, relative to *Aotus* and *Callicebus*, the three pitheciine taxa will exhibit molar adaptations for seed feeding, with the prediction that *Pithecia*, *Chiropotes*, and *Cacajao* will each exhibit relatively low SRA, RFI, and DNE. We also predict that OPCR will be highest among the pitheciines, consistent with occlusal surface complexities for grinding of tough seed particles.

Within pitheciines, we test the hypothesis (Hypothesis 2a) that *Pithecia* will exhibit molar occlusal morphology consistent with increased leaf intake relative to *Chiropotes* and *Cacajao* (Ayres, 1989; Kinzey, 1992; Kinzey and Norconk, 1993), with the prediction that *Pithecia* will exhibit significantly greater SRA, RFI, DNE, and OPCR than the other pitheciines.

As an alternative hypothesis (Hypothesis 2b), *Pithecia* will exhibit molar occlusal topography consistent with the previously observed niche partitioning between sakis and bearded sakis, specifically the tendency of *Pithecia* to masticate seeds with greater crushing resistance than those masticated by *Chiropotes* (Kinzey and Norconk, 1990, 1993; Norconk and Veres, 2011). Indeed, although Kinzey (1992: 508) notes “*Pithecia* appears to be the most folivorous of the pitheciines and also has the least reduction in molar occlusal relief,” he later predicts that “*Pithecia* molars should show features more highly correlated with crushing (vis-à-vis grinding) compared with *Chiropotes*” (509). Under Hypothesis 2b, *Pithecia* is predicted to have significantly lower SRA, RFI, and DNE relative to *Chiropotes*. As grinding of seed particles is central to this alternative hypothesis, it also predicts higher OPCR in *Pithecia* relative to *Chiropotes*.

There are limited data on the fracture mechanics of *Cacajao* foods, and although there are data showing decreased reliance on leaf material in *Cacajao* relative to *Chiropotes*, functional differences in dental anatomy between these taxa should await further study of *Cacajao* feeding ecology. However, comparisons for each variable are made between *Chiropotes* and *Cacajao* to form predictive hypotheses concerning the relative molar function in these taxa.

METHODS

Sample

The entire sample comprises digital models of 81 second mandibular molars from five genera and 11 species

TABLE 2. Taxa comprising study sample^a

| Taxon | <i>n</i> |
|----------------------------|----------|
| <i>A. azarae</i> | 4 |
| <i>A. nigriceps</i> | 14 |
| <i>Cal. donacophilus</i> | 4 |
| <i>Cal. moloch</i> | 9 |
| <i>Cal. torquatus</i> | 10 |
| <i>P. monachus</i> | 9 |
| <i>P. pithecia</i> | 7 |
| <i>Ch. albinus</i> | 6 |
| <i>Ch. satanas</i> | 6 |
| <i>Cac. calvus</i> | 8 |
| <i>Cac. melanocephalus</i> | 4 |

^a Original specimens are housed in the collections of the American Museum of Natural History (AMNH), the National Museum of Natural History (NMNH), and the Harvard Museum of Comparative Zoology (MCZ).

(Table 2). Only lightly worn teeth (i.e., those with limited development of wear facets) were included in the sample. All teeth analyzed exhibit comparable levels of tooth wear, with limited modification of cusp and crest morphology, as judged relative to other members of the same taxon. To create the digital tooth models, molds of platyrrhine mandibular postcanine dentitions were first made using President Jet Light Body polyvinylsiloxane molding gel. High-resolution epoxy casts were created from these molds using EPOTEK 301 epoxy with gray pigment added. Second molars were sectioned from tooth rows, and mounted on 35-mm platforms for efficient μ CT scanning. A ScancoMedical brand μ CT 40 machine (www.scanco.ch) was used to capture tooth surface data at 18- μ m resolution. 3D tooth surface models were then processed using the Scanco, ImageJ (NIH), and Amira (Visage Imaging) software packages to produce models of individual teeth. Cropping and smoothing procedures followed those outlined in Boyer (2008). In addition, Boyer (2008) provides a more detailed discussion of scanning procedures and preparation that were followed here, as well as sensitivity analyses concerning thresholding, cropping, and smoothing.

Variables

Four variables were computed for each specimen: SRA, RFI, OPCR, and DNE. SRAs were measured using Geomagic Studio 11 (Geomagic). Using the surface measurement tool, the following seven shearing crests were measured: the paracristid, protocristid, postmetacristid, pre-entocristid, postentocristid, posthypocristid, and the cristid obliqua. Following Kay (1977), the lingual half of the protocristid was not included in SRA calculation, as this segment functions as an occlusal guide and does not contribute to overall shearing potential. Additionally, as the taxa examined in this study lack a hypoconulid, the boundary between the postentocristid and the posthypocristid was placed at the point where the paraconid or termination of the paracristid on the M_3 contacts the M_2 (Bunn et al., 2011). Shearing crest lengths were summed for each specimen to provide a measure of total shearing potential. Associated 2D occlusal area was measured in ImageJ, and SRAs were calculated as the ratio of total shearing length to the square root of molar area. To calculate RFI, the 2D occlusal surface area embedded in 3D space was measured in Amira. Associated 2D occlusal area projected into the occlusal plane was measured in ImageJ. The RFI was calculated as the natural log of

the ratio of square root of 3D-embedded surface area to the square root of the 2D-projected area. DNE was calculated in Teether, a custom-programmed MATLAB application, using the calculations and formulae described by Bunn et al. (2011). OPCR was calculated using the VisualBasic program SurferManipulator that was written to interface with Surfer (Golden Software) for Windows (Evans et al., 2007). Patch count was averaged following eight successive rotations, and was calculated with a minimum patch size of three grid points.

Data analysis

Kolmogorov–Smirnov and Shapiro–Wilk tests indicate that genus values for each variable approximate the normal distribution, and the results of Levene’s tests indicate homogeneity of population variances. We therefore conducted multiple pairwise comparisons between pitheciine and nonseed predating genera using single-classification analysis of variance (ANOVA) to test the primary hypotheses outlined above using SPSS Statistics 20. Directional hypotheses were tested using a one-tailed analysis, whereas nondirectional comparisons (i.e., *Chiropotes* vs. *Cacajao*) were made using a two-tailed analysis. *Aotus* and *Callicebus* were first compared with the three pitheciine taxa for each variable. *Pithecia*, *Chiropotes*, and *Cacajao* were then compared with each other. This resulted in a total of 36 comparisons. To reduce the risk of Type I error, we adjusted significance values using the Holm–Bonferroni method for multiple comparisons (Holm, 1979). We also analyzed the internal structure of our data in R (R Core Team, 2012) by performing a principal components analysis (PCA) based on the correlation matrix of log-transformed topographic data to highlight the variables that are most responsible for driving shape variation within the sample.

Although we recognize the importance of species-level dietary variation, the comparisons described above focus on the generic level to increase sample size. We conducted an additional set of comparisons to test for any intrageneric differences in molar shape by comparing species within each genus for both the nonseed predators and the pitheciines. As many species distributions were non-normal, we performed these comparisons using the Mann–Whitney *U*-test. Most species have sample sizes of $n < 10$. Therefore, the “exact” variant of *P* is reported below, as asymptotic testing generally yields an incorrect *P*-value in Mann–Whitney *U*-test when sample sizes are small (Mundry and Fischer, 1998). Significance values were again adjusted for each set of comparisons using the Holm–Bonferroni method.

Although the geographic distributions of *Pithecia* spp. overlap with *Chiropotes* in much of eastern Amazonia, sakis and bearded sakis are not sympatric in the western Amazon Basin (Norconk, 2007). Further, *Chiropotes* and *Cacajao* are generally allopatric, but there have been sightings of *Chiropotes* alongside *Cacajao* at several localities in western Amazonia (Boubli, 1997, 2002; Boubli et al., 2008). Therefore, it is possible that the grouping of species within *Pithecia*, *Chiropotes*, and *Cacajao* is masking real niche-related differences in molar morphology. To examine this issue, we conducted a final set of comparisons focusing on all possible species pairs between genera using the same methods used to conduct the intrageneric analyses.

Finally, we performed a phylogenetic MANOVA using the R package “geiger” (Harmon et al., 2008) to test the

TABLE 3. Species means and standard deviations for the four dependent variables

| Taxon | SRA | RFI | DNE | OPCR |
|----------------------------|---------------|---------------|------------------|----------------|
| <i>A. azarae</i> | 2.953 (0.244) | 1.850 (0.000) | 138.129 (5.943) | 47.781 (3.514) |
| <i>A. nigriceps</i> | 2.850 (0.177) | 1.784 (0.036) | 136.662 (11.300) | 48.482 (3.199) |
| <i>Cal. donacophilus</i> | 2.847 (0.213) | 1.813 (0.074) | 169.015 (15.319) | 59.344 (6.465) |
| <i>Cal. moloch</i> | 2.755 (0.159) | 1.771 (0.061) | 145.985 (18.603) | 55.417 (5.986) |
| <i>Cal. torquatus</i> | 2.747 (0.178) | 1.777 (0.027) | 162.266 (19.039) | 63.338 (3.533) |
| <i>P. monachus</i> | 2.307 (0.046) | 1.717 (0.029) | 121.082 (11.067) | 66.444 (5.694) |
| <i>P. pithecia</i> | 2.378 (0.119) | 1.713 (0.022) | 114.363 (12.835) | 78.125 (7.223) |
| <i>Ch. albinasus</i> | 2.383 (0.119) | 1.723 (0.043) | 121.862 (13.881) | 71.063 (8.188) |
| <i>Ch. satanas</i> | 2.314 (0.147) | 1.738 (0.021) | 130.213 (10.077) | 71.600 (2.994) |
| <i>Cac. calvus</i> | 2.411 (0.122) | 1.716 (0.029) | 119.715 (11.833) | 55.393 (4.426) |
| <i>Cac. melanocephalus</i> | 2.362 (0.045) | 1.733 (0.038) | 126.510 (13.498) | 57.333 (3.001) |

significance of differences in mean values (Table 3) between two dietary groups, composed of six species of seed predators (*Pithecia*, *Chiropotes*, and *Cacajao* spp.) and five species of nonseed predators (*Aotus* and *Callicebus* spp.) for the four dependent variables. The phylogenetic MANOVA provides a measure of the mean difference between the two groups for the dependent variables, given the phylogenetic structure of the data. A phylogeny for pitheciines, *Aotus*, and *Callicebus* was downloaded from the 10kTrees website (Arnold et al., 2010) using the consensus phylogeny from the version 3 dataset. *P. monachus* and *Ch. albinasus* are not included in the current 10kTrees database. The divergence date for *P. pithecia*/*P. irrorata* was used as a proxy for *P. pithecia*/*P. monachus*; Hershkovitz (1987) considered *P. irrorata* and *P. monachus* to be more closely related to each other than either is to *P. pithecia*. The consensus tree from the 10kTrees analysis has a polytomy of *Ch. satanas*, *Cac. melanocephalus*, and *Cac. calvus*. *Ch. albinasus* was added as an additional species at this polytomy. To produce the fully resolved tree (Supporting Information Material) required by the statistical analysis, the groupings were then resolved along generic lines, with branch lengths of 0. Significance was assigned based on the simulations under a Brownian motion model (n simulations = 5,000) of trait values along the given phylogeny. As the P -value is based on a simulation and can differ slightly between iterations of analyses using the same data, it is possible that some simulations might produce a different result, depending on how much the probability estimate varies. Therefore, the phylogenetic MANOVA analysis was repeated 10 times, and the averaged phylogenetic P -value is reported below.

RESULTS

Results of the 36 genus-level pairwise comparisons are summarized in Table 4. As predicted, *Pithecia*, *Chiropotes*, and *Cacajao* all exhibit significantly low SRA, RFI, and DNE relative to *Callicebus* and *Aotus*. The pitheciines also exhibit greater OPCR with the exception of comparison 21, which yielded a nonsignificant result. Pitheciines exhibit similar mean values and distributions for SRA, RFI, and DNE (Table 5 and Fig. 3). There is no significant difference between *Pithecia* and *Chiropotes* for any of the shape variables examined, and *Pithecia* only differs from *Cacajao* by having significantly greater OPCR. Although no predictions concerning molar shape differences between *Chiropotes* and *Cacajao* were made, *Chiropotes* was also found to exhibit significantly greater OPCR.

Results of the PCA support the findings of the paired comparisons. Together, the first two principal compo-

nents explain just more than 85% of sample variation (Table 6). PC 1, which accounts for 65.7% of the sample variation, has greater contributions from SRA and DNE. Pitheciines differ from *Aotus* and *Callicebus* along this axis (Fig. 4). PC 2, which accounts for 19.7% of sample variance, is loaded mainly by OPCR and RFI. This axis mainly separates *Aotus* from *Callicebus*. *Cacajao* diverges from *Pithecia* and *Chiropotes* along both axes, particularly PC 2, consistent with their relatively low OPCR.

Results of the intrageneric species comparisons (Table 7) reveal that species within each genus examined have generally similar molar topographies; however, *Aotus azarae* was shown to exhibit greater RFI than *A. nigriceps*, *Callicebus torquatus* differed from *Cal. moloch* by having higher OPCR, and *Pithecia pithecia* had significantly higher OPCR than *P. monachus*.

Results of the individual species comparisons (Table 8) show that there are no significant differences between *Pithecia* spp. and *Chiropotes* spp. for any of the variables examined, despite the apparent interspecific variation in OPCR within *Pithecia*. With the exception of *Ch. satanas* having significantly higher DNE than *Cac. calvus*, *Cacajao* only differs from *Pithecia* spp. and *Chiropotes* spp. by having significantly low OPCR in both *Cac. calvus* and *Cac. melanocephalus*, supporting the findings of our intergeneric comparisons. However, one of these comparisons was only significant at $P = 0.05$.

The results of the phylogenetic MANOVA (Table 9) indicate that the differences between the six species of seed predators and five species of nonseed predators are not a product of their evolutionary history. The P -value assigned to this test statistic after the phylogenetic simulations is still significant at the 0.05 level. The range of values after 10 iterations was between 0.040 and 0.047, with an average phylogenetic P -value of 0.044. The Supporting Information Material provides the phylogeny used in cladogram and Nexus formats, and the R code for the analysis.

DISCUSSION

Topographic variation between- and within-pitheciine and outgroup genera

Our comparisons of topographic variables between the pitheciines and the "nonseed predating" outgroup (*Aotus* and *Callicebus*) yielded results broadly consistent with previous comparative analyses (Hershkovitz, 1985; Kay, 1990; Kinzey, 1992) and ecological studies (Mittermeier and van Roosmalen, 1981; van Roosmalen et al., 1988; Ayres, 1989; Kinzey and Norconk, 1993), documenting specialized seed predation in the pitheciine clade. These

TABLE 4. Results of pairwise comparisons^a

| No. | Comparison | Variable | Prediction | Result ^b |
|-----|------------------------------|----------|--|--|
| 1 | <i>Aotus/Pithecia</i> | DNE | <i>Aotus</i> > <i>Pithecia</i> | <i>Aotus</i> ($t = 4.96$; $P < 0.001$) |
| 2 | | RFI | <i>Aotus</i> > <i>Pithecia</i> | <i>Aotus</i> ($t = 6.53$; $P < 0.001$) |
| 3 | | SRA | <i>Aotus</i> > <i>Pithecia</i> | <i>Aotus</i> ($t = 10.23$; $P < 0.001$) |
| 4 | <i>Aotus/Chiropotes</i> | OPCR | <i>Pithecia</i> > <i>Aotus</i> | <i>Pithecia</i> ($t = -10.68$; $P < 0.001$) |
| 5 | | DNE | <i>Aotus</i> > <i>Chiropotes</i> | <i>Aotus</i> ($t = 2.65$; $P = 0.013$) |
| 6 | | RFI | <i>Aotus</i> > <i>Chiropotes</i> | <i>Aotus</i> ($t = 4.61$; $P < 0.001$) |
| 7 | <i>Aotus/Cacajao</i> | SRA | <i>Aotus</i> > <i>Chiropotes</i> | <i>Aotus</i> ($t = 8.26$; $P < 0.001$) |
| 8 | | OPCR | <i>Chiropotes</i> > <i>Aotus</i> | <i>Chiropotes</i> ($t = -13.38$; $P < 0.001$) |
| 9 | | DNE | <i>Aotus</i> > <i>Cacajao</i> | <i>Aotus</i> ($t = 3.64$; $P = 0.001$) |
| 10 | <i>Callicebus/Pithecia</i> | RFI | <i>Aotus</i> > <i>Cacajao</i> | <i>Aotus</i> ($t = 5.04$; $P < 0.001$) |
| 11 | | OPCR | <i>Cacajao</i> > <i>Aotus</i> | <i>Cacajao</i> ($t = -5.57$; $P < 0.001$) |
| 12 | | SRA | <i>Aotus</i> > <i>Cacajao</i> | <i>Aotus</i> ($t = 7.91$; $P < 0.001$) |
| 13 | <i>Callicebus/Chiropotes</i> | RFI | <i>Callicebus</i> > <i>Pithecia</i> | <i>Callicebus</i> ($t = 4.55$; $P < 0.001$) |
| 14 | | OPCR | <i>Pithecia</i> > <i>Callicebus</i> | <i>Pithecia</i> ($t = -5.11$; $P < 0.001$) |
| 15 | | DNE | <i>Callicebus</i> > <i>Pithecia</i> | <i>Callicebus</i> ($t = 6.86$; $P < 0.001$) |
| 16 | <i>Callicebus/Cacajao</i> | SRA | <i>Callicebus</i> > <i>Pithecia</i> | <i>Callicebus</i> ($t = 9.12$; $P < 0.001$) |
| 17 | | RFI | <i>Callicebus</i> > <i>Chiropotes</i> | <i>Callicebus</i> ($t = 3.07$; $P = 0.004$) |
| 18 | | DNE | <i>Callicebus</i> > <i>Chiropotes</i> | <i>Callicebus</i> ($t = 4.81$; $P < 0.001$) |
| 19 | <i>Callicebus/Cacajao</i> | OPCR | <i>Chiropotes</i> > <i>Callicebus</i> | <i>Chiropotes</i> ($t = -5.25$; $P < 0.001$) |
| 20 | | SRA | <i>Callicebus</i> > <i>Chiropotes</i> | <i>Callicebus</i> ($t = 7.35$; $P < 0.001$) |
| 21 | | OPCR | <i>Cacajao</i> > <i>Callicebus</i> | NS ($t = -1.69$; $P = 0.101$) |
| 22 | <i>Pithecia/Chiropotes</i> | RFI | <i>Callicebus</i> > <i>Cacajao</i> | <i>Callicebus</i> ($t = 3.44$; $P = 0.002$) |
| 23 | | DNE | <i>Callicebus</i> > <i>Cacajao</i> | <i>Callicebus</i> ($t = 5.46$; $P < 0.001$) |
| 24 | | SRA | <i>Callicebus</i> > <i>Cacajao</i> | <i>Callicebus</i> ($t = 6.85$; $P < 0.001$) |
| 25 | <i>Pithecia/Cacajao</i> | OPCR | <i>Pithecia</i> > <i>Chiropotes</i> | NS ($t = 0.08$; $P = 0.935$) |
| 26 | | SRA | <i>Pithecia</i> > <i>Chiropotes</i> ^c | NS ($t = -0.25$; $P = 0.803$) |
| 27 | | RFI | <i>Pithecia</i> > <i>Chiropotes</i> ^c | NS ($t = -1.34$; $P = 0.193$) |
| 28 | <i>Pithecia/Cacajao</i> | DNE | <i>Pithecia</i> > <i>Chiropotes</i> ^c | NS ($t = -1.7$; $P = 0.100$) |
| 29 | | DNE | <i>Pithecia</i> > <i>Cacajao</i> | NS ($t = -0.83$; $P = 0.413$) |
| 30 | | RFI | <i>Pithecia</i> > <i>Cacajao</i> | NS ($t = -1.01$; $P = 0.321$) |
| 31 | <i>Chiropotes/Cacajao</i> | SRA | <i>Pithecia</i> > <i>Cacajao</i> | NS ($t = -1.56$; $P = 0.130$) |
| 32 | | OPCR | <i>Pithecia</i> > <i>Cacajao</i> | <i>Pithecia</i> ($t = 5.35$; $P < 0.001$) |
| 33 | | RFI | No prediction made | NS ($t = 0.6$; $P = 0.557$) |
| 34 | | DNE | No prediction made | NS ($t = 0.81$; $P = 0.428$) |
| 35 | | SRA | No prediction made | NS ($t = -0.96$; $P = 0.347$) |
| 36 | | OPCR | No prediction made | <i>Chiropotes</i> ($t = 6.73$; $P < 0.001$) |

^a For each species comparison, rows are ordered from largest to smallest *P* value corresponding to the four corrected significance levels.

^b Taxon indicated in column has the significantly greater mean value for that particular measure following Holm–Bonferroni correction. If no taxon is listed, the results are not significant (NS).

^c Under the alternative hypothesis (Hypothesis 2b), *Chiropotes* > *Pithecia*.

TABLE 5. Descriptive statistics for SRA, RFI, DNE, and OPCR in our sample of pitheciine and nonseed predating taxa

| | <i>Aotus</i> | <i>Callicebus</i> | <i>Pithecia</i> | <i>Chiropotes</i> | <i>Cacajao</i> |
|-------------|-----------------|-------------------|-----------------|-------------------|-----------------|
| SRA | | | | | |
| <i>x</i> | 2.874 | 2.768 | 2.338 | 2.349 | 2.395 |
| <i>R</i> | 2.606–3.262 | 2.484–3.199 | 2.133–2.474 | 2.147–2.560 | 2.244–2.574 |
| SD | 0.191 | 0.172 | 0.090 | 0.132 | 0.103 |
| RFI | | | | | |
| <i>x</i> | 1.799 | 1.781 | 1.715 | 1.730 | 1.722 |
| <i>R</i> | 1.718–1.891 | 1.688–1.903 | 1.668–1.756 | 1.673–1.777 | 1.675–1.772 |
| SD | 0.044 | 0.052 | 0.025 | 0.033 | 0.032 |
| DNE | | | | | |
| <i>x</i> | 136.988 | 156.526 | 118.142 | 126.038 | 121.980 |
| <i>R</i> | 112.837–155.671 | 120.156–202.153 | 99.337–134.153 | 109.451–148.127 | 105.710–145.170 |
| SD | 10.212 | 19.878 | 11.961 | 12.360 | 12.247 |
| OPCR | | | | | |
| <i>x</i> | 48.326 | 59.544 | 71.555 | 71.307 | 55.975 |
| <i>R</i> | 42.750–54.250 | 47.500–68.750 | 56.500–86.000 | 57.500–81.375 | 47.500–60.750 |
| SD | 3.177 | 6.111 | 8.601 | 6.098 | 3.993 |

^a *x*, mean; *R*, range; SD, standard deviation.

results support our predictions from Hypothesis 1. Unlike in *Callicebus* and *Aotus*, pitheciine molars exhibit low shearing potential (SRA), cusp relief (RFI), occlusal surface curvature (DNE), and high occlusal complexity

(OPCR), consistent with a specialization for the mastication of tough and crushing-resistant seeds. Of the 24 pairwise comparisons, 23 yielded significant differences. The differences between seed predators and nonseed pre-

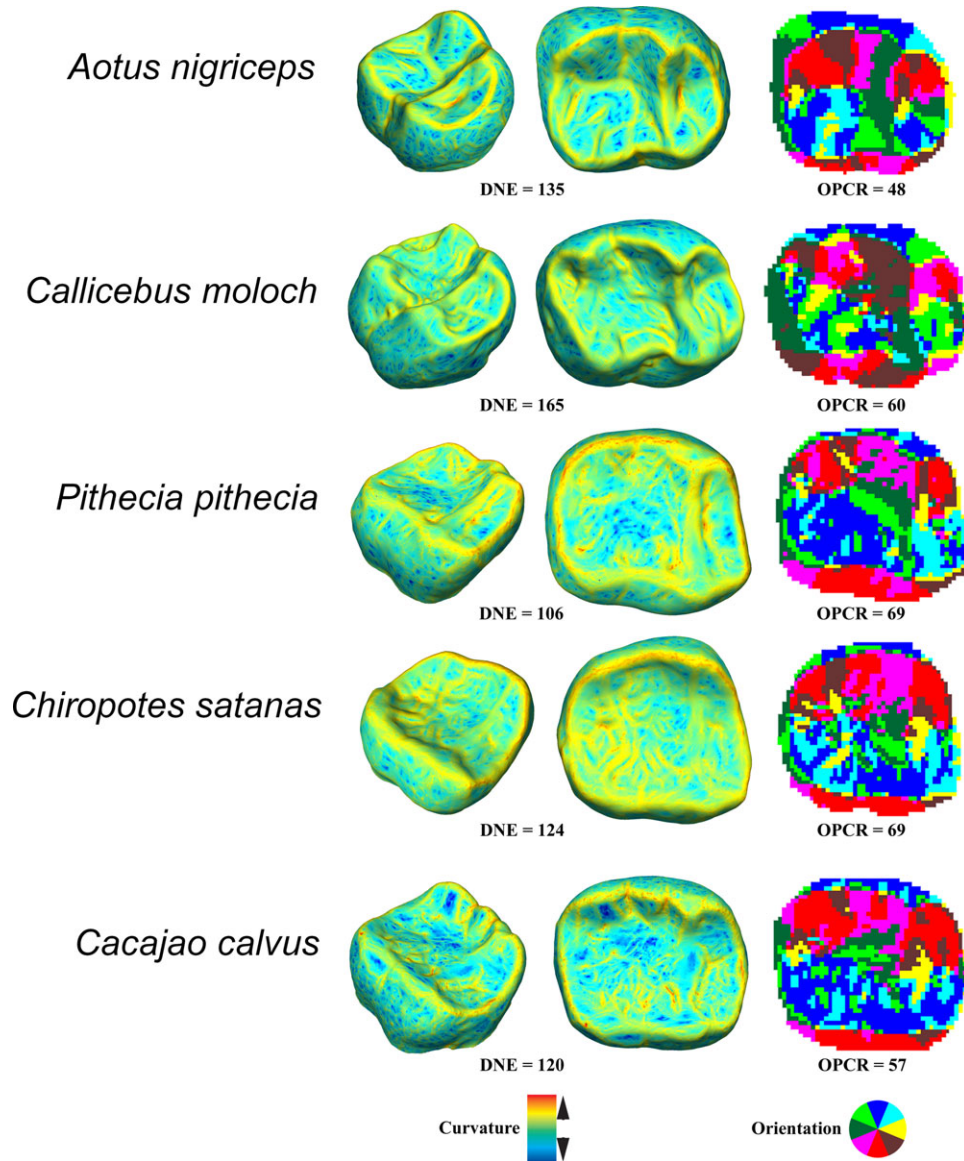


Fig. 2. OPCR complexity map and distribution of DNE in examples of pitheciine and nonseed predator second mandibular molars. For OPCR, a topographic map of a tooth's functional surface is first divided into a series of grid points. Contiguous grid points that share one of the eight compass directions are grouped into patches and counted. For DNE, warmer colors represent high curvatures, and cooler colors represent lower curvature. The DNE value for each represents the average energy of the entire surface of the tooth. For further details, see text.

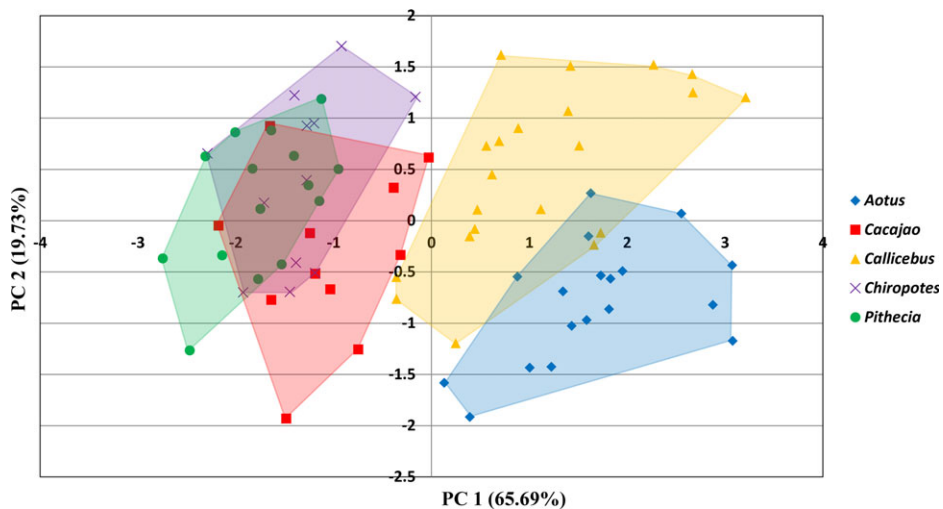


Fig. 4. Scatter plot of the first two principal components. *Aotus*, blue diamond; *Cacajao*, red square; *Callicebus*, orange triangle; *Chiropotes*, purple cross; and *Pithecia*, green circle.

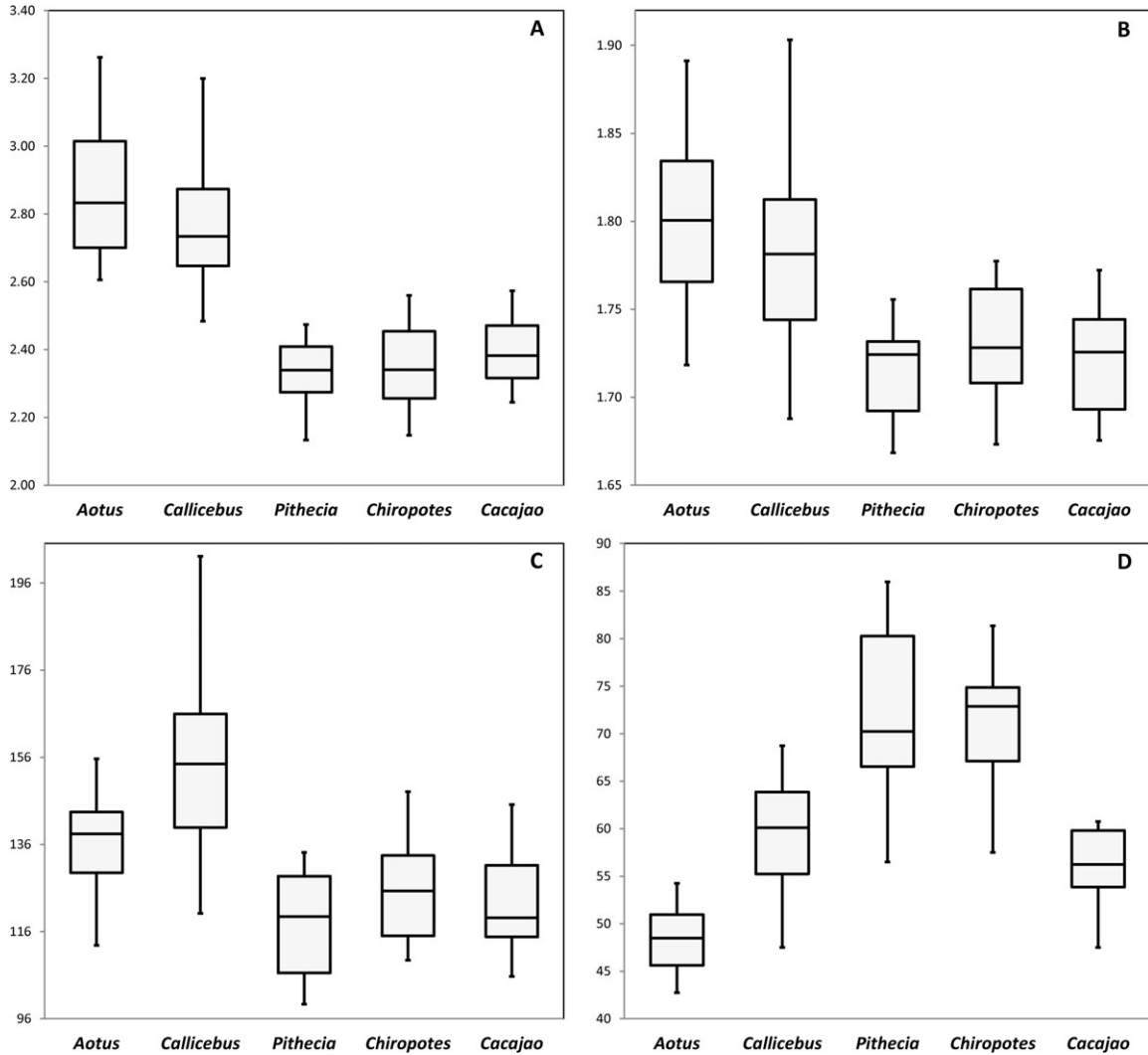


Fig. 3. Box-and-whisker plots showing the sample minimum, first quartile, median, third quartile, and maximum in each taxon examined in this study for (A) SRA, a measure of relative shearing crest length; (B) RFI, a measure of relative occlusal surface area; (C) DNE, a measure of overall occlusal surface curvature; and (D) OPCR, a measure of occlusal surface “complexity.”

TABLE 6. Results of principal components analysis^a

| Component | Eigenvalue | % Variance | Principal component coefficients | | | |
|-----------|------------|------------|----------------------------------|---------|---------|---------|
| | | | SRA | RFI | DNE | OPCR |
| 1 | 2.627650 | 65.6910 | 0.5692 | 0.4642 | 0.5238 | -0.4315 |
| 2 | 0.789164 | 19.7290 | -0.1425 | 0.5870 | 0.2563 | 0.7546 |
| 3 | 0.381572 | 9.5393 | 0.0505 | -0.6374 | 0.7238 | 0.2595 |
| 4 | 0.201616 | 5.0404 | 0.8082 | -0.1836 | -0.3690 | 0.4208 |

^a The first two components explain 85% of the sample variance.

dating frugivores were found to be significant in the phylogenetic MANOVA, which indicates that the results are not simply reflecting the phylogenetic structure of the species sample. This is further supported by the similarity in molar shape between *Aotus* and *Callicebus* despite the close evolutionary relationship between the *Callicebus* and the pitheciine clade (von Dorum and Ruvolo, 1999).

Low SRA, RFI, and DNE in pitheciine molars are a reflection of their almost featureless and low-crowned occlusal topography. Low relief is generally thought to

reflect a diet that includes “hard” objects, including seeds and nuts (e.g., Lucas, 2004; Ungar, 2004). However, for pitheciines, it appears to be an adaptation to their tendency to grind tough seeds with high resistance to crushing (Kinzey, 1992).

Teeth with complex occlusal surfaces (i.e., high OPCR) are adapted to cope with tough foods high in dietary fiber (Evans et al., 2007; Boyer et al., 2010). For most primate species, such diets are characteristic of highly folivorous and herbivorous taxa (e.g., *Hapalemur*; Tan, 1999). However, high OPCR in pitheciines is a reflection

TABLE 7. Results of intrageneric comparisons^a

| Comparison | SRA | RFI | DNE | OPCR |
|---|----------------------------------|---|----------------------------------|--|
| Nonseed predators | | | | |
| <i>A. azarae/A. nigriceps</i> | NS ($U = 19$; $P = 0.382$) | <i>A. azarae</i> ($U = 3$; $P = 0.0005$) | NS ($U = 24$; $P = 0.721$) | NS ($U = 24$; $P = 0.721$) |
| <i>Cal. donacophilus/Cal. moloch</i> | NS ($U = 13$; $P = 0.504$) | NS ($U = 13$; $P = 0.504$) | NS ($U = 4$; $P = 0.1$) | NS ($U = 13$; $P = 0.478$) |
| <i>Cal. donacophilus/Cal. torquatus</i> | NS ($U = 14$; $P = 0.454$) | NS ($U = 9$; $P = 0.199$) | NS ($U = 10$; $P = 0.469$) | NS ($U = 10$; $P = 0.189$) |
| <i>Cal. moloch/Cal. torquatus</i> | NS ($U = 39$; $P = 0.661$) | NS ($U = 9$; $P = 0.73$) | NS ($U = 24$; $P = 0.095$) | <i>Cal. torquatus</i> ($U = 10.5$; $P = 0.003$) |
| Pitheciines | | | | |
| <i>P. monachus/P. pithecia</i> | NS ($U = 13$; $P = 0.055$) | NS ($U = 24$; $P = 0.694$) | NS ($U = 25$; $P = 0.536$) | <i>P. pithecia</i> ($U = 8$; $P = 0.012$) |
| <i>Ch. albinasus/Ch. satanas</i> | NS ($U = 13$; $P = 0.485$) | NS ($U = 14$; $P = 0.589$) | NS ($U = 9$; $P = 0.178$) | NS ($U = 14$; $P = 0.892$) |
| <i>Cac. calvus/Cac. melanocephalus</i> | NS ($U = 13$; $P = 0.623$) | NS ($U = 10$; $P = 0.527$) | NS ($U = 14$; $P = 0.808$) | NS ($U = 8$; $P = 0.667$) |

^a Comparisons that yielded a significant difference are indicated by bold typeface, with the taxon listed having the relatively greater mean value for that particular measure following Holm–Bonferroni correction.

TABLE 8. Results of pitheciine interspecific comparisons^a

| Comparison | SRA | RFI | DNE | OPCR |
|--|----------------------------------|----------------------------------|---|--|
| <i>P. monachus/Ch. albinasus</i> | NS ($U = 18$; $P = 0.327$) | NS ($U = 23$; $P = 0.95$) | NS ($U = 24$; $P = 0.776$) | NS ($U = 16$; $P = 0.212$) |
| <i>P. monachus/Ch. satanas</i> | NS ($U = 25$; $P = 0.863$) | NS ($U = 14$; $P = 0.228$) | NS ($U = 21$; $P = 0.529$) | NS ($U = 8.5$; $P = 0.065$) |
| <i>P. monachus/Cac. calvus</i> | NS ($U = 17$; $P = 0.074$) | NS ($U = 26$; $P = 0.867$) | NS ($U = 27$; $P = 0.423$) | <i>P. monachus</i> ($U = 5$; $P = 0.003$)** |
| <i>P. monachus/Cac. melanocephalus</i> | NS ($U = 7$; $P = 0.105$) | NS ($U = 9$; $P = 0.283$) | NS ($U = 12$; $P = 0.414$) | <i>P. monachus</i> ($U = 2$; $P = 0.036$)* |
| <i>P. pithecia/Ch. albinasus</i> | NS ($U = 20$; $P = 0.945$) | NS ($U = 20$; $P = 0.945$) | NS ($U = 13$; $P = 0.295$) | NS ($U = 9$; $P = 0.093$) |
| <i>P. pithecia/Ch. satanas</i> | NS ($U = 14$; $P = 0.366$) | NS ($U = 8$; $P = 0.073$) | NS ($U = 8$; $P = 0.073$) | NS ($U = 6$; $P = 0.073$) |
| <i>P. pithecia/Cac. calvus</i> | NS ($U = 25$; $P = 0.779$) | NS ($U = 23$; $P = 0.902$) | NS ($U = 20$; $P = 0.396$) | <i>P. pithecia</i> ($U = 0$; $P < 0.001$)** |
| <i>P. pithecia/Cac. melanocephalus</i> | NS ($U = 8$; $P = 0.315$) | NS ($U = 9$; $P = 0.412$) | NS ($U = 6$; $P = 0.164$) | <i>P. pithecia</i> ($U = 0$; $P = 0.017$)** |
| <i>Ch. albinasus/Cac. calvus</i> | NS ($U = 20$; $P = 0.662$) | NS ($U = 20$; $P = 0.945$) | NS ($U = 20$; $P = 0.662$) | <i>Ch. albinasus</i> ($U = 2$; $P = 0.005$)** |
| <i>Ch. albinasus/Cac. melanocephalus</i> | NS ($U = 10$; $P = 0.762$) | NS ($U = 10$; $P = 0.762$) | NS ($U = 8$; $P = 0.476$) | <i>Ch. albinasus</i> ($U = 1$; $P = 0.048$)** |
| <i>Ch. satanas/Cac. calvus</i> | NS ($U = 15$; $P = 0.282$) | NS ($U = 10$; $P = 0.138$) | <i>Ch. satanas</i> ($U = 6$; $P = 0.02$)** | <i>Ch. satanas</i> ($U = 0$; $P = 0.003$)** |
| <i>Ch. satanas/Cac. melanocephalus</i> | NS ($U = 8$; $P = 0.476$) | NS ($U = 12$; $P = 1$) | NS ($U = 9$; $P = 0.61$) | <i>Ch. satanas</i> ($U = 0$; $P = 0.036$)** |

^a Comparisons that yielded a significant difference are indicated by bold typeface, with the taxon listed having the relatively greater mean value for that particular measure.

* Significant at $P = 0.05$.

** Significant following Holm–Bonferroni correction.

of their crenulated occlusal surfaces that aid the breakdown of fibrous seed material. Crenulated enamel may improve the extent to which teeth can fracture tough foods (Lucas and Luke, 1984; Vogel et al., 2008), and they may help position seeds along the tooth row (Lucas and Teaford, 1994). Leaves and other tough foods in the diets of folivorous primate species are typically broken down through an increase in molar crest length and occlusal surface relief (Kay, 1975, 1978; Anthony and Kay, 1993; Ungar and Williamson, 2000). However, high relief in pitheciines could potentially interfere with transverse grinding of seed particles through the interlocking of steep molar cusps, and might increase the risk of tooth crown fracture during the forceful biting of crushing-resistant seed tissues (Lawn and Lee, 2009; Berthaume

et al., 2010). Pitheciine molars, characterized by their complex occlusal topography and low grinding surfaces, therefore appear ideally suited for a specialized diet that includes both tough and crushing-resistant foods (Kinzey, 1992).

As demonstrated by Bunn et al. (2011), OPCR may not have the resolution to distinguish between dietary categories such as folivory and insectivory, but it is a useful indicator of toughness in the diet (Evans et al., 2007). Bunn et al. (2011) find that *Hapalemur simus*, with an OPCR range of 63–84, has the highest occlusal complexity in their sample. Notably, the diet of *Hapalemur* includes incredibly tough and fibrous bamboo (Tan, 1998). Yamashita et al. (2009) show that *H. simus* consumes the outer culm of giant bamboo with toughness

TABLE 9. Results of the phylogenetic MANOVA used to compare the significance of differences between pitheciine species and five species of nonseed predators for the four dependent variables^a

| Wilks' λ | df | Approx. F | Pr > F | |
|------------------|------|-------------|--------------|------------------|
| | | | Standard P | Phylogenetic P |
| 0.023065 | 4, 6 | 63.533 | 0.000048 | 0.044 |

^a The significance level in this test is assessed relative to a set of simulations of the data along the phylogeny. This allows the observed level of difference to be judged as significant or not compared to the level of difference that would be expected given the phylogenetic structure of the data.

values approaching 20,000 J m⁻². *Pithecia* and *Chiropotes* both have OPCR ranges similar to those demonstrated for *Haplemur* (Table 5), suggesting that their diets also include exceedingly tough foods.

The only comparison between the pitheciines and the nonseed predators that failed to conform to prediction was comparison 21 (Table 4). Here, *Cacajao* was predicted to exhibit greater OPCR than *Callicebus*, but there was no significant difference. In fact, Table 5 summarizes that *Callicebus* exhibits a greater mean OPCR (59.54) than *Cacajao* (55.98). One possible explanation for this is that the semi-granivorous *Callicebus* requires a slightly more "complex" occlusal surface when compared with other ripe fruit feeding taxa, such as *Aotus*. Although *Callicebus* is not a traditional "seed predator," some species are known to include a high proportion of seeds in their diet (Müller 1996; Palacios et al., 1997). Palacios et al. (1997) note that *Cal. torquatus*, with 27% seeds consumed during the periods of resource scarcity, should be classified as a "frugivore-granivore" and a potential competitor of *Cacajao* at Estación Biológica Caparú where their distributions overlap. Among the three *Callicebus* species we examine, *Cal. torquatus* was found to have the greatest average OPCR (63.3) compared with *Cal. donacophilus* (59.3) and *Cal. moloch* (55.4), and this difference is significant for *Cal. moloch* (Table 7). This result might also be a reflection of the greater proportion of leaf material or insect prey in the diet of *Cal. torquatus* (Table 1). However, Bunn et al. (2011) show that OPCR might not be reliable at distinguishing between folivory and insectivory in primates.

In addition to the intragenetic variation in OPCR observed between *Callicebus* species, *A. azarae* was found to have significantly greater RFI than *A. nigriceps*, which might correspond to its proportionately higher leaf intake (Table 1). The intragenetic comparisons also reveal that *P. pithecia* differs from *P. monachus* by having significantly higher OPCR. This could also reflect a greater reliance on leaf material in *P. pithecia*, as a result of the increased competition with sympatric *Ch. satanas* in Suriname (Kinzey and Norconk, 1993) not likely to be experienced by *P. monachus* in the western Amazon Basin (Norconk, 2007). Nonetheless, *P. pithecia* did not differ from *Chiropotes* spp. for any of the topographic variables we examine in this study (see below).

Pitheciine genus-level and interspecific comparisons

We tested two sets of functional hypotheses (Hypotheses 2a and 2b) based on different forms of data that predict differences in molar form between *Pithecia* and

Chiropotes, and neither hypothesis was supported. Based on the observation that *Pithecia* includes a greater proportion of leaves in its diet, Hypothesis 2a predicts relatively greater SRA, RFI, DNE, and OPCR in *Pithecia* relative to *Chiropotes* and *Cacajao*. Based on the observation that *Pithecia* masticates seeds with greater crushing resistance than those preferred by *Chiropotes* (Kinzey and Norconk, 1990, 1993), our alternative hypothesis (Hypothesis 2b) predicts that *Pithecia* would exhibit short shearing crests, low relief, low surface energy, and high OPCR relative to *Chiropotes*. Contrary to both sets of predictions, *Pithecia*, *Chiropotes*, and *Cacajao* share a similar topographic pattern, suggesting adaptation to foods with similar fracture mechanics.

These findings do not support previous qualitative studies that report greater occlusal relief in *Pithecia* relative to other pitheciines (Kinzey, 1992), nor do they support previous quantitative analyses that report longer shearing crest length in *Pithecia* relative to *Chiropotes*. Our results are also not consistent with data on folivory (Table 1) or the structural properties of seeds in the diets of *Pithecia* and *Chiropotes* (Kinzey and Norconk, 1993; Norconk and Veres, 2011). Overall, the molars of pitheciine taxa appear adapted to cope with foods with similar structural and/or mechanical properties. All three pitheciine taxa have similarly low SRA, RFI, and DNE. However, *Cacajao* exhibits significantly lower OPCR than other pitheciines, which suggests a less fibrous dietary intake relative to other pitheciine species. Additionally, *Cac. calvus* was found to have significantly lower DNE than *Ch. satanas*. The morphological divergence of *Cacajao* from *Pithecia* and *Chiropotes* is also demonstrated by the PCA.

The mechanical properties of foods eaten by *Cacajao* spp. have yet to be formally investigated, and low surface complexity in this taxon relative to *Pithecia* and *Chiropotes* is difficult to interpret. It is possible that decreased sympatry between *Cacajao* and the sakis has led to relaxed competition over preferred foods (Ayres, 1989). For instance, Norconk and Conklin-Brittain (2004) show that *Pithecia* increases its intake of dietary fiber during the early dry season by increasing its predation on the mature seeds of *Licania discolor* and *Ouratea roraimae*. This dietary shift might be the result of direct competition with sympatric *Chiropotes* (Kinzey and Norconk, 1993). The relaxed level of dietary resource competition faced by *Cacajao* spp. therefore might allow them to procure more preferred foods, including soft fruits and seeds with low fracture toughness. Indeed, some research suggests that *Cacajao* occupies a nearly competition-free dietary niche (Kinzey, 1992; Barnett and Brandon-Jones, 1997), and although several studies demonstrate the importance of hard fruits to the diet of *Cacajao* (e.g., Ayres, 1986, 1989), some recent work suggests that *Cacajao* spp. might not rely on these resources to the extent previously thought (Barnett and de Castilho, 2000; Barnett et al., 2005).

A second, nonmutually exclusive possibility is that low OPCR in *Cacajao* is explained by differences in folivory. Table 1 summarizes that leaf material can make up around 18% of the *Pithecia* diet. Leaves might form 16% of the *Chiropotes* diet in some species (although this includes bark and stems; see Ayres, 1981), but these resources are generally exploited less frequently than in *Pithecia*. On the other hand, *Cacajao* is almost exclusively frugivorous-granivorous, with a mere 4% leaves recorded in one recent study (Boubli, 1999). More data

on the fracture properties of *Cacajao* foods, as well as foods of other primate species, are required to better understand the relationship between diet and dental complexity in the pitheciine clade.

Our results conflict with previous analyses of pitheciine molar shape. For example, *Pithecia* is typically cited to exhibit the greatest molar relief of the pitheciine clade (Kinzey, 1992). Moreover, Anthony and Kay (1993) report a higher shearing quotient for *P. monachus* than *Ch. satanas* although this was not tested for a statistical difference. Shearing quotients are highly sample-dependent as the results per sample require an allometry correction created from the sample itself, whereas calculation of the SRA requires no allometry correction and is thus not sample-dependent. There are also some additional reasons to suspect that Anthony and Kay's (1993) results might not be directly comparable to those presented here. First, the Anthony and Kay (1993) study calculates shearing quotients using mesiodistal molar length. Our quantification of shearing potential, the SRA, scales total crest length by the square root of occlusal area (Strait, 1991). In addition, Anthony and Kay's (1993) sample includes only *P. monachus* and *Ch. satanas*, whereas our sample includes two species per genus. Nonetheless, our data reveal no significant difference in SRA between *Pithecia* and *Chiropotes* when focusing our comparison on these species alone (Table 8).

If *Pithecia* is reported to consume proportionally more leaves than other pitheciine genera, why do its postcanine teeth not exhibit morphology consistent with such behavior? Although pitheciine molar topographies are generally similar across species, postcanine teeth are large for body size in *Pithecia* (Anapol and Lee, 1994; Ledogar, 2009; Norconk et al., 2009). Previous work demonstrates that relative molar size is greater in folivores compared with more frugivorous taxa (Kay, 1975; Lucas et al., 1986; Anthony and Kay, 1993). This increases the surface over which leaf material can be broken down, and prolongs the life of the tooth in animals that chew more frequently and wear their teeth faster. Along these lines, Anapol and Lee (1993) interpret broad occlusal surfaces in *Pithecia* as an adaptation for increased folivory, or possibly as being related to increased seed predation. Our results support the former interpretation, and suggest that increased molar occlusal area in *Pithecia* relative to the other pitheciines can be explained by its more folivorous dietary intake.

With respect to Hypothesis 2b, if seeds in the diet of *Pithecia* exhibit higher crushing resistance than seeds preferred by *Chiropotes*, why do the molars of *Pithecia* not appear more adapted to seed crushing and grinding? It is possible that the mechanical properties of the foods *Pithecia* species rely on during resource scarcity impose functional demands on the postcanine teeth that select for opposing but similarly important morphologies. As discussed above, *Pithecia* increases its reliance on both tough foods (leaves and seeds) and crushing-resistant foods (seeds) during periods of low fruit abundance, whereas *Chiropotes* focuses to a greater extent on fruits with hard pericarps that require more anterior tooth processing (Kinzey, 1992; Kinzey and Norconk, 1993). Although there are differences in overall tooth size, which might correspond to variation in leaf consumption, the range of demands imposed on the postcanine teeth of *Pithecia* may therefore select for an average topography, one that converges on that of *Chiropotes*.

New research on primate feeding is exploring the relationship between various food structural/mechanical properties and their ecological significance (e.g., Lambert et al., 2004; Wright, 2004, 2005; Dominy et al., 2008; Vogel et al., 2008; Norconk et al., 2009). Norconk and colleagues (Kinzey and Norconk, 1990, 1993; Norconk and Veres, 2011) quantify fruit and seeds eaten by *Pithecia* and *Chiropotes* in terms of their puncture and crushing resistance (i.e., structural properties). These variables have been described as being mechanical properties (Lambert et al., 2004; Wiczowski, 2009), but this is not strictly accurate. Lucas (2004) notes that the mechanical properties E (Young's modulus, a measure of material stiffness) and R (fracture toughness, a measure of resistance to fracture propagation) more accurately describe a food's resistance to fragmentation (in an engineering sense) during ingestion and mastication, and may have more of a direct influence on the evolution of dental form. Nonetheless, variation in tissue puncture and crushing resistance is associated with differences in foraging and feeding behaviors in these monkeys. It is therefore a pertinent question as to whether E and R explain niche partitioning in these genera equally well.

CONCLUSIONS

Compared with *Callicebus* and *Aotus*, two taxa that do not regularly masticate seeds, our results show that pitheciines (*Pithecia*, *Chiropotes*, and *Cacajao*) exhibit significantly low molar shearing potential, occlusal surface relief, and overall surface curvature. These findings concur with previous comparative analyses, and support the hypothesis that pitheciine molars are adapted to a specialized diet of unripe seeds that are both tough and crushing-resistant (Kinzey, 1992). Pitheciine molars were also found to have highly "complex" occlusal surface topography. This complexity is a reflection of extensive enamel surface crenulations that promote efficient breakdown of tough seed particles without compromising grinding ability through the interlocking of molar cusps. However, *Cal. torquatus* also has a complex occlusal surface, which might be related to the semi-granivorous nature of its diet. Our results further demonstrate that differences in molar topography between pitheciines and New World primate taxa that do not specialize on seed predation appear to be related to differences in dietary ecology rather than being the result of their evolutionary history.

Although *Cacajao* exhibits a less complex occlusal surface compared with *Pithecia* and *Chiropotes*, which could reflect some difference in the fracture properties of seeds in the *Cacajao* diet and/or their decreased reliance on leaf material compared with other pitheciines, our results show that the molars of *Pithecia*, *Chiropotes*, and *Cacajao* exhibit a broadly similar topographic pattern, which suggests that this clade is adapted to cope with foods that exhibit similar structural and/or mechanical properties.

The results of our pitheciine comparisons fail to provide evidence of either adaptation to increased leaf intake, or to mastication of seeds with greater crushing resistance in *Pithecia*. This could be an indication that the broad range of functional demands imposed by the *Pithecia* diet selects for an average occlusal topography that converges on that of *Chiropotes*. Enlarged postcanine teeth for body size in *Pithecia* might also compensate for its increased reliance on leaves compared with *Chiropotes* and *Cacajao*. This has implications for die-

tary reconstruction in fossil specimens only represented by isolated teeth.

The postcanine teeth of fossil pitheciines have yet to be examined using dental topographic techniques, and hence it is not entirely clear what similarities and differences they would share with extant species. Seed predation in pitheciines is thought to have evolved sometime during the early Miocene (Rosenberger, 1992). However, anterior tooth specialization related to the opening of hard fruits is thought to have preceded the emergence of postcanine modifications related to seed feeding behavior (Kinzey, 1992; Rosenberger, 1992), and this is supported by the fossil record. Several fossil pitheciine species, including *Cebupithecia sarmientoi* (Orlosky, 1973), *Nuciraptor rubricae* (Meldrum and Kay, 1997), and *Propithecia neuquenensis* (Kay et al., 1998) all exhibit canine and incisor form consistent with hard fruit feeding, yet the evidence for seed predation in these taxa is less compelling. Future studies investigating dental topography in these fossil specimens will shed new light on the evolution of pitheciine feeding behavior.

Mechanical testing on a broader range of foods and across a greater number of primate species, as well as more detailed examination of the relationship between diet and dental form in living taxa can also enhance our ability to reconstruct the dietary ecology of fossil species. For example, as we demonstrate for pitheciines, dental complexity is also high among some late Paleocene to early Eocene plesiadapids (Boyer et al., 2010), supporting the hypothesis that tough foods were an important component of their diets (Gingerich, 1976).

ACKNOWLEDGMENTS

Access to specimens in museum collections was made possible by E. Westwig and D. Lunde at the AMNH, J. Chupasko at the MCZ (Harvard), and L. Gordon at the Smithsonian Institution. Additional facilities and assistance were provided by D. Krause and J. Groenke (Stony Brook University Vertebrate Paleontology Fossil Preparation Laboratory), D. Strait (University at Albany, Human Paleobiology Lab), and C. Rubin, S. Judex and S. Tommasini (Stony Brook University, Center for Biotechnology). The authors thank the AnthroTree Workshop for training in phylogenetic comparative methods. Finally, the authors thank the three anonymous reviewers for their helpful comments and critique on an earlier draft of this paper.

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