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 pred- ators 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.


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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 Callirhinchus as the most basal member of the pitheciine clade (von Dorn and Ruvolo, 1999). However, we reserve the subfamily Callirhinchinae 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-fruit 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, 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 triturating 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 Calliebus spp.a

<table>
<thead>
<tr>
<th>Species</th>
<th>% Seeds</th>
<th>% Pericarp</th>
<th>% Flowers</th>
<th>% Leaves</th>
<th>% Insects</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. azarae</td>
<td>–</td>
<td>16</td>
<td>33</td>
<td>40</td>
<td>–</td>
<td>Wright (1986)</td>
</tr>
<tr>
<td>A. azarae</td>
<td>–</td>
<td>45</td>
<td>14</td>
<td>41</td>
<td>–</td>
<td>Arditi (1992)</td>
</tr>
<tr>
<td>A. nigriceps</td>
<td>–</td>
<td>60</td>
<td>–</td>
<td>–</td>
<td>0.4</td>
<td>Solano (1995)</td>
</tr>
<tr>
<td>Cal. brunneus</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>(23–66)</td>
<td>–</td>
<td>Wright (1986)</td>
</tr>
<tr>
<td>Cal. personatus</td>
<td>21.9</td>
<td>54.7</td>
<td>–</td>
<td>17.2</td>
<td>–</td>
<td>Muller (1996)</td>
</tr>
<tr>
<td>Cal. personatus</td>
<td>–</td>
<td>81</td>
<td>1</td>
<td>18</td>
<td>–</td>
<td>Kinzey and Becker (1983)</td>
</tr>
<tr>
<td>Cal. torquatus</td>
<td>26.9</td>
<td>59.4</td>
<td>3.9</td>
<td>6.4</td>
<td>3.4</td>
<td>Palacios et al. (1997)</td>
</tr>
<tr>
<td>P. albicans</td>
<td>46.2</td>
<td>28.6</td>
<td>6.5</td>
<td>9.5</td>
<td>0.4</td>
<td>Peres (1993)</td>
</tr>
<tr>
<td>P. monachus</td>
<td>38</td>
<td>55</td>
<td>3</td>
<td>4</td>
<td>–</td>
<td>Soini (1986)</td>
</tr>
<tr>
<td>P. pithecia</td>
<td>(26–31)</td>
<td>15.9</td>
<td>(4–18.4)</td>
<td>–</td>
<td>–</td>
<td>Setz (1993)</td>
</tr>
<tr>
<td>P. pithecia</td>
<td>53.3</td>
<td>31</td>
<td>2</td>
<td>10.4</td>
<td>3.7</td>
<td>Homburg (1997)</td>
</tr>
<tr>
<td>P. pithecia</td>
<td>60.6</td>
<td>27.8</td>
<td>2.2</td>
<td>7.1</td>
<td>2.3</td>
<td>Kinzey and Norconk (1993); Norconk (1996)</td>
</tr>
<tr>
<td>Ch. albinasus</td>
<td>35.9</td>
<td>53.9</td>
<td>3</td>
<td>7.2</td>
<td>–</td>
<td>Ayres (1981, 1989, 1991)</td>
</tr>
<tr>
<td>Ch. satanas</td>
<td>63.3</td>
<td>9.3</td>
<td>11.4</td>
<td>(16.1)</td>
<td>–</td>
<td>Ayres (1981)</td>
</tr>
<tr>
<td>Ch. satanas</td>
<td>66.4</td>
<td>27.6</td>
<td>4.6</td>
<td>–</td>
<td>–</td>
<td>van Roosmalen et al. (1981)</td>
</tr>
<tr>
<td>Ch. satanas</td>
<td>50.7</td>
<td>(4–60)</td>
<td>(0–32)</td>
<td>(0–8.1)</td>
<td>(0–1.5)</td>
<td>(1–21) Peetz (2001)</td>
</tr>
<tr>
<td>Ch. satanas</td>
<td>74.8</td>
<td>21.6</td>
<td>0.4</td>
<td>0.2</td>
<td>0.5</td>
<td>Kinzey and Norconk (1993); Norconk (1996)</td>
</tr>
<tr>
<td>Cal. calvus</td>
<td>66.9</td>
<td>18.4</td>
<td>–</td>
<td>3.3</td>
<td>5.2</td>
<td>Ayres (1989)</td>
</tr>
<tr>
<td>Cal. calvus</td>
<td>46</td>
<td>50</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>Aquino and Encarnacion (1999)</td>
</tr>
<tr>
<td>Cal. melanocephalus</td>
<td>67</td>
<td>28.8</td>
<td>5</td>
<td>4</td>
<td>2</td>
<td>Boulli (1999)</td>
</tr>
</tbody>
</table>

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).

Pithecia 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 (Kaminski 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 macerate 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; Boulli, 1999, 1997; 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 American Journal of Physical Anthropology
mandibular molar topography within this specialized clade of seed predators. Pithecine molar form is interpreted relative to two Neotropical primate frugivores that do not occupy a specialized seed-feeding niche: Callithrix and Aotus. Recent molecular phylogenies identify Callithrix 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 closest 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 Callithrix are found to be relatively similar.

Table 1 provides an overview of dietary ecology in Aotus spp., Callithrix spp., Pithecia spp., Chiroptes spp., and Cacajao spp. Fleshy fruit surface energy (DNE) and orientation patch count rotated (OPCR) in Pithecia, Chiroptes, and Cacajao, as well as in Callithrix 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, 1985; Kay and Hylander, 1978; Kay and Covert, 1985; Kay and Hylander, 1978; Kay and Covert, 1985; Kay and Hylander, 1978; Kay and Covert, 1985). 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 surface 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 platyrhines (Boyer et al., 2011).

We test the hypothesis (Hypothesis 1) that, relative to Aotus and Callithrix, the three pithecine taxa will exhibit molar adaptations for seed feeding, with the prediction that Pithecia, Chiroptes, 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 Chiroptes and Cacajao (Arens, 1989; Kinzey and Norconk, 1992; Kinzey and Norconk, 1996), 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 Chiroptes (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 Chiroptes” (509). Under Hypothesis 2b, Pithecia is predicted to have significantly lower SRA, RFI, and DNE relative to Chiroptes. As grinding of seed particles is central to this alternative hypothesis, it also predicts higher OPCR in Pithecia relative to Chiroptes.

There are limited data on the fracture mechanics of Cacajao foods, and although these data showing decreased reliance on leaf material in Cacajao relative to Chiroptes, functional differences in dental anatomy between these taxa should await further study of Cacajao feeding ecology. However, comparisons for each variable are made between Chiroptes 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). 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 roots, and mounted on 35-µm platforms for efficient µCT scanning. A ScancoMedical brand µCT 40 machine (www.scanco.ch) was used to capture tooth surface data at 18-µm 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 M3 contacts the M2 (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–Wilks 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; Boublí 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
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 Cal. 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 other than either is to P. pithecia. The consensus tree from the 10kTrees analysis has a polytomy of Ch. satanas, Cac. melanocephalus, and Cal. 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 (5,000 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 components 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. nigripes, 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 C. 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


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-

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

<table>
<thead>
<tr>
<th>No.</th>
<th>Comparison</th>
<th>Variable</th>
<th>Aotus</th>
<th>Callicebus</th>
<th>Pithecia</th>
<th>Chiropotes</th>
<th>Cacajao</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Aotus/Pithecia</td>
<td>DNE</td>
<td>2.874</td>
<td>2.606–3.262</td>
<td>2.768</td>
<td>2.388</td>
<td>2.394</td>
</tr>
<tr>
<td>2</td>
<td></td>
<td>RFI</td>
<td>0.191</td>
<td>2.484–3.199</td>
<td>0.172</td>
<td>2.133–2.474</td>
<td>0.900</td>
</tr>
<tr>
<td>3</td>
<td></td>
<td>SRA</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>4</td>
<td></td>
<td>OPCR</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

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

* 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).

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

*TABLE 4. Results of pairwise comparisons*

<table>
<thead>
<tr>
<th>No.</th>
<th>Taxon Comparison</th>
<th>Variable</th>
<th>Aotus</th>
<th>Callicebus</th>
<th>Pithecia</th>
<th>Chiropotes</th>
<th>Cacajao</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Aotus/Pithecia</td>
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<td>2.484–3.199</td>
<td>0.172</td>
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<td>0.900</td>
</tr>
<tr>
<td>3</td>
<td>SRA</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>OPCR</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

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

* 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).

* Under the alternative hypothesis (Hypothesis 2b), *Chiropotes > Pithecia*.
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; *Chiroptes*, purple cross; and *Pithecia*, green circle.
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

**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**

<table>
<thead>
<tr>
<th>Component</th>
<th>Eigenvalue</th>
<th>% Variance</th>
<th>Principal component coefficients</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>SRA</td>
</tr>
<tr>
<td>1</td>
<td>2.627650</td>
<td>65.6910</td>
<td>0.5692</td>
</tr>
<tr>
<td>2</td>
<td>0.789164</td>
<td>19.7290</td>
<td>−0.1425</td>
</tr>
<tr>
<td>3</td>
<td>0.381572</td>
<td>9.5393</td>
<td>0.0505</td>
</tr>
<tr>
<td>4</td>
<td>0.201616</td>
<td>5.0404</td>
<td>0.8082</td>
</tr>
</tbody>
</table>

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

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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 their sample. Notably, the diet of *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\(a\)

<table>
<thead>
<tr>
<th>Wilks’ (\lambda)</th>
<th>df</th>
<th>Approx. (F)</th>
<th>Standard (P)</th>
<th>Phylogenetic (P)</th>
<th>(Pr &gt; F)</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.023065</td>
<td>4</td>
<td>63.533</td>
<td>0.000048</td>
<td>0.044</td>
<td></td>
</tr>
</tbody>
</table>

\(a\) 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 Hapalemur (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 (55.04) 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. moloč (55.4), and this difference is significant for Cal. moloč (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 intrageneric 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 intrageneric comparisons also reveal that P. pithecus differs from P. monachus by having significantly higher OPCR. This could also reflect a greater reliance on leaf material in P. pithecus, as a result of the increased competition with sympatric Ch. satanas in Suriname (Kinzy and Norconk, 1993) not likely to be experienced by P. monachus in the western Amazon Basin (Norconk, 2007). Nonetheless, P. pithecus 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 (Kinzy and Norconk, 1990, 1993), our alternative hypothesis (Hypothesis 2b) predicts that Pithecia would exhibit shorter 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 (Kinzy, 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 (Kinzy and Norconk, 1993; Norconk and Veres, 2011). Overall, the molaras 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, Cacajao 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 sympathy 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 (Kinzy 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 (Kinzy, 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 Castillo, 2000; Barnett et al., 2005).

Another, 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 (Kinzezy, 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 larger 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 (Kinziey, 1992; Kinziey 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 (Kinziey 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; Wyczkowski, 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 Callucebus 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 (Kinziey, 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 (Kinsey, 1992; Rosenberger, 1992), and this is supported by the fossil record. Several fossil pitheciine species, including Cebupithecus sarmientoi (Orlosky, 1973), Nuciruptor rubriceae (Meldrum and Kay, 1997), and Propithecus nequenensis (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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