

Canine and Incisor Microwear in Pitheciids and *Ateles* Reflects Documented Patterns of Tooth Use

Lucas K. Delezene,^{1*} Mark F. Teaford,² and Peter S. Ungar¹

¹Department of Anthropology, University of Arkansas, Fayetteville, AR, 72701

²Department of Basic Sciences, Touro University California, Vallejo, CA, 94592

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ABSTRACT

Objectives: Platyrrhine species differ in the extent to and the manner in which they use their incisors and canines during food ingestion. For example, *Ateles* uses its anterior teeth to process mechanically nondemanding soft fruits, while the sclerocarp-harvesting pitheciids rely extensively on these teeth to acquire and process more demanding foods. Pitheciids themselves vary in anterior tooth use, with the pitheciines (*Cacajao*, *Chiropotes*, and *Pithecia*) noted to use their robust canines in a variety of ways to predate seeds, while *Callicebus*, which rarely predate seeds, uses its incisors and exceptionally short canines to scrape tough mesocarp from fruits. To investigate the relationship between tooth use and dental wear, microwear textures were investigated for the anterior teeth of these five genera of platyrrhine primates.

Methods: Using a white light confocal microscope, 12 microwear texture attributes that reflect feature size, anisotropy, density, and complexity were recorded from high-resolution epoxy casts of the incisors and canines of adult wild-collected Brazilian specimens of *Ateles*, *Callicebus*, *Cacajao*, *Chiropotes*, and *Pithecia*.

Results: Pitheciine canines tend to have deep microwear features and complex, anisotropic microwear textures, while *Ateles* anterior teeth tend to have very small features, low feature density, and less complex and anisotropic surfaces. *Callicebus* incisor and canine microwear is generally intermediate in size and complexity between those extremes.

Conclusions: These findings align with expectations from reported field observations of tooth use and illustrate the potential for using microwear texture analysis to infer patterns of anterior tooth use in extinct primates. *Am J Phys Anthropol* 000:000–000, 2016. © 2016 Wiley Periodicals, Inc.

Dental microwear analysis, the study of microscopic wear patterns that form on teeth, is a valuable tool for reconstructing the feeding behaviors of extinct vertebrates. However, the ability to decipher the relationship between wear patterns and dental function depends on understanding how teeth are used by extant taxa. For primates, this relationship has been studied extensively for the molars; although, it remains understudied for other tooth classes. Fieldwork examining primates in the wild has provided data on food preferences and on the fracture properties of masticated foods (e.g., Teaford et al., 2006; Lucas et al., 2008); this, combined with insights from studies of masticatory biomechanics (e.g., Hua et al., 2015), permits an understanding of molar microwear patterning. Years of study have shown that molar microwear distinguishes primates on the basis of broad dietary preferences. For example, Teaford and Walker (1984; Walker and Teaford, 1989) found that frugivorous anthropoids typically have more pitting on their Phase II facets than do folivorous taxa, which have more striations. Moreover, harder-object feeders tend to have higher pit-to-scratch ratios and higher frequencies of large pits on those surfaces than do soft-fruit eaters (e.g., Teaford and Walker, 1984; Teaford and Runestad, 1992; King et al., 1999). Recent analyses using scale-sensitive fractal analysis show that harder-object feeders typically exhibit more complex microwear surfaces and larger features on average than do soft- or tough-object feeders (e.g., Scott et al., 2006, 2012). Indeed, molar microwear in primates and other mammals has been shown to reflect rather subtle

variation in diet (Teaford, 1985, 1993; Daegling and Grine, 1999; King et al., 1999), including seasonal and ecological zone differences within taxa (e.g., Teaford and Robinson, 1989; Teaford and Glander, 1996; Merceron et al., 2004; Nystrom et al., 2004; Estalrich et al., 2015; Burgman et al., 2016).

In contrast to the molars, far fewer studies have examined the relationship between microwear patterning and incisor use. For primates, incisor microwear has been related to patterns of ingestive behavior and feeding height in the canopy. Kelley (1990) suggested that microwear feature density is related to the degree of incisor use in ingestion, which was confirmed by combined studies of microwear and anterior tooth use in numerous primates (Ungar, 1990, 1994, 1995). Further, Walker (1976), Teaford (1983), and Ungar (1994) all associated striation direction with ingestive behaviors. And Ryan (1980, 1981) suggested that some behaviors involving the incisors,

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*Correspondence to: Lucas K. Delezene; 330 Old Main, University of Arkansas, Fayetteville AR 72701. E-mail: delezene@uark.edu

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such as leaf stripping and seed crushing, create distinctive microwear signatures. Incisor microwear may distinguish terrestrial from arboreal primates given different abrasives associated with foods on or near the ground and those high in the canopy (Walker, 1976; Ungar, 1994). Analyses of human bioarchaeological samples, as well as those of Neandertals, demonstrate that incisor use as part of dietary and non-dietary behaviors is associated with microwear patterning (Krueger et al., 2008; Krueger and Ungar, 2010). Further, texture attributes (e.g., complexity, anisotropy, feature volume) vary in their utility for inferring aspects of tooth use between anterior and posterior teeth. For example, Krueger and Ungar (2010) found that microwear complexity, which tends to separate groups with different diets based on molar microwear, may not separate them based on incisor microwear, whereas some other variables, such as anisotropy and heterogeneity, often do.

Despite the demonstrated value of molar and incisor microwear studies, much less has been done on canines. Walker (1984) used striation orientation to infer the mechanics of maxillary canine honing, and subsequent canine microwear studies focused on changes in function that accompanied the loss of honing in early hominins (e.g., Puech and Albertini, 1984; Ryan and Johanson, 1989; Greenfield, 1990; Delezene et al., 2013). Puech et al. (1989) also examined extinct hominoid canine microwear in relation to dietary choice. By and large, though, these studies were qualitative and included little comparative analysis, which restricted their value for interpreting patterns of tooth use in fossil hominins. Limited study of canine use in wild primates has also hampered understanding microwear patterns for these teeth. A notable exception in this regard is for the family Pitheciidae, which includes the subfamilies Callicebinae (*Callicebus*) and Pitheciinae (*Cacajao*, *Chiropotes*, and *Pithecia*) (see Schneider and Sampaio, 2015 for a review of platyrrhine systematics). Differences in canine form and size between these genera are well studied (Kinzey, 1992; Rosenberger, 1992; Anapol and Lee, 1994; Spencer, 2003; Plavcan and Ruff, 2008) and have been related to adaptations to sclerocarp harvesting and seed predation (Kinzey, 1992; Anapol and Lee, 1994).

This study examines incisor and canine microwear textures in five platyrrhine genera that present a continuum of dietary use of the anterior dentition, ranging from a soft-fruit specialist (*Ateles*), through sclerocarp harvesters that run the gamut from occasional canine use in food ingestion (*Callicebus*) to more specialized sclerocarp and seed-predating adaptations involving the canines (*Pithecia*, *Chiropotes*, and *Cacajao*). Unlike adaptive lines of evidence, such as occlusal morphology or enamel thickness, dental microwear provides a record of what a specific individual ate over a particular period of time in the past (e.g., Teaford, 1991, 1994). That period is typically on the order of days or weeks depending on what was eaten (e.g., Teaford and Oyen, 1989a), and this has led some to call microwear a “last supper phenomenon” (e.g., Grine, 1986). With sufficient sample sizes, this can be an asset, as it can provide insights into both central tendencies and also dietary dispersion (Ungar, 2009). Gathering microwear data from these taxa is an essential step in revealing the relationship between anterior tooth use and microwear formation in primates.



Fig. 1. Lateral views of male specimens of genera examined in this study. Clockwise from upper left, *Chiropotes*, *Pithecia*, *Callicebus*, and *Ateles*. The white bar equals 5 cm.

Feeding ecology and craniodental morphology of studied taxa

Ateles species are ripe-fruit specialists. Indeed, the percentage of fruit flesh in their diets has been estimated to be between 60% and 90% (e.g., Peres, 1994; Nunes, 1996; Stevenson et al., 2000; Iwanaga and Ferrari, 2001; Dew, 2005; Russo et al., 2005; Wallace, 2005; Felton et al., 2008; González-Zamora et al., 2009). *Ateles* maximizes fruit pulp intake through less careful food processing and mastication, in essence, swallowing so many fruits whole that their accompanying seeds have been referred to as “ballast” that may impact their locomotion and foraging patterns (Dew, 2005). When ripe fruits are unavailable, *Ateles* often turns to young leaves or flowers (Chapman, 1987; Symington, 1988; Nunes, 1996; Wallace, 2005; Suarez, 2006; Felton et al., 2008, 2009); however, they have rarely been observed to masticate seeds (Russo et al., 2005; Wallace, 2005; Felton et al., 2008).

Ateles species have relatively broad and spatulate incisors (Anthony and Kay, 1993; Meldrum and Kay, 1997; Swindler, 2002; Norconk et al., 2009) that are used to peel the exocarp from ripe fruits (Eaglen, 1984; Anapol and Lee, 1994; Norconk et al., 2009). *Ateles* canines are slender and vertically implanted (Fig. 1) and exhibit substantial height dimorphism, especially for a platyrrhine (Plavcan, 1990). *Ateles* canines are not used regularly in food acquisition or processing (Anapol and Lee, 1994), though they are well buttressed to resist lateral bending stresses (Kinzey and Norconk, 1990).

The pitheciines (*Cacajao*, *Chiropotes*, *Pithecia*) comprise a subfamily (Schneider and Sampaio, 2015) of highly frugivorous sclerocarp harvesters that often consume fruits with stony endocarps (e.g., Mittermeier and van Roosmalen, 1981; Kinzey and Norconk, 1990; Kinzey, 1992). Unlike other platyrrhines that swallow fruit seeds whole and derive little nutritional value from their consumption, pitheciines are predispersal seed predators that target seeds as a dietary resource (e.g., Rosenberger et al., 1996; Norconk et al., 1998; Norconk and Veres, 2011), often consuming unripe fruit with hard pericarps (Ayres, 1986, 1989; van Roosmalen et al., 1988; Kinzey and Norconk, 1990, 1993; Kinzey, 1992; Rosenberger,

1992). This feeding strategy mitigates the effects of reduced fruit availability during the dry season (Norconk, 1996, 2011; Rosenberger et al., 1996; Norconk et al., 2009) and allows them to avoid competition with sympatric platyrrhines, such as *Ateles* (Kinzey and Norconk, 1990; Rosenberger, 1992; Kinzey and Norconk, 1993; Norconk et al., 1998; Norconk and Conklin-Brittain, 2004). Field observations confirm that seeds are important dietary resources throughout the year for *Pithecia*, *Cacajao*, and *Chiropotes* (e.g., Ayres, 1989; Kinzey, 1992; Norconk et al., 1997; Boubli, 1999; Norconk and Conklin-Brittain, 2004; Barnett et al., 2005; Cunningham and Janson, 2006; Norconk and Veres, 2011).

Pitheciines have tall, narrow, styliform, procumbent incisors (Fig. 1) (Kinzey, 1992; Rosenberger, 1992; Anapol and Lee, 1994) that are used to pierce fruit husks, scrape mesocarp from hard nuts, and pry resistant seeds from fruits (Kinzey and Norconk, 1990; Anapol and Lee, 1994). Pitheciine canines are tall, robust, wedge-like (i.e., broad at their base and tapered toward the tip), laterally splayed, and separated from the incisors by diastemata in both the maxilla and mandible (Fig. 1) (Kinzey, 1992; Plavcan and Ruff, 2008). Further, the canine crowns are anchored in the jaws by large roots (Spencer, 2003). Pitheciines have modest canine size dimorphism compared with most other anthropoids because both male and female canines are relatively large, presumably a reflection of the specialized use of the canines for food acquisition and processing by both sexes (Plavcan and Ruff, 2008). Pitheciine canines are used to open soft fruits, to extract small seeds, to puncture and open hard pericarp, to scrape mesocarp from hard seeds, and to pry open the woody casing that may protect those seeds (Kinzey and Norconk, 1990; Rosenberger, 1992; Norconk et al., 1998; Barnett et al., 2005; Norconk, 2011). Seed processing involving the canines occurs between the maxillary and mandibular canines and is also reported to occur between the maxillary canine and mesial-most mandibular premolar (Rosenberger, 1992; Norconk, 2007).

Among the pitheciines, *Pithecia* is a less specialized seed predator than either *Chiropotes* or *Cacajao*. In fact, Kinzey (1992) noted that fruits eaten by *Pithecia* tend to have a lower resistance to puncturing and, further, that *Pithecia* is “apparently not capable of biting through pericarps as hard as those punctured by *Chiropotes* and *Cacajao*” (Kinzey, 1997b, p. 284); though, Norconk and Veres (2011) found no significant difference between the puncture resistance of foods consumed by *Pithecia* and *Chiropotes*. It is perhaps unsurprising also that while *Pithecia* consumes few leaves, it does so more than either *Chiropotes* or *Cacajao* (e.g., van Roosmalen et al., 1981; Happel, 1982; Soini, 1986; Ayres, 1989; Kinzey, 1992; Kinzey and Norconk, 1993; Peres, 1993; Norconk, 1996; Rosenberger et al., 1996; Boubli, 1999). *Cacajao* and *Chiropotes* evince the most specialized sclerocarp-harvesting adaptations, having more robust canine crowns and roots than *Pithecia* (Fig. 1) (Anapol and Lee, 1994; Spencer, 2003).

Callicebus is also a sclerocarp harvester, though it consumes ripe-fruit flesh more frequently than do the pitheciines (Müller, 1996; Kinzey, 1997a). While it is not a specialized seed predator, *Callicebus* eats seeds more frequently than most other platyrrhines, especially at times of resource stress during the “fruit bottleneck” (Palacios et al., 1997; Norconk, 2007; Norconk et al., 2009; Norconk, 2011). *Callicebus* species have tall, labio-

lingually expanded incisors compared with most other platyrrhines; though, they are not as tall or thick as those of pitheciines and are more vertically implanted (Fig. 1) (Rosenberger, 1992). *Callicebus* incisors are reportedly used to peel back moderately tough husks from fruit and to scrape mesocarp from the external surface of hard nuts, as well as to scrape the thin edible tissue from nut casings (Kinzey, 1974, 1977, 1992; Rosenberger, 1992). *Callicebus* has small, non-dimorphic canines that project less than expected for a platyrrhine of its body size (Fig. 1) (Kinzey, 1972; Kay et al., 1988). No, or very small, diastemata separate the canines from either the incisors or postcanine teeth; further, as the mandibular canine occludes tip-to-tip with the maxillary lateral incisor and apex of the maxillary canine (Greenfield, 1992c), their canines appear to be functionally integrated with the adjacent incisors (Kinzey, 1972; Greenfield, 1992a,b). As a result of this occlusal pattern, their canines wear flat rapidly from their apices (Greenfield 1992a,1996). *Callicebus* canines are used along with their incisors to peel fruit husks and to scrape edible mesocarp from the hard nuts within them (Kinzey, 1974, 1977; Rosenberger, 1992).

Hypotheses

The pitheciid genera present a well-studied dietary and anatomical continuum. As Kinzey (1992, p. 512) noted, “the progressive sharing of derived characters from *Callicebus* to *Pithecia* to *Chiropotes* and *Cacajao* represents a morphocline of increasingly specialized features for fruit husking and seed predation-sclerocarpic foraging or harvesting.” By including *Ateles*, the analyzed sample spans a broad range of incisor size and shape, canine size and shape, canine size dimorphism, and use of the anterior teeth in dietary contexts.

Incisor microwear textures should differentiate *Ateles*, which mostly consumes soft ripe fruit, from the sclerocarp-harvesting pitheciids. Reflecting their use in processing soft fruits, *Ateles* incisors should have the lowest density of microwear features, the smallest microwear features, and the least complex microwear surfaces. Further, since *Ateles* species have broader diets than the pitheciines, microwear features should be less anisotropic (i.e., not have a consistent orientation). Because pitheciines use their incisors to puncture and pry open resistant pericarp, they should have complex incisor microwear surfaces dominated by deep parallel scratches (i.e., higher anisotropy than *Ateles*). Given the use of the incisors in scraping behaviors, *Callicebus* incisors should have microwear surfaces dominated by parallel features (i.e., higher anisotropy than *Ateles*); further, as *Callicebus* is noted to process a more mechanically demanding diet than *Ateles* and a less demanding diet than the pitheciines, *Callicebus* microwear feature size is expected to be intermediate in size between *Ateles* and the pitheciines.

Canine microwear should reflect the continuum of use. Species that use their canines more in ingestive behaviors should have more complex microwear surfaces with larger features than those that use these teeth less, or with lower magnitude forces [following inferences about incisor use from Krueger and Ungar (2010)]. Thus, as compared with *Ateles*, pitheciid canines should have a higher density of features, more complex microwear surfaces, and larger microwear features. Further, given

their specialized use, *Pithecia*, *Cacajao*, and *Chiropotes* canines should have larger features and more complex microwear surfaces than *Callicebus*. Since *Cacajao* and *Chiropotes* are more specialized seed predators than *Pithecia*, their canines should be more extreme in these regards. Finally, given the use of their anterior teeth in sclerocarp harvesting, pitheciine canines and incisors should show greater functional differentiation than those of either *Callicebus* or *Ateles*, especially in terms of feature size and complexity. This functional differentiation should be reflected by deeper and more complex microwear surfaces for pitheciine canines than their central incisors.

MATERIALS AND METHODS

Specimens of *Ateles marginatus*, *Cacajao calvus*, *Callicebus brunneus*, *Callicebus moloch*, *Chiropotes satanas*, *Pithecia irrorata*, *Pithecia monachus*, and *Pithecia pithecia* were examined (Table 1). All specimens are wild-collected Brazilian primates that are curated at the Museu Paraense Emílio Goeldi in Belem, Brazil, with the exception of *Callicebus moloch*, which is kept at the American Museum of Natural History, New York. Individuals of *Chiropotes satanas* and *Pithecia pithecia* were collected near the confluence of the Rios Amazonas and Trombetas and near the municipality of Oriximiná in the state of Pará. Specimens of *Callicebus moloch* were collected from the state of Pará at localities along the Rio Tapajos in the counties of Santarem, Aveiro, Igarape Mirim, and Baiao. The *Ateles marginatus* specimens were collected near Fazenda Taperinha in the state of Pará along the Rio Amazonas and downstream from its confluence with the Rio Tapajos [more information on the site is available in Estalrich et al. (2015)]. Specimens of *Cacajao calvus* and *Pithecia monachus* were collected from the state of Amazonas near Estirão do Equado along the Rio Javari. Specimens of *Callicebus brunneus* and *Pithecia irrorata* are from the area flooded by the Samuel Hydroelectric dam on the Rio Jamari in the state of Rondônia. Only adult specimens, here defined by eruption of the third permanent molar into occlusion, were molded and included in this analysis.

Given the lack of direct observations of tooth use and diet in the wild for the analyzed individuals, the design of this study only permits the examination of broad, generalized patterns of tooth use (e.g., Teaford and Runestad, 1992). Further, as evidence reviewed above indicates that congeners in this study typically have similar diets and tooth use behaviors, all analyses were conducted at the level of the genus. Finally, given the small sample size available for *Cacajao calvus* (Table 1) and observations of similar patterns of tooth use, diet, ecology (Kinzey, 1997c), and functional morphology (e.g., Spencer, 2003) for *Cacajao* and *Chiropotes*, these two genera were pooled for analysis.

To prepare for molding, teeth were cleaned with alcohol-soaked cotton swabs; then, molds were made with polysiloxane vinyl (President's Jet Regular Body; Coltene-Whaledent Corp., Mawah, NJ). High-resolution epoxy-polymer casts (Epotek 301; Epoxy Technologies, Inc., Billerica, MA) were prepared from these molds (e.g., Rose, 1983; Teaford and Oyen, 1989b; Galbany et al., 2006; Goodall et al., 2015).

Microwear texture data were generated from wear surfaces along the labial faces of the maxillary central

incisor and canine. Preference was not given to left or right teeth (only those in the best condition) and teeth from both sides were pooled in analyses. Wear was examined near the biting (incisal) edge of each maxillary incisor and at the apex of each maxillary canine. A Sensofar Plμ white-light scanning confocal profiler (Solarius, Inc.) fitted with a 100× objective was used to scan the surface of the polymer casts and generate microwear texture data in the form of three-dimensional point clouds with a lateral (x, y) sampling interval of 0.18 μm, a vertical resolution (z) of 0.005 μm, and a total work envelop of 138 μm × 102 μm (e.g., Scott et al., 2006; Grine et al., 2010; Scott et al., 2012). Data for four microwear texture variables [area scale fractal complexity ($Asfc$), textural fill volume (Tfv), and two measures of heterogeneity of complexity ($HAsfc_9$ and $HAsfc_{81}$)] were derived from scale-sensitive fractal analysis (SSFA) software programs (ToothFrax and SFrax, Surfcraft Corp.; Scott et al., 2006; Ungar et al., 2008). Detail on the procedures used to calculate SSFA variables is found in Scott et al. (2006). Additionally, surface textures were characterized by eight International Organization for Standardization (2010) (ISO 25178-2) texture measurements, which were generated using Sensomap v6 (Sensofar Corp.) (e.g., Calandra et al., 2012; Schulz et al., 2013). The ISO parameters used include five-point pit height ($S5v$), maximum pit height (Sv), mean daled area (Sda), mean daled volume (Sdv), pit void volume (Vvv), texture-aspect ratio (Str), developed interfacial area ratio (Sdr), and skewness (Ssk) (ISO/FDIS 25178-2, International Organization for Standardization, 2010; Țălu et al., 2013). Such parameters are increasingly being employed in microwear analyses (e.g., Calandra et al., 2012; Schulz et al., 2013) to complement SSFA. For the ISO variables, the curvature of the scanned surface was removed by using the "form removal" operator of Sensomap v6. Thus, parameters analyzed in this study include two measures of feature complexity ($Asfc$, Sdr), two measures of heterogeneity of textures ($HAsfc_9$, $HAsfc_{81}$), three measures of feature volume (Tfv , Vvv , Sdv), a measure of feature area (Sda), two measures of feature depth (Sv , $S5v$), a measure of feature anisotropy (Str), and a measure of the density of scratches (Ssk).

As microwear textures are usually not normally distributed, statistical analyses were performed on rank-transformed data. First, a two-way MANOVA with tooth (canine, incisor), taxon (*Ateles*, *Callicebus*, *Pithecia*, *Cacajao/Chiropotes*), and the interaction between the two factors was employed to determine whether there was significant variation in the model. Then, pairwise comparisons were carried out for each tooth type among species and between tooth types within species to elucidate the sources of variation. All pairwise comparisons were conducted using Mann-Whitney U tests. In addition to comparisons of central tendency, the homogeneity of variances was compared among species and between teeth within species using Levene's tests. As twelve variables were analyzed, multicollinearity was investigated to determine whether each variable provides an independent characterization of surface parameters; then, a multivariate principal components analysis was performed. As the parameters are measured on different scales and have unequal variances, the principal components were computed from the correlation matrix. All statistical analyses were performed in JMP Pro v11.2 and Systat v12.0.

RESULTS

The overall model

Results of the MANOVA indicate that taxon (Wilks $\lambda = 0.52$; $P < 0.0001$), tooth (Wilks $\lambda = 0.14$; $P < 0.0001$), and their interaction (Wilks $\lambda = 0.58$; $P < 0.0001$) all have significant effects on the response variables. Thus, pairwise comparisons were used to examine the source(s) of significant variation in the overall model.

Interspecific comparisons of incisor textures

Twelve microwear variables were analyzed for each incisor. Results are presented below first for general surface characteristics (i.e., complexity [*Sdr*, *Asfc*], anisotropy [*Str*], heterogeneity of complexity [*HAsfc₉*, *HAsfc₈₁*], and feature density [*Ssk*]), then for aspects of feature size (i.e., feature volume [*Tfv*, *Vvv*, *Sdv*], area [*Sda*], and depth [*S5v*, *Sv*]), and, finally, a summary of textures attributes is provided.

For the incisors (Fig. 2), measures of surface anisotropy, complexity, and feature density capture significant

variation among species. The measure of anisotropy (*Str*) ranges from zero to one; with a value of one indicating an isotropic surface (i.e., with no discernible pattern of feature orientation), and a value of zero indicating an anisotropic surface (i.e., with a pattern of feature orientation). As predicted, the *Ateles* median, 0.63, is the most isotropic among all analyzed taxa (Table 1; Fig. 3); however, significant differences are only observed between *Ateles* and *Callicebus* (Table 2). Levels of variance for *Str* are similar across taxa, as only a single comparison, *Pithecia* versus *Cacajao/Chiropotes*, yields a significant difference. In this case, *Cacajao/Chiropotes* has a higher variance (Table 1). For *Ssk*, a proxy of feature density, negative values indicate surfaces characterized by valleys, while positive values indicate surfaces dominated by peaks. With the exception of *Ateles*, all taxa have highly negative *Ssk* values, indicating surfaces with a high density of scratches (Table 1; Fig. 3). The *Ateles* median *Ssk*, 0.04, indicates a surface with a low density of both peaks and valleys; though significant differences are seen only between *Ateles* and *Cacajao/Chiropotes* (Table 2). For *Ssk*, no

TABLE 1. Summary data for texture-aspect ratio (*Str*), skewness (*Ssk*), area-scale fractal complexity (*Asfc*), developed interfacial area ratio (*Sdr*) [%], heterogeneity of area-scale fractal complexity (*HAsfc₉*, *HAsfc₈₁*), mean dale volume (*Sdv*) [μm^3], pit void volume (*Vvv*) [$\mu\text{m}^3/\mu\text{m}^2$], textural fill volume (*Tfv*), five-point pit height (*S5v*) [μm], maximum pit height (*Sv*) [μm], and mean dale area (*Sda*) [μm^2]

Genus	Tooth	<i>n</i>		<i>Str</i>	<i>Ssk</i>	<i>Asfc</i>	<i>Sdr</i>	<i>HAsfc₉</i>	<i>HAsfc₈₁</i>
<i>Ateles</i>	Incisor	19	Median	0.63	0.04	1.18	0.60	1.14	1.13
			Mean	0.61	-0.06	1.28	0.75	1.25	1.17
			Std	0.22	0.44	0.61	0.42	0.62	0.54
	Canine	20	Median	0.54	-0.07	1.72	0.88	0.20	0.35
			Mean	0.49	-0.10	1.63	0.90	0.24	0.39
			Std	0.22	0.38	0.56	0.38	0.10	0.13
<i>Callicebus</i>	Incisor	23	Median	0.48	-0.25	1.85	1.02	1.85	1.69
			Mean	0.47	-0.30	1.99	1.11	1.88	1.73
			Std	0.23	0.50	1.00	0.57	0.97	0.76
	Canine	36	Median	0.27	-0.56	2.77	1.52	0.30	0.54
			Mean	0.35	-0.49	3.65	2.41	0.37	0.57
			Std	0.24	0.44	3.07	2.81	0.18	0.22
<i>Pithecia</i>	Incisor	27	Median	0.58	-0.12	1.62	0.86	1.65	1.45
			Mean	0.56	-0.14	2.20	1.81	2.10	1.98
			Std	0.19	0.37	1.86	3.35	1.75	1.67
	Canine	23	Median	0.24	-0.41	3.34	2.36	0.57	0.86
			Mean	0.37	-0.52	3.76	2.59	0.60	0.87
			Std	0.27	0.46	1.50	1.29	0.42	0.43
<i>Cacajao</i>	Incisor	5	Median	0.26	-0.27	1.91	1.19	1.69	1.34
			Mean	0.36	-0.57	1.87	1.27	1.80	1.53
			Std	0.30	0.54	0.41	0.47	0.54	0.47
	Canine	4	Median	0.49	-0.36	3.90	2.80	0.44	0.63
			Mean	0.41	-0.57	3.95	2.90	0.44	0.63
			Std	0.21	0.78	1.19	1.00	0.17	0.16
<i>Chiropotes</i>	Incisor	15	Median	0.55	-0.11	1.69	0.94	1.52	1.56
			Mean	0.52	-0.22	2.31	1.38	2.15	2.15
			Std	0.27	0.45	1.57	1.08	1.55	1.52
	Canine	20	Median	0.39	-0.48	4.17	3.32	0.35	0.70
			Mean	0.41	-0.45	4.72	3.55	0.38	0.76
			Std	0.27	0.41	2.12	1.85	0.21	0.35
<i>Cacajao/Chiropotes</i>	Incisor	20	Median	0.51	-0.22	1.76	0.95	1.55	1.54
			Mean	0.48	-0.31	2.20	1.36	2.06	1.99
			Std	0.28	0.48	1.38	0.95	1.36	1.35
	Canine	24	Median	0.44	-0.45	4.17	3.24	0.36	0.69
			Mean	0.41	-0.47	4.60	3.45	0.39	0.74
			Std	0.25	0.47	2.01	1.74	0.20	0.33

TABLE 1. Continued

Genus	Tooth	<i>n</i>		<i>Sdv</i>	<i>Vvv</i>	<i>Tfv</i>	<i>S5v</i>	<i>Sv</i>	<i>Sda</i>
<i>Ateles</i>	Incisor	19	Median	0.62	1.59	10546.11	0.30	0.59	89.90
			Mean	1.59	1.77	10063.55	0.34	0.74	121.93
			Std	2.30	0.70	5420.86	0.14	0.38	79.81
	Canine	20	Median	0.61	1.76	12634.56	0.34	0.77	66.04
			Mean	0.71	1.90	12756.18	0.35	0.75	74.70
			Std	0.64	0.90	4932.27	0.12	0.26	42.77
<i>Callicebus</i>	Incisor	23	Median	0.65	2.06	14901.47	0.31	0.79	77.74
			Mean	0.73	2.21	14307.23	0.35	0.79	92.65
			Std	0.42	1.02	3817.46	0.10	0.28	50.30
	Canine	36	Median	0.54	2.64	13324.15	0.56	1.17	47.71
			Mean	0.81	3.10	13971.24	0.61	1.28	71.19
			Std	0.66	1.93	3844.96	0.27	0.63	53.80
<i>Pithecia</i>	Incisor	27	Median	0.35	1.57	8997.86	0.29	0.63	56.62
			Mean	0.40	1.64	9003.63	0.34	0.69	60.08
			Std	0.22	0.61	5196.65	0.21	0.32	31.68
	Canine	23	Median	0.94	3.51	15507.87	0.61	1.25	71.26
			Mean	1.26	3.58	14321.50	0.67	1.45	85.94
			Std	1.15	1.08	4607.20	0.26	0.63	52.06
<i>Cacajao</i>	Incisor	5	Median	1.29	3.64	10073.73	0.43	1.04	194.66
			Mean	4.34	3.45	10897.25	0.55	1.36	175.96
			Std	6.12	1.25	4695.88	0.27	0.62	66.22
	Canine	4	Median	2.73	4.87	16820.72	0.73	1.69	171.87
			Mean	3.31	4.77	16697.57	0.79	1.73	156.61
			Std	2.54	0.77	635.21	0.23	0.28	50.16
<i>Chiropotes</i>	Incisor	15	Median	0.76	2.19	14368.08	0.44	0.81	68.54
			Mean	1.12	2.59	13114.97	0.45	0.99	90.02
			Std	0.97	1.42	5059.10	0.17	0.51	50.47
	Canine	20	Median	0.98	3.92	17288.59	0.84	1.56	73.56
			Mean	1.16	4.22	17197.67	0.83	1.61	79.34
			Std	0.72	1.79	3212.95	0.33	0.56	31.35
<i>Cacajao/Chiropotes</i>	Incisor	20	Median	0.91	2.43	12915.35	0.44	0.93	85.05
			Mean	1.92	2.81	12560.54	0.48	1.09	111.51
			Std	3.26	1.40	4946.93	0.20	0.54	65.25
	Canine	27	Median	1.22	4.10	16992.38	0.81	1.63	85.10
			Mean	1.52	4.31	17117.65	0.83	1.63	92.22
			Std	1.39	1.66	2947.54	0.31	0.52	44.78

Values for *Vvv* are multiplied by 100, but analyses are performed on the raw data.

comparisons of variance are significantly different (Table 3). For both measures of surface complexity, *Asfc* and *Sdr*, the *Ateles* median is significantly smaller than that for *Callicebus* and *Cacajao/Chiropotes* (Tables 1 and 2; Fig. 3); no other comparisons yielded significant differences. For each complexity variable, only a single comparison of variance showed significant differences and both indicate lower variance for *Ateles* (Table 3). For the measures of the heterogeneity of complexity across the surface, *HAsfc*₉ and *HAsfc*₈₁, the *Ateles* median is significantly smaller than that of both *Callicebus* and *Cacajao/Chiropotes* (Tables 1 and 2; Fig. 3). Levels of variance are similar among taxa for the measures of heterogeneity; no comparisons of *HAsfc*₉ yield significant differences, and only a single comparison for *HAsfc*₈₁, *Ateles* versus *Pithecia*, yielded significant results, with *Pithecia* showing higher values than *Ateles* (Table 3).

For the incisors, measures of feature volume capture differences among the taxa (Table 1; Fig. 4). For *Sdv*, *Pithecia* is significantly lower than all other taxa and *Callicebus* is significantly lower than *Cacajao/Chiropotes* (Table 2). For *Vvv*, both *Ateles* and *Pithecia* are significantly lower than *Cacajao/Chiropotes* and, further, *Pithecia* is

significantly lower than *Callicebus* (Table 2). *Ateles* and *Pithecia* both have significantly lower *Tfv* than *Callicebus*; further, *Pithecia* is also significantly lower than *Cacajao/Chiropotes* (Table 2). Comparisons of variance (Table 3) are inconsistent for measures of feature volume. For *Sdv*, *Ateles* has a significantly higher variance than *Callicebus* and *Pithecia*, and *Cacajao/Chiropotes* have a significantly higher variance than *Callicebus*. For *Vvv*, *Cacajao/Chiropotes* has significantly higher variance than *Ateles* and *Pithecia*. And no comparisons of variance yield significant differences for *Tfv*.

Measures of feature depth, *S5v* and *Sv*, also indicate significant differences among species. For *Sv*, which measures the deepest pit on the scanned surface, *Ateles* and *Pithecia* are both significantly shallower than *Cacajao/Chiropotes*; further, *Pithecia* is also significantly shallower than *Callicebus* (Tables 1 and 2; Fig. 4). For *S5v*, the average of the five deepest pits, *Cacajao/Chiropotes* is significantly deeper than all other samples (Tables 1 and 2; Fig. 4); no other comparisons are significant. No comparisons of variance involving *S5v* show significant differences; while for *Sv* *Cacajao/Chiropotes* has higher variance than *Callicebus* and *Pithecia*.

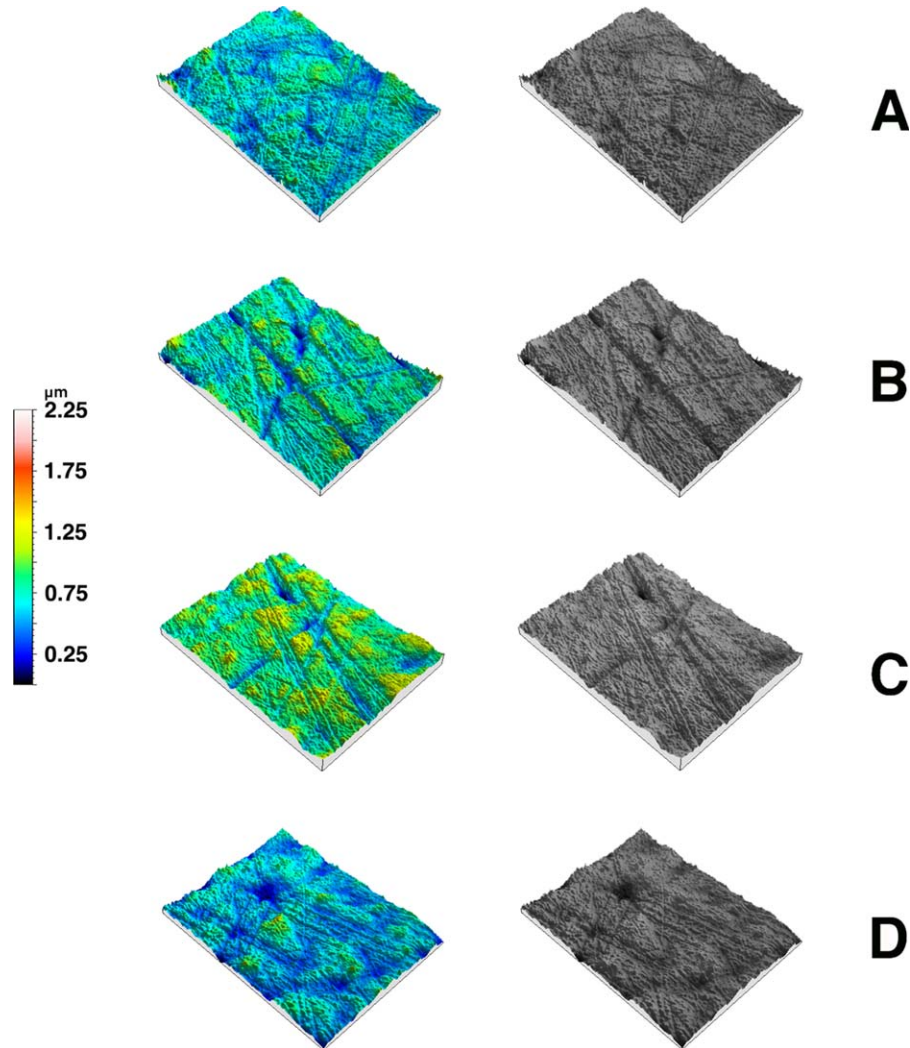


Fig. 2. Simulations of wear surfaces on central incisor labial surfaces. (A) *Ateles*, (B) *Callicebus*, (C) *Cacajao*, and (D) *Pithecia*. Each image is $138 \mu\text{m} \times 102 \mu\text{m}$.

For the measure of feature area, *Sda*, *Pithecia* is significantly smaller than all other taxa (Tables 1 and 2; Fig. 4); no other comparisons are significant. Comparisons of variance (Table 3) indicate significantly higher variance for *Ateles* than *Pithecia* and significantly higher variance for *Cacajao/Chiropotes* than *Callicebus* and *Pithecia*.

In sum, microwear textures considerably overlap among the analyzed species; though, some patterns are evident. For example, *Ateles* microwear textures are relatively simple and isotropic. For measures of size, including volume and depth, *Cacajao/Chiropotes* has the largest features, *Callicebus* is intermediate, and *Ateles* and *Pithecia* have the smallest features (Table 1; Figs. 3 and 4). Contrary to prediction, *Pithecia* microwear resembles that of *Ateles* and not *Cacajao/Chiropotes* to which it is ecologically more similar; in fact, only two of twelve variables (*Sda* and *Sdv*) are significantly different between *Ateles* and *Pithecia*, while six variables (*Sdv*, *Vvv*, *Tfv*, *S5v*, *Sv*, *Sda*) are significantly different between *Pithecia* and *Cacajao/Chiropotes* and all indicate smaller features for *Pithecia* than for *Cacajao/Chiropotes*.

Interspecific comparisons of canine textures

For the canines (Fig. 5), measures of surface anisotropy, feature density, and complexity indicate significant differences between samples. The measure of anisotropy, *Str*, indicates that *Ateles* is significantly more isotropic than *Callicebus*; no other comparisons are significant (Tables 1 and 4; Fig. 3). No comparisons of variance for this variable yield significant differences (Table 5). For *Ssk*, the proxy of feature density, *Ateles* is significantly different from all other taxa but no differences are observed among the pitheciids (Tables 1 and 4; Fig. 3). No comparisons of variance for this variable yield significant differences (Table 5). For both measures of complexity, *Asfc* and *Sdr*, *Ateles* has significantly lower complexity than all other taxa; at the other extreme, *Cacajao/Chiropotes* is more complex than all others except for *Pithecia*. *Callicebus* falls intermediate in *Asfc* and *Sdr* values between *Ateles* and the pitheciines and is generally significantly different from both (Tables 1 and 4; Fig. 3). For *Asfc* and *Sdr*, a common pattern emerges for comparisons of variance (Table 5). *Ateles* has significantly lower variance than all other taxa, while all other comparisons yield no significant differences. For *HAsfc*₉, *Ateles* is significantly different from

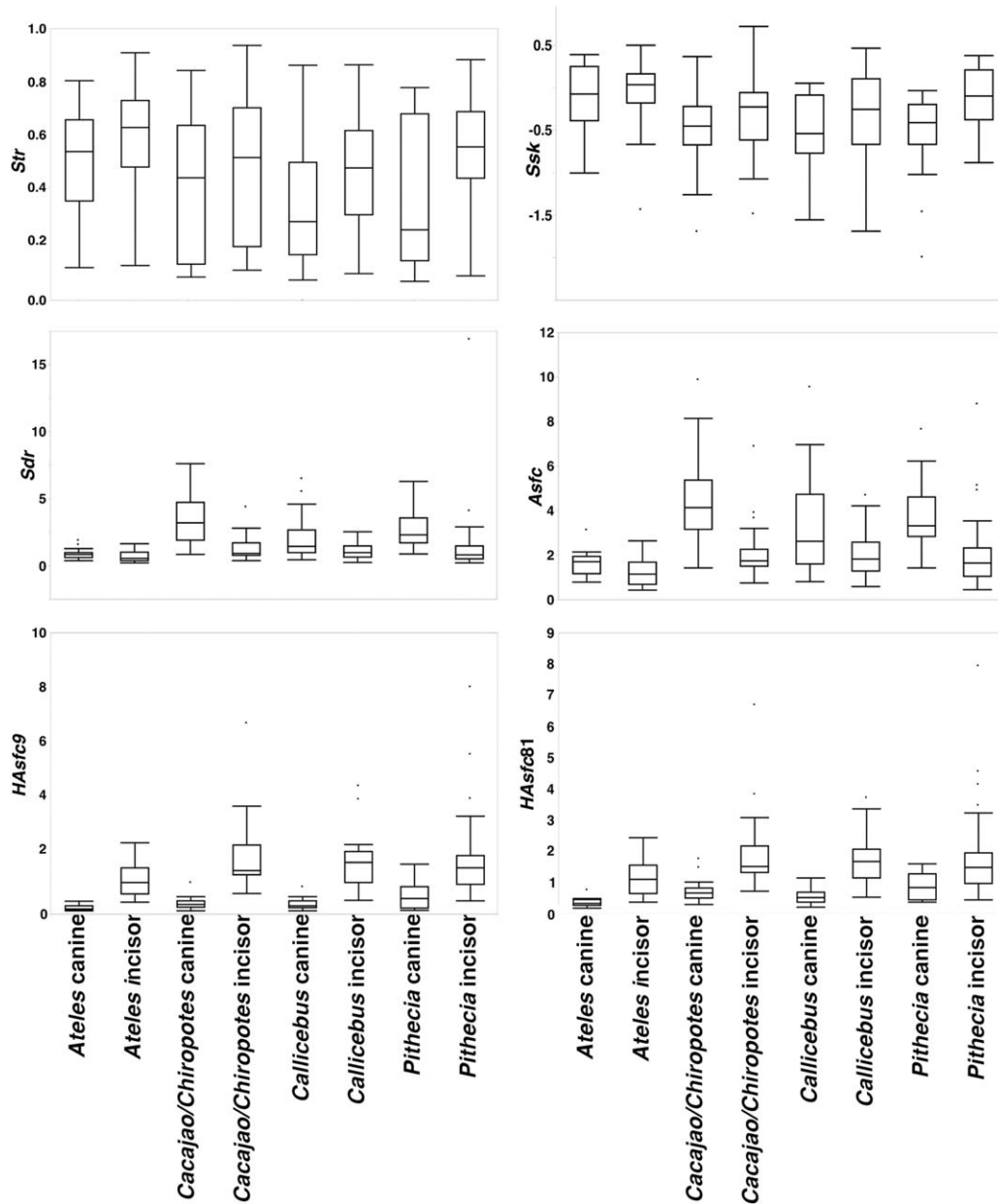


Fig. 3. Box and Whisker plots for a measure of feature anisotropy (*Str*), a measure of feature density (*Ssk*), two measures of complexity (*Sdr*, *Asfc*), and two measures of heterogeneity (*HASfc₉*, *HASfc₈₁*).

all other taxa (Tables 1 and 4; Fig. 3), indicating low variance of complexity across the surface for *Ateles*. And for *HASfc₈₁*, the medians are arranged as *Ateles* < *Callicebus* < *Cacajao/Chiropotes* ≤ *Pithecia* as all pairwise comparisons are significantly different except for that of *Pithecia* and *Cacajao/Chiropotes* (Table 4). Comparisons of variance for the two measures of heterogeneity indicate significant differences among taxa (Table 5). For *HASfc₉*, two comparisons involving *Ateles* and two comparisons involving *Pithecia* are significantly different. For this variable, *Ateles* has lower variance and *Pithecia* has higher variance. For *HASfc₈₁*, *Ateles* has lower variance than all of the other taxa with *Callicebus* in between *Ateles* and *Pithecia* and *Cacajao/Chiropotes*.

Proxies for feature volume (*Tfv*, *Vvv*, *Sdv*) indicate significant differences among taxa (Fig. 4). For *Tfv*, *Caca-*

jao/Chiropotes is significantly different from all other taxa; for *Vvv*, all comparisons yield significant differences except for that of *Pithecia* and *Cacajao/Chiropotes*; and for *Sdv*, all comparisons yield significant differences except for that of *Ateles-Callicebus* and *Pithecia-Cacajao/Chiropotes* (Table 4). These results generally indicate larger features for the pitheciines, with *Cacajao/Chiropotes* more extreme than *Pithecia*, smaller features for *Ateles*, and intermediate feature size for *Callicebus*. No comparisons of variance for *Tfv* yield significant differences and single comparisons of variance for *Vvv* and *Sdv* yield significant differences, and both indicate higher variance in *Cacajao/Chiropotes* (Table 5).

Indicators of feature depth (*Sv*, *S5v*) mirror the results for feature volume (Fig. 4). And for both variables, *Ateles*

TABLE 2. Pairwise comparisons of incisor microwear textures

Variable	Comparison	Z	Variable	Comparison	Z
<i>Str</i>	<i>Ateles</i> – <i>Callicebus</i>	2.12*	<i>Sdv</i>	<i>Ateles</i> – <i>Callicebus</i>	0.28
	<i>Ateles</i> – <i>Pithecia</i>	1.28		<i>Ateles</i> – <i>Pithecia</i>	2.70**
	<i>Ateles</i> – <i>Cacajao</i> / <i>Chiropotes</i>	1.50		<i>Ateles</i> – <i>Cacajao</i> / <i>Chiropotes</i>	0.77
	<i>Callicebus</i> – <i>Pithecia</i>	1.20		<i>Callicebus</i> – <i>Pithecia</i>	3.67***
	<i>Callicebus</i> – <i>Cacajao</i> / <i>Chiropotes</i>	0.26		<i>Callicebus</i> – <i>Cacajao</i> / <i>Chiropotes</i>	2.06*
	<i>Pithecia</i> – <i>Cacajao</i> / <i>Chiropotes</i>	0.65		<i>Pithecia</i> – <i>Cacajao</i> / <i>Chiropotes</i>	3.96****
<i>Ssk</i>	<i>Ateles</i> – <i>Callicebus</i>	1.72	<i>Vvv</i>	<i>Ateles</i> – <i>Callicebus</i>	1.42
	<i>Ateles</i> – <i>Pithecia</i>	0.85		<i>Ateles</i> – <i>Pithecia</i>	0.28
	<i>Ateles</i> – <i>Cacajao</i> / <i>Chiropotes</i>	2.29*		<i>Ateles</i> – <i>Cacajao</i> / <i>Chiropotes</i>	2.60**
	<i>Callicebus</i> – <i>Pithecia</i>	1.16		<i>Callicebus</i> – <i>Pithecia</i>	2.58**
	<i>Callicebus</i> – <i>Cacajao</i> / <i>Chiropotes</i>	0.13		<i>Callicebus</i> – <i>Cacajao</i> / <i>Chiropotes</i>	1.57
	<i>Pithecia</i> – <i>Cacajao</i> / <i>Chiropotes</i>	1.40		<i>Pithecia</i> – <i>Cacajao</i> / <i>Chiropotes</i>	3.44***
<i>Asfc</i>	<i>Ateles</i> – <i>Callicebus</i>	2.48*	<i>Tfv</i>	<i>Ateles</i> – <i>Callicebus</i>	2.65**
	<i>Ateles</i> – <i>Pithecia</i>	1.92		<i>Ateles</i> – <i>Pithecia</i>	0.31
	<i>Ateles</i> – <i>Cacajao</i> / <i>Chiropotes</i>	2.77**		<i>Ateles</i> – <i>Cacajao</i> / <i>Chiropotes</i>	1.48
	<i>Callicebus</i> – <i>Pithecia</i>	0.45		<i>Callicebus</i> – <i>Pithecia</i>	3.38***
	<i>Callicebus</i> – <i>Cacajao</i> / <i>Chiropotes</i>	0.33		<i>Callicebus</i> – <i>Cacajao</i> / <i>Chiropotes</i>	1.06
	<i>Pithecia</i> – <i>Cacajao</i> / <i>Chiropotes</i>	0.70		<i>Pithecia</i> – <i>Cacajao</i> / <i>Chiropotes</i>	2.09*
<i>Sdr</i>	<i>Ateles</i> – <i>Callicebus</i>	2.30*	<i>S5v</i>	<i>Ateles</i> – <i>Callicebus</i>	0.76
	<i>Ateles</i> – <i>Pithecia</i>	1.56		<i>Ateles</i> – <i>Pithecia</i>	0.00
	<i>Ateles</i> – <i>Cacajao</i> / <i>Chiropotes</i>	2.49*		<i>Ateles</i> – <i>Cacajao</i> / <i>Chiropotes</i>	2.43*
	<i>Callicebus</i> – <i>Pithecia</i>	0.56		<i>Callicebus</i> – <i>Pithecia</i>	1.09
	<i>Callicebus</i> – <i>Cacajao</i> / <i>Chiropotes</i>	0.52		<i>Callicebus</i> – <i>Cacajao</i> / <i>Chiropotes</i>	2.50*
	<i>Pithecia</i> – <i>Cacajao</i> / <i>Chiropotes</i>	1.08		<i>Pithecia</i> – <i>Cacajao</i> / <i>Chiropotes</i>	2.96**
<i>HAsfc₉</i>	<i>Ateles</i> – <i>Callicebus</i>	2.35*	<i>Sv</i>	<i>Ateles</i> – <i>Callicebus</i>	1.08
	<i>Ateles</i> – <i>Pithecia</i>	1.94		<i>Ateles</i> – <i>Pithecia</i>	0.40
	<i>Ateles</i> – <i>Cacajao</i> / <i>Chiropotes</i>	2.32*		<i>Ateles</i> – <i>Cacajao</i> / <i>Chiropotes</i>	2.45*
	<i>Callicebus</i> – <i>Pithecia</i>	0.56		<i>Callicebus</i> – <i>Pithecia</i>	2.02*
	<i>Callicebus</i> – <i>Cacajao</i> / <i>Chiropotes</i>	0.13		<i>Callicebus</i> – <i>Cacajao</i> / <i>Chiropotes</i>	1.72
	<i>Pithecia</i> – <i>Cacajao</i> / <i>Chiropotes</i>	0.35		<i>Pithecia</i> – <i>Cacajao</i> / <i>Chiropotes</i>	3.25*
<i>Hasfc₈₁</i>	<i>Ateles</i> – <i>Callicebus</i>	2.55*	<i>Sda</i>	<i>Ateles</i> – <i>Callicebus</i>	0.88
	<i>Ateles</i> – <i>Pithecia</i>	1.78		<i>Ateles</i> – <i>Pithecia</i>	3.03**
	<i>Ateles</i> – <i>Cacajao</i> / <i>Chiropotes</i>	2.46*		<i>Ateles</i> – <i>Cacajao</i> / <i>Chiropotes</i>	0.32
	<i>Callicebus</i> – <i>Pithecia</i>	0.62		<i>Callicebus</i> – <i>Pithecia</i>	2.48*
	<i>Callicebus</i> – <i>Cacajao</i> / <i>Chiropotes</i>	0.01		<i>Callicebus</i> – <i>Cacajao</i> / <i>Chiropotes</i>	0.45
	<i>Pithecia</i> – <i>Cacajao</i> / <i>Chiropotes</i>	0.56		<i>Pithecia</i> – <i>Cacajao</i> / <i>Chiropotes</i>	2.87**

Those comparisons where $P \leq \alpha = 0.05$ are bolded. P -values are indicated as *(≤ 0.05), **(≤ 0.01), ***(≤ 0.001), and ****(≤ 0.0001).

is significantly different from all other taxa, *Callicebus* is different from all except *Pithecia*, and *Cacajao*/*Chiropotes* is significantly different from all except for *Pithecia* (Table 4). The direction of difference indicates the deepest features for *Cacajao*/*Chiropotes*, intermediate feature depth for *Pithecia* and *Callicebus*, and the shallowest features for *Ateles*. Comparisons of variance indicate a single difference for *Sv*, *Pithecia*–*Ateles*, in which *Pithecia* has higher variance (Table 5). For *S5v*, *Ateles* has significantly lower variance than all other taxa (Table 5).

The measure of feature area, *Sda*, shows that *Callicebus* and *Cacajao*/*Chiropotes* are significantly different (Tables 1 and 4; Fig. 4), indicating relatively narrower scratches on *Callicebus* canines. Comparisons of variance indicate no significant differences for *Sda*.

In sum, the pitheciid canines are clearly distinct from *Ateles* in terms of anisotropy, feature density, and complexity; further, feature complexity separates the pitheciines from *Callicebus*, which falls between them and *Ateles*. As predicted, measures of feature volume indicate that *Cacajao*/*Chiropotes* canines have the largest features, *Ateles* canines have, in general, the smallest, *Pithecia* canines are similar to *Cacajao*/*Chiropotes*, and *Callicebus* canines tend to be intermediate between the pitheciines and *Ateles* (Figs. 3 and 4).

Intraspecific comparisons of incisor textures to canine textures

Ateles incisors and canines are characterized by low complexity surfaces with shallow features that are more isotropic than in the other analyzed taxa (Table 1; Figs. 3 and 4). Not surprisingly, few variables indicate significant differences between their incisors and canines. *Ateles* canine textures do tend to be more complex (i.e., significantly higher *Asfc*), more heterogeneous (i.e., significantly higher *HAsfc₉* and *HAsfc₈₁*), and to have higher *Sda* (Table 6). No significant differences are observed between *Ateles* incisors and canines for measures of feature volume (*Vvv*, *Tfv*, *Sdv*) or depth (*S5v*, *Sv*).

The pitheciids (*Callicebus*, *Pithecia*, *Cacajao*/*Chiropotes*) all show roughly the same pattern of difference between their canines and incisors. Pitheciid canines have larger features, more complex surfaces, and more heterogeneous surfaces than their incisors (Table 1; Figs. 3 and 4), which are reflected by significantly higher canine *Asfc*, *Sdr*, *Vvv*, *Sv*, *S5v*, *HAsfc₉*, and *HAsfc₈₁* than incisor values for all of pitheciid samples (Table 6). The magnitude of difference between the canine and incisor textures is, however, more pronounced for the pitheciines (*Pithecia*, *Cacajao*/*Chiropotes*) than for *Callicebus* (Table 6; Figs. 3 and 4). In addition, *Pithecia* canines

TABLE 3. Levene's test of incisor microwear textures

Variable	Comparison	F	Variable	Comparison	F
<i>Str</i>	<i>Ateles–Callicebus</i>	0.15	<i>Sdv</i>	<i>Ateles–Callicebus</i>	12.22**
	<i>Ateles–Pithecia</i>	0.04		<i>Ateles–Pithecia</i>	15.38***
	<i>Ateles–Cacajao/Chiropotes</i>	2.80		<i>Ateles–Cacajao/Chiropotes</i>	0.06
	<i>Callicebus–Pithecia</i>	0.42		<i>Callicebus–Pithecia</i>	0.95
	<i>Callicebus–Cacajao/Chiropotes</i>	1.95		<i>Callicebus–Cacajao/Chiropotes</i>	6.28*
<i>Ssk</i>	<i>Pithecia–Cacajao/Chiropotes</i>	4.22*	<i>Vvu</i>	<i>Pithecia–Cacajao/Chiropotes</i>	7.61**
	<i>Ateles–Callicebus</i>	1.06		<i>Ateles–Callicebus</i>	0.09
	<i>Ateles–Pithecia</i>	<0.01		<i>Ateles–Pithecia</i>	2.15
	<i>Ateles–Cacajao/Chiropotes</i>	0.33		<i>Ateles–Cacajao/Chiropotes</i>	6.14*
	<i>Callicebus–Pithecia</i>	1.67		<i>Callicebus–Pithecia</i>	1.68
<i>Asfc</i>	<i>Callicebus–Cacajao/Chiropotes</i>	0.18	<i>Tfv</i>	<i>Callicebus–Cacajao/Chiropotes</i>	3.38
	<i>Pithecia–Cacajao/Chiropotes</i>	0.48		<i>Pithecia–Cacajao/Chiropotes</i>	12.77***
	<i>Ateles–Callicebus</i>	1.90		<i>Ateles–Callicebus</i>	1.98
	<i>Ateles–Pithecia</i>	4.84*		<i>Ateles–Pithecia</i>	<0.01
	<i>Ateles–Cacajao/Chiropotes</i>	2.69		<i>Ateles–Cacajao/Chiropotes</i>	0.16
<i>Sdr</i>	<i>Callicebus–Pithecia</i>	2.25	<i>S5v</i>	<i>Callicebus–Pithecia</i>	2.86
	<i>Callicebus–Cacajao/Chiropotes</i>	0.44		<i>Callicebus–Cacajao/Chiropotes</i>	0.97
	<i>Pithecia–Cacajao/Chiropotes</i>	0.66		<i>Pithecia–Cacajao/Chiropotes</i>	0.27
	<i>Ateles–Callicebus</i>	0.88		<i>Ateles–Callicebus</i>	2.91
	<i>Ateles–Pithecia</i>	3.43		<i>Ateles–Pithecia</i>	0.20
<i>HAsfc₉</i>	<i>Ateles–Cacajao/Chiropotes</i>	4.78*	<i>Sv</i>	<i>Ateles–Cacajao/Chiropotes</i>	0.21
	<i>Callicebus–Pithecia</i>	3.56		<i>Callicebus–Pithecia</i>	2.19
	<i>Callicebus–Cacajao/Chiropotes</i>	2.59		<i>Callicebus–Cacajao/Chiropotes</i>	2.70
	<i>Pithecia–Cacajao/Chiropotes</i>	1.83		<i>Pithecia–Cacajao/Chiropotes</i>	<0.01
	<i>Ateles–Callicebus</i>	1.20		<i>Ateles–Callicebus</i>	0.90
<i>Hasfc₈₁</i>	<i>Ateles–Pithecia</i>	3.75	<i>Sda</i>	<i>Ateles–Pithecia</i>	0.49
	<i>Ateles–Cacajao/Chiropotes</i>	2.81		<i>Ateles–Cacajao/Chiropotes</i>	2.34
	<i>Callicebus–Pithecia</i>	1.87		<i>Callicebus–Pithecia</i>	<0.01
	<i>Callicebus–Cacajao/Chiropotes</i>	0.76		<i>Callicebus–Cacajao/Chiropotes</i>	6.78*
	<i>Pithecia–Cacajao/Chiropotes</i>	0.29		<i>Pithecia–Cacajao/Chiropotes</i>	4.53*
	<i>Ateles–Callicebus</i>	0.74		<i>Ateles–Callicebus</i>	6.01*
	<i>Ateles–Pithecia</i>	5.15*		<i>Ateles–Pithecia</i>	12.97***
	<i>Ateles–Cacajao/Chiropotes</i>	3.89		<i>Ateles–Cacajao/Chiropotes</i>	0.45
	<i>Callicebus–Pithecia</i>	3.85		<i>Callicebus–Pithecia</i>	0.17
	<i>Callicebus–Cacajao/Chiropotes</i>	2.26		<i>Callicebus–Cacajao/Chiropotes</i>	4.62**
	<i>Pithecia–Cacajao/Chiropotes</i>	0.30		<i>Pithecia–Cacajao/Chiropotes</i>	13.61***

Those comparisons where $P \leq \alpha = 0.05$ are bolded. P -values are indicated as *(<0.05), **(<0.01), ***(<0.001), and ****(<0.0001).

can be distinguished from their incisors by having significantly more anisotropic surfaces (i.e., lower *Str*) and a significantly greater density of scratches (i.e., lower *Ssk*).

Comparisons of variance (Table 7) reflect a few consistent patterns. First, for heterogeneity of complexity, *HAsfc₉* and *HAsfc₈₁*, all comparisons yield significant differences and indicate higher variance for the incisors than the canines for all taxa. For *Ateles*, the other significant differences (for *Sda* and *Sdv*) also indicate higher variance for the incisors. For the pitheciids, the pattern is reversed and all significant comparisons, excluding *HAsfc₉* and *HAsfc₈₁*, indicate higher variance for the canines.

Multivariate analysis

Many of the analyzed variables exhibit substantial multicollinearity when all specimens and teeth are pooled (Table 8); thus, a multivariate principal components analysis (PCA) of the combined sample of incisors and canines for all taxa was performed to investigate groupings within the sample. Four principal components (PCs) contain factor loadings greater than |0.7001|; combined, these four PCs explain 82.4% of the variance in the sample (Table 9). However, separation among taxa or tooth types is only evident when the first two PCs are graphed.

In multivariate space, there is substantial overlap between canine and incisor textures; although, general trends are evident. The first PC separates those surfaces that are the most complex and with the largest features, which plot to the right along the x -axis, from those that have less complex surfaces with smaller features, which plot to the left (Fig. 6). As observed with the univariate analyses, the PCA reveals greater interspecific dispersion of data values for canine textures (Fig. 6B) than incisor textures (Fig. 6A) on the x -axis (PC 1). In fact, in multivariate space the incisors are poorly separated among species. The incisors of all taxa tend to be skewed to the lower left quadrant of the PC 1 versus PC 2 graph, which emphasizes simple wear textures with small features. The pitheciids show greater dispersion along the PC 2 axis, which emphasizes more heterogeneous wear surfaces (i.e., higher *HAsfc₉* and *HAsfc₈₁*) in some individuals.

Both *Pithecia* and *Cacajao/Chiropotes* canines overlap in their distributions and plot to the right of the PC 1 axis, with little overlap observed with *Ateles* canine textures (Fig. 6B). The center of the pitheciine, *Pithecia* and *Chiropotes/Cacajao*, canine cluster overlaps with that of *Callicebus* canines; though, the pitheciine canines present more extreme positive values on PC 1, which emphasizes their complex surfaces with deep features (Fig. 6B). *Callicebus* canine textures overlap

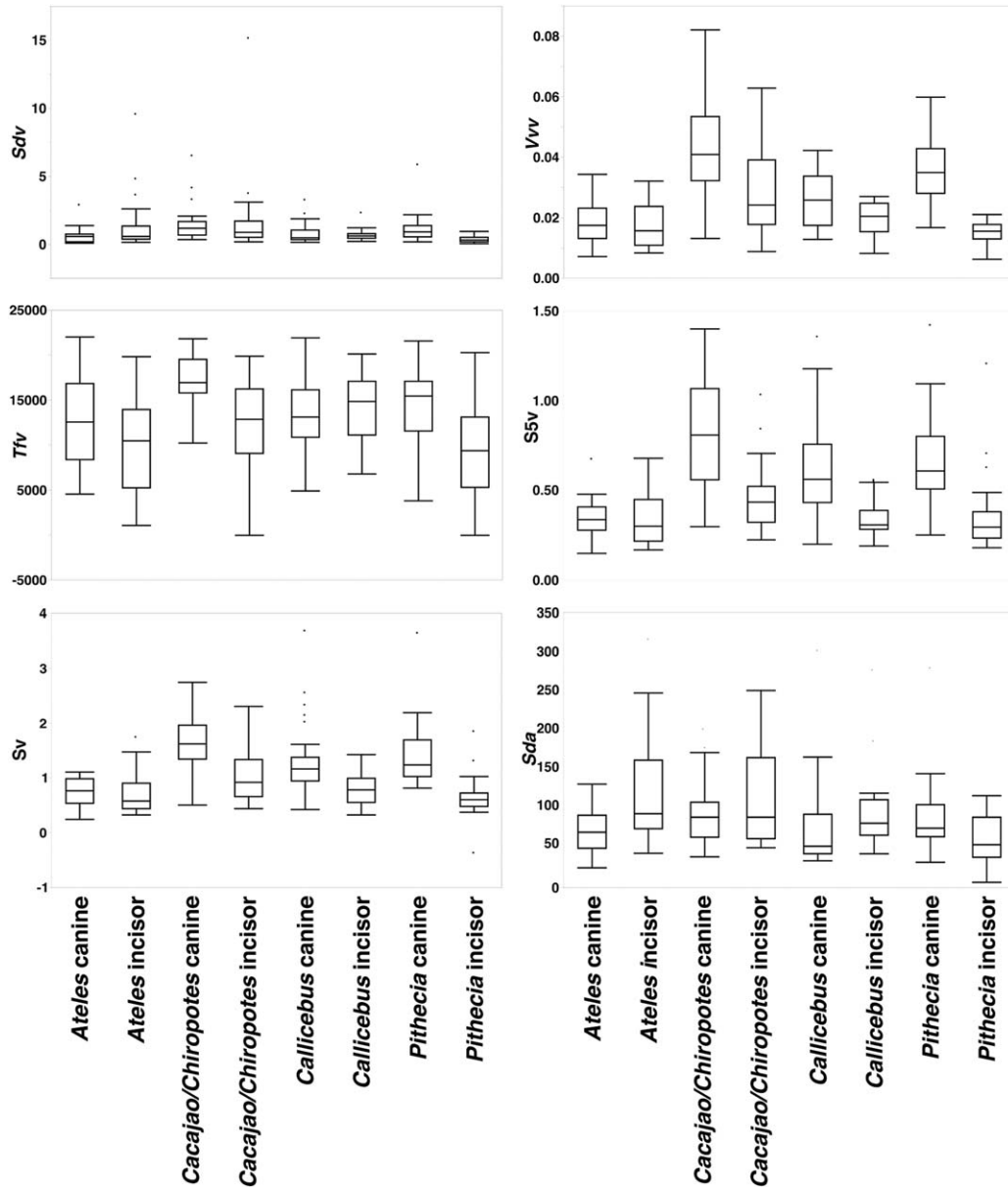


Fig. 4. Box and Whisker plots for three measures of feature volume (Sdv , Vvv , Tfv), two measures of feature depth (Su , $S5v$), and a measure of feature area (Sda).

both *Ateles* and the pitheciines, emphasizing the intermediacy of the canine texture values.

A univariate analysis of PC 1 scores reinforces the pattern described above and shows that the pitheciine canines have the largest microwear features and the most complex microwear surfaces on average. Indeed, the PC 1 scores (Fig. 7) reflect a continuum of feature size and complexity. In fact, for PC 1 scores, the largest observed differences are between pitheciine (*Pithecia* and *Cacajao/Chiropotes*) canines and the incisors of *Ateles*, *Pithecia*, and *Callicebus* (Table 10). The similarity of pitheciine canine textures in multivariate space is reflected by the absence of significance differences between *Pithecia* and *Cacajao/Chiropotes* canines. Further, the strong overlap between the incisor textures of all taxa in the univariate analysis is also reflected by the general lack of significant differences among them

for PC 1 scores. The only significant differences for incisor PC 1 scores is between *Cacajao/Chiropotes* and *Ateles* and *Pithecia*, indicating more positive PC 1 values for *Cacajao/Chiropotes*, and between *Callicebus* and *Pithecia* incisors, indicating more positive values for *Callicebus* (Table 10). In summary, the multivariate analysis shows that microwear textures overlap significantly for the incisors of all analyzed taxa but show greater dispersion for the canines.

DISCUSSION

Incisor and especially canine data separate the taxa in some expected ways that give confidence that microwear textures can be used as a proxy to reconstruct anterior tooth use behaviors in some fossil primates.

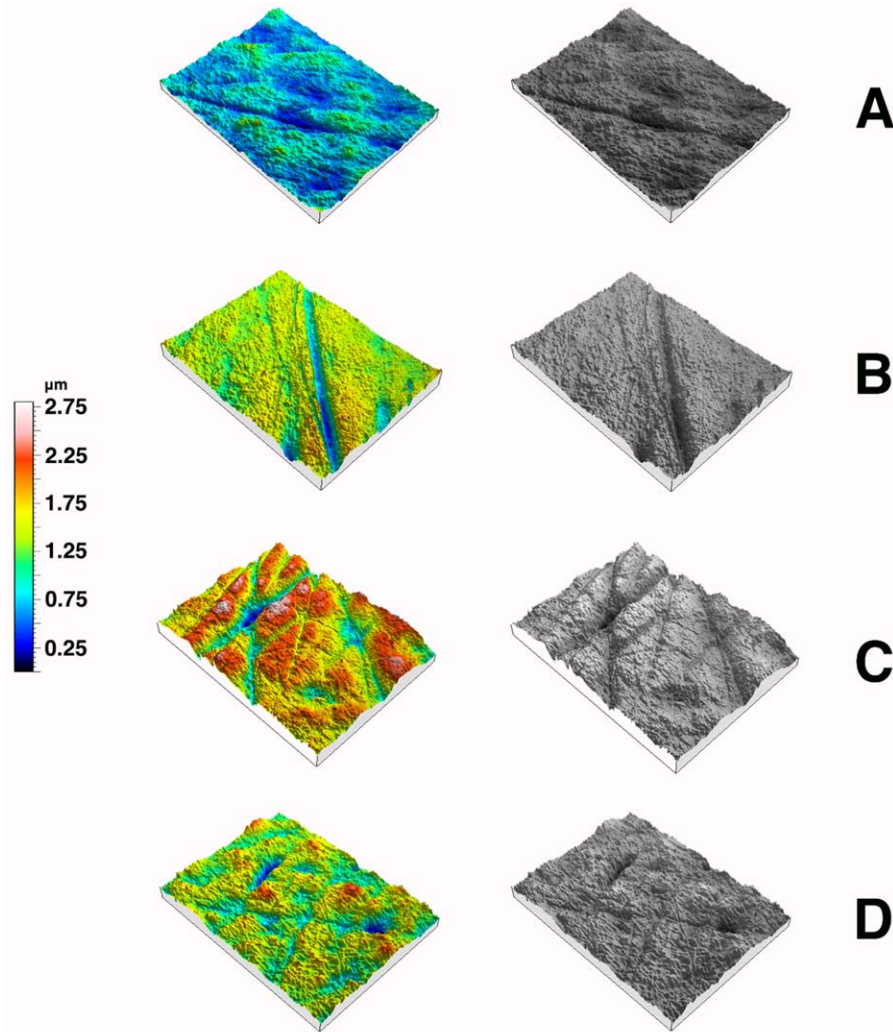


Fig. 5. Simulations of wear surfaces on maxillary canine labial surfaces. (A) *Ateles*, (B) *Callicebus*, (C) *Cacajao*, and (D) *Pithecia*. Each image is $138 \mu\text{m} \times 102 \mu\text{m}$.

Incisor microwear and tooth use

Although incisor microwear textures overlap substantially among the analyzed taxa in both univariate and multivariate space (Table 1; Figs. 3, 4, and 6A), the pattern observed in this study reflects a continuum of feature size and complexity. *Pithecia* and *Ateles* tend to lie at one extreme of feature size, *Cacajao/Chiropotes* lies at the other, and *Callicebus* is intermediate for many measures. *Ateles* incisors are further distinguished from the other taxa by having microwear surfaces with lower heterogeneity, lower anisotropy, and lower feature density (Tables 1 and 2, Figs. 3 and 4). These findings are consistent with the observed *Ateles* dietary focus on soft foods, like ripe fruits, that do not require extensive preparation with the anterior teeth (Eaglen, 1984; Anapol and Lee, 1994; Norconk et al., 2009). The larger, more anisotropic, and more variable features for *Callicebus* and *Cacajao/Chiropotes* incisors are consistent with their use as part of sclerocarpic-feeding behaviors (Kinzey and Norconk, 1990; Anapol and Lee, 1994; Norconk, 2011).

Counter to predictions, both measures of feature complexity, *Asfc* and *Sdr*, poorly separate the incisors of the examined taxa (Table 2). The finding that incisor complexity poorly separates taxa in this study is, however, in agreement with the results of Krueger and Ungar (2010) who also found that *Asfc* poorly separated the incisors of bioarchaeological human samples with differences in anterior tooth use. Further in contrast to predictions, *Pithecia* incisor microwear texture sizes (*Sdv*, *Vvv*, *Tfv*, *Sda*, *Sv*, *S5v*) were found to be significantly smaller than those of *Cacajao/Chiropotes* (Table 2). This is consistent with observations that *Pithecia* consumes a less demanding diet (Kinzey, 1992, 1997b; Rosenberger et al., 1996); however, the general similarity of *Pithecia* and *Ateles* for these measures and the magnitude of differences between *Pithecia* and the sclerocarpic-harvesting *Cacajao/Chiropotes*, which are anatomically and behaviorally comparable, still defies expectations. The discordance may be explained by distinct patterns of incisor use in the two pitheciine groups that we examined; though, it is not clear from the published literature what that pattern

TABLE 4. Pairwise comparisons of canine microwear textures

Variable	Comparison	Z	Variable	Comparison	Z
<i>Str</i>	<i>Ateles–Callicebus</i>	2.18*	<i>Sdv</i>	<i>Ateles–Callicebus</i>	0.59
	<i>Ateles–Pithecia</i>	1.40		<i>Ateles–Pithecia</i>	2.50*
	<i>Ateles–Cacajao/Chiropotes</i>	1.17		<i>Ateles–Cacajao/Chiropotes</i>	2.93**
	<i>Callicebus–Pithecia</i>	0.04		<i>Callicebus–Pithecia</i>	2.28*
	<i>Callicebus–Cacajao/Chiropotes</i>	0.81		<i>Callicebus–Cacajao/Chiropotes</i>	3.12**
<i>Ssk</i>	<i>Pithecia–Cacajao/Chiropotes</i>	0.37	<i>Vvv</i>	<i>Pithecia–Cacajao/Chiropotes</i>	0.56
	<i>Ateles–Callicebus</i>	2.98**		<i>Ateles–Callicebus</i>	2.86**
	<i>Ateles–Pithecia</i>	3.03**		<i>Ateles–Pithecia</i>	4.37****
	<i>Ateles–Cacajao/Chiropotes</i>	2.60**		<i>Ateles–Cacajao/Chiropotes</i>	4.63****
	<i>Callicebus–Pithecia</i>	0.18		<i>Callicebus–Pithecia</i>	2.45*
<i>Asfc</i>	<i>Callicebus–Cacajao/Chiropotes</i>	0.26	<i>Tfv</i>	<i>Callicebus–Cacajao/Chiropotes</i>	3.28**
	<i>Pithecia–Cacajao/Chiropotes</i>	0.18		<i>Pithecia–Cacajao/Chiropotes</i>	1.59
	<i>Ateles–Callicebus</i>	3.46***		<i>Ateles–Callicebus</i>	0.90
	<i>Ateles–Pithecia</i>	4.66****		<i>Ateles–Pithecia</i>	1.16
	<i>Ateles–Cacajao/Chiropotes</i>	5.36****		<i>Ateles–Cacajao/Chiropotes</i>	2.96**
<i>Sdr</i>	<i>Callicebus–Pithecia</i>	1.39	<i>S5v</i>	<i>Callicebus–Pithecia</i>	0.91
	<i>Callicebus–Cacajao/Chiropotes</i>	2.56*		<i>Callicebus–Cacajao/Chiropotes</i>	3.26**
	<i>Pithecia–Cacajao/Chiropotes</i>	1.40		<i>Pithecia–Cacajao/Chiropotes</i>	2.27*
	<i>Ateles–Callicebus</i>	3.62***		<i>Ateles–Callicebus</i>	4.13****
	<i>Ateles–Pithecia</i>	5.00****		<i>Ateles–Pithecia</i>	4.37****
<i>HAsfc₉</i>	<i>Ateles–Cacajao/Chiropotes</i>	5.24****	<i>Sv</i>	<i>Ateles–Cacajao/Chiropotes</i>	4.84****
	<i>Callicebus–Pithecia</i>	2.01*		<i>Callicebus–Pithecia</i>	0.92
	<i>Callicebus–Cacajao/Chiropotes</i>	3.25**		<i>Callicebus–Cacajao/Chiropotes</i>	2.60**
	<i>Pithecia–Cacajao/Chiropotes</i>	1.61		<i>Pithecia–Cacajao/Chiropotes</i>	1.73
	<i>Ateles–Callicebus</i>	3.32***		<i>Ateles–Callicebus</i>	4.08****
<i>Hasfc₈₁</i>	<i>Ateles–Pithecia</i>	3.59***	<i>Sda</i>	<i>Ateles–Pithecia</i>	4.50****
	<i>Ateles–Cacajao/Chiropotes</i>	3.12**		<i>Ateles–Cacajao/Chiropotes</i>	4.96****
	<i>Callicebus–Pithecia</i>	1.83		<i>Callicebus–Pithecia</i>	0.95
	<i>Callicebus–Cacajao/Chiropotes</i>	0.51		<i>Callicebus–Cacajao/Chiropotes</i>	3.01**
	<i>Pithecia–Cacajao/Chiropotes</i>	1.30		<i>Pithecia–Cacajao/Chiropotes</i>	1.77
<i>Hasfc₈₁</i>	<i>Ateles–Callicebus</i>	3.41***	<i>Sda</i>	<i>Ateles–Callicebus</i>	0.88
	<i>Ateles–Pithecia</i>	4.35****		<i>Ateles–Pithecia</i>	0.84
	<i>Ateles–Cacajao/Chiropotes</i>	4.49****		<i>Ateles–Cacajao/Chiropotes</i>	1.50
	<i>Callicebus–Pithecia</i>	2.42*		<i>Callicebus–Pithecia</i>	1.93
	<i>Callicebus–Cacajao/Chiropotes</i>	2.24*		<i>Callicebus–Cacajao/Chiropotes</i>	2.54*
	<i>Pithecia–Cacajao/Chiropotes</i>	0.62		<i>Pithecia–Cacajao/Chiropotes</i>	0.73

Those comparisons where $P \leq \alpha = 0.05$ are bolded. P -values are indicated as *(≤ 0.05), **(≤ 0.01), ***(≤ 0.001), and ****(≤ 0.0001).

would be. *Cacajao* and *Chiropotes* are ecological vicars and tend to be allopatrically distributed (Kinzey, 1997c; Norconk, 2011), while *Pithecia* is variably sympatric with both of them. *Pithecia* has been indicated to be more folivorous than either *Cacajao* or *Chiropotes*. For *Cacajao* and *Chiropotes*, leaves are generally reported to account for less than 5% of consumed resources (e.g., Ayres, 1989; van Roosmalen et al., 1981; Kinzey and Norconk, 1993; Norconk, 1996; Boubli, 1999); while low, the percentage of leaves in the diets of *Pithecia* species is generally greater than 5% and is reported to be as high as 16% (Happel, 1982; Soini, 1986; Kinzey and Norconk, 1993; Peres, 1993). Both Ungar (1994) and Kelley (1990) found that leaf ingestion produces distinctive microwear signatures—typically lower feature densities compared with fruit eaters. This may indicate that *Pithecia* and *Chiropotes/Cacajao* are using their incisors to process foods with different degrees of mechanical protection, or are using those teeth in different manners or extents for food acquisition. It is unclear if the slightly higher rates of folivory for *Pithecia* than *Cacajao/Chiropotes* could account for their differences in incisor microwear. Further, more detailed observational data documenting the ways in which primates considered in this study use their incisors during food acquisition and processing (sensu Ungar, 1994) could provide insight into why *Pithecia* incisor microwear textures differ

substantially from other pitheciids. It should also be noted that the analyzed taxa span a small range of the total dietary breadth present in extant platyrrhines; specifically, all of the taxa included in this study are highly frugivorous and, as such, may frequently use their incisors in similar ways (in contrast to the canines, which are discussed below). Broadening the analysis to include taxa spanning a broader range of observed platyrrhine diets, including folivores, will provide some insight into the greater than expected overlap among incisor microwear textures observed in this study.

Canine microwear and tooth use

Interpretations of anterior dental microwear always require a baseline of observations derived from extant taxa with documented variation in tooth use in dietary and nondietary contexts. However, this is an especially formidable challenge for canines where patterns are complicated because primates use these teeth in more than one biological role, from sexual display and fighting (e.g., McGraw et al., 2002; Leigh et al., 2008; Galbany et al., 2015) to ingestion and food fracture (e.g., Kinzey and Norconk, 1990; Rosenberger, 1992; Norconk et al., 1998; Barnett et al., 2005).

Results clearly indicate that, as predicted, canine microwear textures lie along a continuum, with *Ateles*

TABLE 5. Levene's test of canine microwear textures

Variable	Comparison	F	Variable	Comparison	F
<i>Str</i>	<i>Ateles-Callicebus</i>	0.33	<i>Sdv</i>	<i>Ateles-Callicebus</i>	0.26
	<i>Ateles-Pithecia</i>	2.92		<i>Ateles-Pithecia</i>	1.36
	<i>Ateles-Cacajao/Chiropotes</i>	1.17		<i>Ateles-Cacajao/Chiropotes</i>	3.78
	<i>Callicebus-Pithecia</i>	1.72		<i>Callicebus-Pithecia</i>	1.26
	<i>Callicebus-Cacajao/Chiropotes</i>	0.41		<i>Callicebus-Cacajao/Chiropotes</i>	4.76*
<i>Ssk</i>	<i>Pithecia-Cacajao/Chiropotes</i>	0.37	<i>Vvv</i>	<i>Pithecia-Cacajao/Chiropotes</i>	0.63
	<i>Ateles-Callicebus</i>	0.95		<i>Ateles-Callicebus</i>	2.73
	<i>Ateles-Pithecia</i>	0.00		<i>Ateles-Pithecia</i>	1.17
	<i>Ateles-Cacajao/Chiropotes</i>	0.18		<i>Ateles-Cacajao/Chiropotes</i>	6.50*
	<i>Callicebus-Pithecia</i>	0.67		<i>Callicebus-Pithecia</i>	1.28
<i>Asfc</i>	<i>Callicebus-Cacajao/Chiropotes</i>	0.14	<i>Tfv</i>	<i>Callicebus-Cacajao/Chiropotes</i>	0.05
	<i>Pithecia-Cacajao/Chiropotes</i>	0.13		<i>Pithecia-Cacajao/Chiropotes</i>	3.30
	<i>Ateles-Callicebus</i>	10.16**		<i>Ateles-Callicebus</i>	0.83
	<i>Ateles-Pithecia</i>	10.97**		<i>Ateles-Pithecia</i>	0.01
	<i>Ateles-Cacajao/Chiropotes</i>	15.03***		<i>Ateles-Cacajao/Chiropotes</i>	3.65
<i>Sdr</i>	<i>Callicebus-Pithecia</i>	3.35	<i>S5v</i>	<i>Callicebus-Pithecia</i>	0.77
	<i>Callicebus-Cacajao/Chiropotes</i>	1.09		<i>Callicebus-Cacajao/Chiropotes</i>	1.88
	<i>Pithecia-Cacajao/Chiropotes</i>	1.50		<i>Pithecia-Cacajao/Chiropotes</i>	4.03
	<i>Ateles-Callicebus</i>	6.55*		<i>Ateles-Callicebus</i>	7.94**
	<i>Ateles-Pithecia</i>	14.37***		<i>Ateles-Pithecia</i>	8.87**
<i>HAsfc₉</i>	<i>Ateles-Cacajao/Chiropotes</i>	20.84****	<i>Sv</i>	<i>Ateles-Cacajao/Chiropotes</i>	12.52****
	<i>Callicebus-Pithecia</i>	1.51		<i>Callicebus-Pithecia</i>	0.05
	<i>Callicebus-Cacajao/Chiropotes</i>	0.22		<i>Callicebus-Cacajao/Chiropotes</i>	1.06
	<i>Pithecia-Cacajao/Chiropotes</i>	1.94		<i>Pithecia-Cacajao/Chiropotes</i>	0.54
	<i>Ateles-Callicebus</i>	4.45*		<i>Ateles-Callicebus</i>	3.11
<i>Hasfc₈₁</i>	<i>Ateles-Pithecia</i>	17.62****	<i>Sda</i>	<i>Ateles-Pithecia</i>	5.36*
	<i>Ateles-Cacajao/Chiropotes</i>	2.17		<i>Ateles-Cacajao/Chiropotes</i>	4.00
	<i>Callicebus-Pithecia</i>	15.80***		<i>Callicebus-Pithecia</i>	0.11
	<i>Callicebus-Cacajao/Chiropotes</i>	0.01		<i>Callicebus-Cacajao/Chiropotes</i>	0.06
	<i>Pithecia-Cacajao/Chiropotes</i>	10.44**		<i>Pithecia-Cacajao/Chiropotes</i>	0.37
	<i>Ateles-Callicebus</i>	5.78*		<i>Ateles-Callicebus</i>	0.39
	<i>Ateles-Pithecia</i>	46.51****		<i>Ateles-Pithecia</i>	0.10
	<i>Ateles-Cacajao/Chiropotes</i>	5.70*		<i>Ateles-Cacajao/Chiropotes</i>	0.17
	<i>Callicebus-Pithecia</i>	29.34****		<i>Callicebus-Pithecia</i>	0.07
	<i>Callicebus-Cacajao/Chiropotes</i>	1.17		<i>Callicebus-Cacajao/Chiropotes</i>	0.08
	<i>Pithecia-Cacajao/Chiropotes</i>	6.96*		<i>Pithecia-Cacajao/Chiropotes</i>	<0.01

Those comparisons where $P \leq \alpha = 0.05$ are bolded. P -values are indicated as *(<0.05), **(<0.01), ***(<0.001), and ****(<0.0001).

having a low density of features, small features, low surface anisotropy, and low texture variation across the scanned surface. The pitheciids, in contrast, have a higher density of features, larger features, and features that are more anisotropic in orientation (Tables 1 and 4; Figs. (3 and 4), and 6B). Among the pitheciids, *Cacajao/Chiropotes* and *Callicebus* are the most divergent and *Pithecia* lies intermediate for several measures. These results appear to capture the specialized use of the pitheciine canines in seed predation activities, while comparisons of

incisor and canine textures within taxa may also capture the specialized use of the pitheciid canines in food processing. In this case, morphology (e.g., Kinzey, 1972, 1992; Greenfield, 1992a, b, 1996; Spencer, 2003; Plavcan and Ruff, 2008), field observations (e.g., Kinzey, 1974, 1992, 1997b; Kinzey and Norconk, 1990; Rosenberger, 1992; Norconk et al., 1998; Barnett et al., 2005; Norconk, 2007, 2011), and microwear textures are in agreement, which indicates that microwear will be useful for inferring patterns of specialized canine use in extinct primates.

TABLE 6. Pairwise comparisons of microwear textures between canines and incisors

Variable	<i>Ateles</i>	<i>Callicebus</i>	<i>Pithecia</i>	<i>Cacajao/Chiropotes</i>
<i>Str</i>	Z = 1.64	Z = 1.95	Z = 2.00*	Z = 1.19
<i>Ssk</i>	Z = 0.52	Z = 1.58	Z = 3.14**	Z = 1.43
<i>Asfc</i>	Z = 1.98*	Z = 2.67**	Z = 3.67***	Z = 4.26****
<i>Sdr</i>	Z = 1.33	Z = 2.77**	Z = 3.98****	Z = 4.33****
<i>HAsfc₉</i>	Z = 5.27****	Z = 6.29****	Z = 4.73****	Z = 5.65****
<i>HAsfc₈₁</i>	Z = 4.96****	Z = 5.94****	Z = 3.55***	Z = 4.85****
<i>Sdv</i>	Z = 1.17	Z = 0.60	Z = 4.44****	Z = 0.41
<i>Vvv</i>	Z = 0.38	Z = 2.35*	Z = 5.37***	Z = 3.03**
<i>Tfv</i>	Z = 1.64	Z = 0.58	Z = 3.34***	Z = 3.30**
<i>S5v</i>	Z = 0.55	Z = 4.39****	Z = 4.42****	Z = 3.64****
<i>Sv</i>	Z = 0.77	Z = 3.75***	Z = 5.16****	Z = 3.15**
<i>Sda</i>	Z = 2.04*	Z = 2.73**	Z = 1.92	Z = 0.55

Those comparisons where $P \leq \alpha = 0.05$ are bolded. P -values are indicated as *(<0.05), **(<0.01), ***(<0.001), and ****(<0.0001).

TABLE 7. Levene's test of microwear textures between canines and incisors

Variable	<i>Ateles</i>	<i>Callicebus</i>	<i>Pithecia</i>	<i>Cacajao/Chiropotes</i>
<i>Str</i>	$F = 0.12$	$F = 0.28$	$F = 5.68^*$	$F = 0.24$
<i>Ssk</i>	$F = 0.02$	$F = 0.12$	$F = 0.02$	$F = 0.01$
<i>Asfc</i>	$F = 0.31$	$F = 7.59^{**}$	$F = 0.01$	$F = 3.50$
<i>Sdr</i>	$F = 0.98$	$F = 5.77^*$	$F = 0.90$	$F = 6.43^*$
<i>HAsfc₉</i>	$F = 40.41^{****}$	$F = 26.13^{****}$	$F = 8.15^{**}$	$F = 15.46^{***}$
<i>HAsfc₈₁</i>	$F = 29.19^{****}$	$F = 19.15^{****}$	$F = 7.74^{**}$	$F = 11.46^{**}$
<i>Sdv</i>	$F = 7.67^{**}$	$F = 4.65^*$	$F = 7.45^{**}$	$F = 1.68$
<i>Vvv</i>	$F = 0.17$	$F = 2.99$	$F = 8.20^{**}$	$F = 0.53$
<i>Tfv</i>	$F = 0.36$	$F = 0.07$	$F = 0.88$	$F = 5.49^*$
<i>S5v</i>	$F = 1.93$	$F = 9.69^{**}$	$F = 2.01$	$F = 4.51^*$
<i>Sv</i>	$F = 1.00$	$F = 3.37$	$F = 4.65^*$	$F = 0.14$
<i>Sda</i>	$F = 7.36^*$	$F = 0.23$	$F = 0.44$	$F = 5.45^*$

Those comparisons where $P \leq \alpha = 0.05$ are bolded. P -values are indicated as $^*(\leq 0.05)$, $^{**}(\leq 0.01)$, $^{***}(\leq 0.001)$, and $^{****}(\leq 0.0001)$.

TABLE 8. Correlation coefficients among variables for all teeth and taxa pooled

<i>Tfv</i>	0.30^{****}										
<i>HAsfc₉</i>	0.13	-0.18[*]									
<i>HAsfc₈₁</i>	0.22^{**}	-0.15[*]	0.97^{****}								
<i>Ssk</i>	-0.24^{**}		-0.08	0.01	-0.01						
<i>Vvv</i>	0.64^{****}	0.29^{****}	-0.05	0.02	-0.47^{****}						
<i>Sda</i>	-0.22^{**}	0.06	-0.01	-0.04	-0.09	0.23^{**}					
<i>Sdv</i>	0.04	0.05	0.06	0.05	-0.09	0.33^{****}	0.69^{****}				
<i>S5v</i>	0.79^{****}	0.38^{****}	-0.08	0.02	-0.31^{****}	0.72^{****}	0.02	0.31^{****}			
<i>Str</i>	-0.21^{**}	-0.12	0.06	0.03	0.54^{****}	-0.52^{****}	-0.07	-0.05	-0.26^{***}		
<i>Sdr</i>	0.96^{****}	0.31^{****}	0.04	0.12	-0.21^{**}	0.63^{****}	-0.16[*]	0.06	0.77^{****}	-0.18[*]	
<i>Sv</i>	0.71^{****}	0.34^{****}	-0.07	0.02	-0.43^{****}	0.85^{****}	0.26^{***}	0.40^{****}	0.84^{****}	-0.35^{****}	0.70^{****}
	<i>Asfc</i>	<i>Tfv</i>	<i>HAsfc₉</i>	<i>HAsfc₈₁</i>	<i>Ssk</i>	<i>Vvv</i>	<i>Sda</i>	<i>Sdv</i>	<i>S5v</i>	<i>Str</i>	<i>Sdr</i>

Those comparisons where $P \leq \alpha = 0.05$ are bolded. P -values are indicated as $^*(\leq 0.05)$, $^{**}(\leq 0.01)$, $^{***}(\leq 0.001)$, and $^{****}(\leq 0.0001)$.

TABLE 9. Loadings for the principal components analysis of the pooled sample of canines and incisors

	PC 1	PC 2	PC 3	PC 4
<i>Asfc</i>	0.847	0.300	-0.338	0.154
<i>Tfv</i>	0.420	-0.246	-0.173	0.261
<i>HAsfc₉</i>	-0.012	0.929	0.318	-0.060
<i>HAsfc₈₁</i>	0.077	0.939	0.279	-0.052
<i>Ssk</i>	-0.489	0.094	-0.137	0.684
<i>Vvv</i>	0.890	-0.090	0.129	-0.130
<i>Sda</i>	0.128	-0.299	0.854	0.173
<i>Sdv</i>	0.330	-0.160	0.781	0.318
<i>S5v</i>	0.901	-0.014	-0.095	0.205
<i>Str</i>	-0.473	0.163	-0.103	0.717
<i>Sdr</i>	0.836	0.202	-0.339	0.204
<i>Sv</i>	0.934	-0.079	0.121	0.074
% variance explained	38.5	17.5	15.4	11.0

Those variables with loading greater than |0.700| are bolded.

Implications for inferring tooth use in fossil primates

Some extinct platyrrhines have been suggested to be pitheciines (e.g., *Cebupithecia*, *Nuciraptor*) or to be anatomically convergent with them (e.g., *Mohanimico*, *Soriacebus*), and many of these fossils preserve anterior teeth (Meldrum and Kay, 1997). Other, more distantly related, extinct primates are craniodentally reminiscent of pitheciines, including the Eocene amphipithecids *Myanmarpithecus*, *Pondongia* and, especially, *Ganlea*, which all have large, robust canines with apical surfaces that tend to wear heavily (Beard et al., 2009; Ramdarshan et al., 2010). Additionally, the African Miocene hominoids *Afropithecus* and *Kenyapithecus*, which share

procumbent incisors and large, stout, splayed canines with the pitheciines, have been suggested to be sclerocarp foragers (e.g., Leakey and Leakey, 1986; Leakey and Walker, 1997; McCrossin and Benefit, 1997; Deane, 2009). On the other hand, these apes differ from pitheciines in having thick molar enamel, and, at least in *Kenyapithecus*, marked canine sexual dimorphism (McCrossin and Benefit, 1997; Martin et al., 2003; Smith et al., 2003). Thus, it is unclear if the shared features indicate a sclerocarp-harvesting diet; though, as Leakey and Walker (1997, p. 231) noted, "tooth microwear studies might shed light on this." If the data from this study are incorporated into a broader baseline of comparative taxa, microwear texture analysis of the anterior dentition may help to elucidate the diet of these extinct taxa.

Small, minimally dimorphic canines have long been recognized as a hominin feature (e.g., Darwin, 1871; Greenfield, 1992c; White et al., 2006, 2015; Suwa et al., 2009; Ward et al., 2010; Simpson et al., 2015). For hominins, reduction in canine size and canine size sexual dimorphism (e.g., White et al., 2015) was coupled with changes in shape so that the maxillary canine was no longer honed (Greenfield, 1990). The origin of small, non-honing canines has historically been thought to be associated with a loss of their function as weapons, either because tools replaced them or because males no longer competed for mates (e.g., Plavcan, 2012; White et al., 2015). Alternatively, small hominin canines may have been co-opted for ingestive behaviors, essentially functioning as additional incisors (e.g., Le Gros Clark, 1967; Greenfield, 1992c; Ward et al., 2010; Manthi et al., 2012; Plavcan, 2012). Among the taxa analyzed in this study, *Ateles* and the pitheciines are poor analogs for

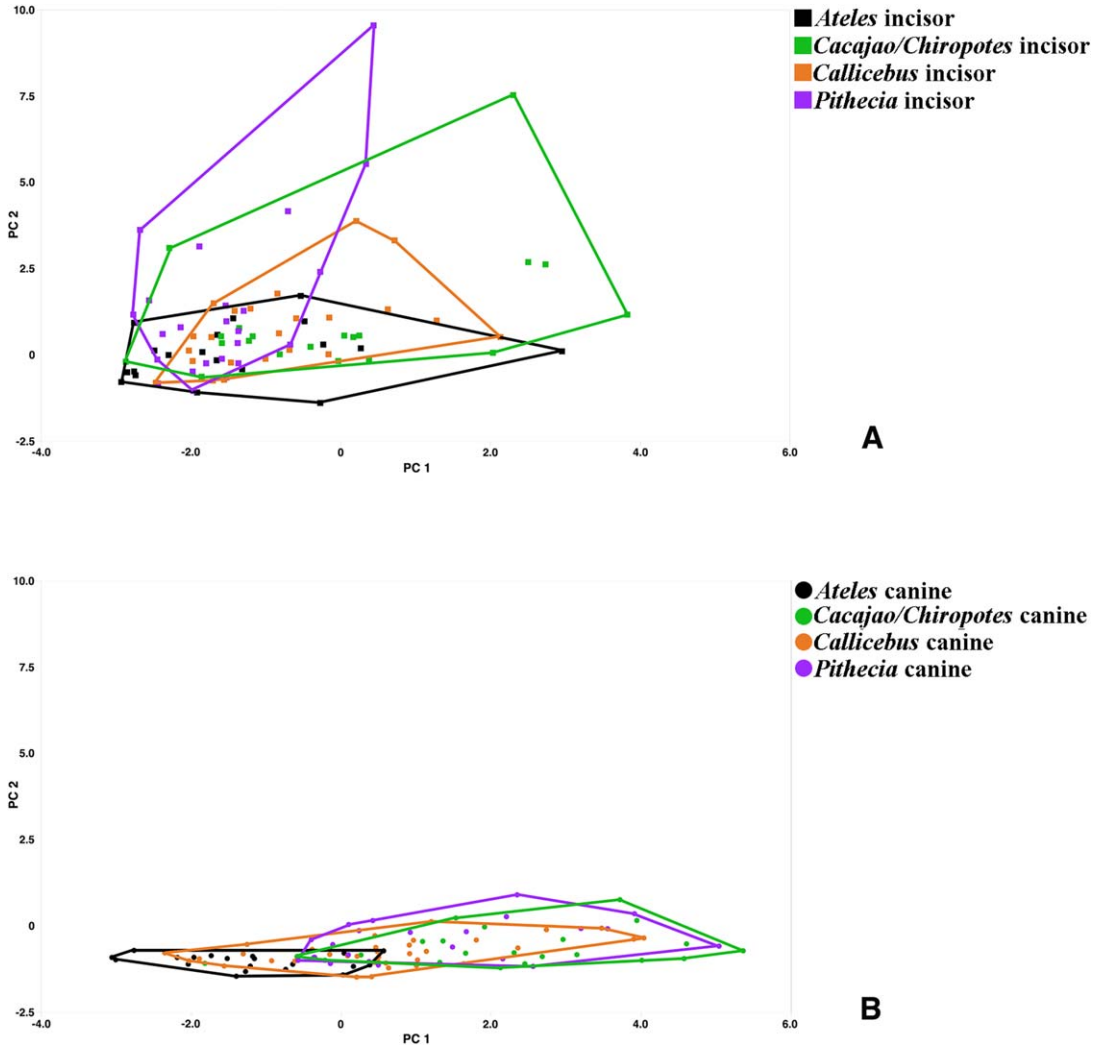


Fig. 6. Plot of first two principal components. Incisors and canines of all taxa were pooled for the computation of the principal components; however, the data for the incisors (A) and canines (B) are plotted separately to ease visualization.

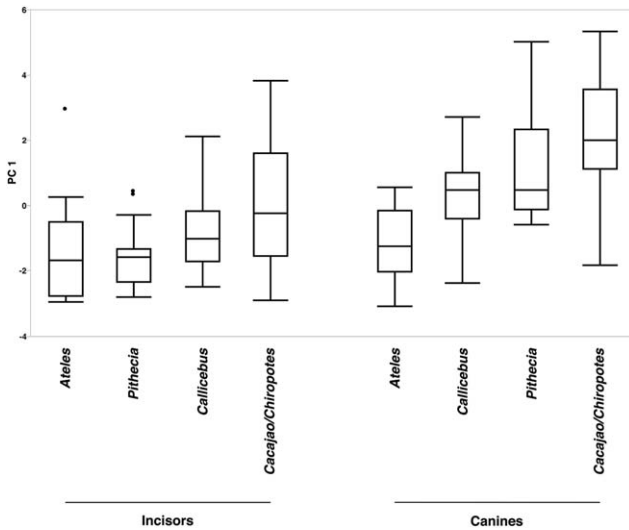


Fig. 7. Box and whisker plots for scores on first principal component. Results are ordered by median value and separated by tooth type.

hominin canine size, dimorphism, and use; however, *Callicebus* shares small, minimally-dimorphic canines with hominins and has been noted as a potential analog (e.g., Kinzey, 1974; Greenfield, 1992c). Dental microwear has been used to investigate canine use in fossil hominins (e.g., Puech and Albertini, 1984; Ryan and Johanson, 1989); however, those studies were generally qualitative in nature and only put results within a limited comparative context. With the addition of other taxa that vary in anterior dental use, including catarrhines, anterior dental microwear analyses will hopefully provide a missing piece of this puzzle needed to determine if/how hominins were using their canines in food acquisition and processing (e.g., Ward et al., 2010). Such data are especially important for testing hypotheses of tooth use given the absence of extant primate analogs with the functional morphology needed for direct comparison with fossil hominins.

CONCLUSION

This study compared patterns of incisor and canine microwear in a group of taxa for whom patterns of

TABLE 10. Results of Mann–Whitney *U* tests for loadings on PC 1

Comparison	<i>Z</i>
<i>Cacajao/Chiropotes</i> canine vs. <i>Pithecia</i> incisor	5.39****
<i>Pithecia</i> canine vs. <i>Pithecia</i> incisor	5.16****
<i>Cacajao/Chiropotes</i> canine vs. <i>Ateles</i> canine	5.06****
<i>Cacajao/Chiropotes</i> canine vs. <i>Ateles</i> incisor	4.93****
<i>Cacajao/Chiropotes</i> canine vs. <i>Callicebus</i> incisor	4.93****
<i>Pithecia</i> canine vs. <i>Ateles</i> canine	4.81****
<i>Callicebus</i> canine vs. <i>Pithecia</i> incisor	4.76****
<i>Pithecia</i> canine vs. <i>Ateles</i> incisor	4.73****
<i>Callicebus</i> canine vs. <i>Ateles</i> incisor	4.33****
<i>Pithecia</i> canine vs. <i>Callicebus</i> incisor	4.26****
<i>Callicebus</i> canine vs. <i>Ateles</i> canine	4.13****
<i>Cacajao/Chiropotes</i> canine vs. <i>Cacajao/Chiropotes</i> incisor	3.48***
<i>Callicebus</i> canine vs. <i>Callicebus</i> incisor	3.26**
<i>Cacajao/Chiropotes</i> canine vs. <i>Callicebus</i> canine	3.24**
<i>Cacajao/Chiropotes</i> incisor vs. <i>Pithecia</i> incisor	3.13**
<i>Pithecia</i> canine vs. <i>Cacajao/Chiropotes</i> incisor	2.79**
<i>Cacajao/Chiropotes</i> incisor vs. <i>Ateles</i> incisor	2.66**
<i>Callicebus</i> incisor vs. <i>Pithecia</i> incisor	2.33*
<i>Cacajao/Chiropotes</i> incisor vs. <i>Ateles</i> canine	2.04*
<i>Callicebus</i> incisor vs. <i>Ateles</i> incisor	1.95
<i>Cacajao/Chiropotes</i> canine vs. <i>Pithecia</i> canine	1.82
<i>Callicebus</i> canine vs. <i>Cacajao/Chiropotes</i> incisor	1.75
<i>Cacajao/Chiropotes</i> incisor vs. <i>Callicebus</i> incisor	1.33
<i>Ateles</i> canine vs. <i>Pithecia</i> incisor	1.19
<i>Pithecia</i> canine vs. <i>Callicebus</i> canine	1.13
<i>Callicebus</i> incisor vs. <i>Ateles</i> canine	1.06
<i>Ateles</i> incisor vs. <i>Ateles</i> canine	0.91
<i>Pithecia</i> incisor vs. <i>Ateles</i> incisor	0.46

Those comparisons where $P \leq \alpha = 0.05$ are bolded. *P*-values are indicated as *(≤ 0.05), **(≤ 0.01), ***(≤ 0.001), and ****(≤ 0.0001). Comparisons are sorted in decreasing order by their *Z*-values.

anterior tooth use in dietary contexts are relatively well documented. Incisor microwear strongly overlaps among taxa. Canine microwear shows greater separation among taxa than incisor microwear and is in line with expectations based on field observations of tooth use. This study is among the first to examine canine microwear within a comparative context and represents a step toward an understanding how extinct primates used these teeth as part of masticatory and non-masticatory behaviors.

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