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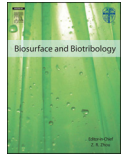
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Dental topography and microwear texture in *Sapajus apella*

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Abstract

Dental microwear texture pattern has been associated with aspects of diet for a broad range of mammalian taxa. The basic idea is that soft, tough foods are sheared with a steeper angle of approach between opposing occlusal surfaces, whereas hard, brittle items are crushed with forces perpendicular to those surfaces; and this difference is manifested in anisotropic, striated microwear textures for tough foods, and complex, pitted ones for hard objects. Other factors may, however, influence microwear texture pattern and confound diet signals. For example, if tooth surface slope influences angle of approach between opposing teeth, then perhaps wear-related changes in tooth shape could affect microwear pattern. This study evaluates the effects of occlusal topography on microwear texture for a series of variably worn upper second molars of one primate species, *Sapajus apella*. Results indicate no significant covariation between any measured topographic attribute (average slope, angularity, relief) and microwear texture variable (complexity, anisotropy, textural fill volume). This suggests that, for this taxon at least, wear-related changes in tooth form do not affect microwear pattern in a consistent manner. This implies that variably worn teeth can be included in samples for comparisons aimed at distinguishing groups by diet.

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Keywords: Tooth wear; Occlusal form; Masticatory kinematics

1. Introduction

1.1. Tooth form and function

Mammalian cheek teeth function to break down food into parcels small enough to swallow, and to increase nutrient accessibility. Teeth rupture protective casings, such as plant cell walls and insect exoskeletons, to release nutrients that could otherwise pass through the gut undigested. Fragmentation also increases exposed surface area for digestive enzymes to act on, which can lead to more complete assimilation of energy stored in foods [1–7]. Dental functional morphologists assume that nature selects for biological structures that maximize efficiency in the functions they perform in a given

environment [8]. Because different foods have different defenses against fracture [9] that are most effectively overcome in different ways [10], nature should select for mammals to evolve teeth of different shapes for different diets. This is the rationale by which paleontologists use tooth form to retrodict diets of fossil species.

Mammalian tooth form relates to function on two complementary levels [11]. These correspond to Butler's [12] “external” and “internal” environment, or Evans and Sanson's [13] “geometry of occlusion” and “geometry of function”. In these cases, teeth are considered to be guides for chewing and tools for breaking, respectively. The idea of teeth as guides for chewing dates to Aristotle, who associated “grinder-teeth” with lateral motions [14]. The basic model was developed, though, by Simpson [15], who contrasted mammalian cheek teeth with opposing crests from those with cusps that fit into basins, and vertical movement of the jaw from horizontal chewing motion. Vertical movements were said to combine with steep crests parallel to the plane of motion to allow opposing teeth to slide

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past one another in shearing. This is common for carnivorous mammals. Vertical movements combined with broad cusps and deep basins perpendicular to the plane of motion, on the other hand, were said to result in opposition, or crushing. This is typical of omnivores, such as pigs and primates. Finally, horizontal movements combined with lophs, or small crests, were said to result in grinding. This combination is most often seen in herbivores.

Subsequent *in vivo* experiments and cineradiographic studies by Crompton and Hiiemae [16,17] confirmed that tooth form effectively guides jaw movements, and that those movements are important for processing food. Hiiemae [18] went so far as to consider that teeth are “an essentially passive element in the active masticatory apparatus and are dependent on the movements of the mandible for their functional interactions” [883]. We now recognize, due in large part to Lucas [19] and his colleagues, that teeth are much more than this; they are also complex surfaces that interact directly with foods to accomplish fracture. Nevertheless, the two sets of functions are not mutually exclusive – while the sharp blades of a carnivorous carnassial form wedges for spreading cracks through tough foods, they also effectively limit relative movements of opposing teeth to vertical shearing.

The relationship between molar form and function has been well studied in primates. The take-home message is that those primates that shear tough foods, such as leaves or insect exoskeletons, typically have steeper sloping occlusal surfaces and long crests, whereas those that crush hard objects, such as some seeds or nuts, more often have shorter crests and blunt cusps fit into opposing basins [20–26]. The shapes of these basic tooth types mirror the chewing actions associated with different food types [27,28].

1.1.1. The worn tooth conundrum

Early studies of tooth form and function did not account for wear-related shape changes, however. If we can assume that teeth get flatter with wear, this should, in principle, affect chewing actions and efficiency. On the other hand, if we can assume that selective pressure continues to operate into and through adulthood, mammals should have teeth that wear in a manner that keeps them functionally efficient for whatever foods they evolved to eat. Some species even depend on tooth wear to make and keep them sharp. This has been termed *secondary morphology* by Fortelius [29], and holds for the selenodont cheek teeth of camels and pecorans, the dilambdodont forms of microchiropteran bats, and even the bunodont molars of many primates [29–34]. Indeed, some rodents, such as the guinea pig, actually brux *in utero* so that their teeth are worn and ready for use shortly after birth [35]. In these various cases, localized and genetically-mediated differences in enamel microstructure (e.g., prism orientation at the surface) and/or enamel thickness guide changes in tooth wear given differential resistance of these tissues. In this way, dental structure can evolve such that wear sculpts teeth in a specific manner to maintain functional efficiency. Myomorph rodents, for example, have very thin enamel over their cusp tips and softer dentin horns protruding

close to the surface to lead quickly to sharp edges for food processing [11].

Dental topographic analysis was initially developed to track changes in dental functional morphology with wear and thus address the “worn tooth conundrum” [31,32]. The basic idea was to characterize whole occlusal surfaces as landscapes using geographic information systems [36]. Average surface slope, angularity (slope of slope, or jaggedness), and relief were all measured and compared among variably worn teeth of given species to assess variation in functionally relevant aspects of occlusal topography over time [31,32,37]. Other measures, such as orientation patch count rotated (OPCR) [38] and Dirichlet normal energy [39], have since been developed to describe crown complexity and surface curvature (see [40,41] for review). These attributes in aggregate do an excellent job of distinguishing living primates with different dietary preferences and fallback food adaptations [42,43]. Again, sharper, more jagged teeth often correspond to a tough food diet, whereas blunter, flatter ones are associated with hard objects.

Perhaps the most important contribution of primate dental topographic analysis is the discovery that while some aspects of occlusal form change with wear, others tend not to. Occlusal slope and relief are lower in more worn specimens – teeth get flatter as they wear. But angularity and OPCR, which measure change in slope and aspect, are relatively insensitive to wear, at least until the bulk of occlusal surface enamel is lost and dental senescence sets in [33]. Extreme wear certainly affects food processing efficiency [44]. It can require longer chewing or consumption of more food, and can reduce fitness by leaving less time for other activities, or inhibiting mother's ability to produce milk [33,45–48]. Nevertheless, molar occlusal jaggedness is often preserved throughout much of life in primates, presumably to maintain functional efficiency in chewing to the degree possible. And this general pattern holds reasonably well for species representing all higher-level primate taxa, from lemurs [33,49–51] to platyrrhines [32,43,44,52,53], ceropithecoids [44,54,55], and hominoids [31,37,56,57].

1.2. Dental microwear and occlusal topography

Just as dental functional morphology has been used as a proxy for masticatory movement and, by extension, diet, so too has dental microwear. Indeed, the basic idea behind molar microwear is (like that behind teeth as guides for chewing) also credited to Simpson [58]. He reasoned that the direction of microscopic scratches on tooth facets could be used to determine how past mammals chewed. Indeed, microwear became something of the “go to” approach for reconstructing jaw movements in fossil mammals during the mid-20th century [59–62]. Grine [63] took this approach one step further in an effort to settle debate concerning whether the therapsid *Diademodon* evinced only reptile-like vertical opening-and-closing movements of the mandible, or chewed with mammal-like lateral excursion. He argued that horizontal (grinding) movements would have led opposing teeth to slide past one another, resulting in striations as abrasives were dragged along

the surface, whereas vertical movements (crushing) would have left only pits.

This perspective is the basis for explanations as to why mammals that shear tough foods tend to have microwear surfaces dominated by scratches, whereas those that crush hard objects typically have more pits, at least on “Phase II” facets. The power stroke of mastication has traditionally been divided into two intervals, “Phase I” and “Phase II”, which immediately precede and follow centric occlusion, respectively [59]. Wear facets produced as mandibular molars move upward and lingually into centric occlusion were associated with “Phase I” of mastication whereas those formed from centric occlusion onward were associated with “Phase II”. Research from the 1980s onward has shown that these “Phase II” facets best separate primates with differing diets [64,65], presumably because crushing occurs between these surfaces as opposing teeth enter centric occlusion, thus resulting in more perpendicular contact between wear surfaces than during “Phase I”.

This bears repeating given recent discussion of the relationships between microwear pattern and type of abrasive – e.g., phytoliths versus grit [66,67]. While abrasives provide the medium for forming microwear, the resulting pattern still reflects the angle of contact between opposing teeth and whatever is between them [65]. As experimental study has confirmed, a steep angle of approach (crushing) causes pits, whereas a shallow angle (shearing) causes scratches [68]. Taking this a step further, the main connection between microwear pattern and diet then comes from food fracture properties (hard foods are crushed, tough ones are sheared), *not* from attributes of the abrasives that cause the microwear per se (though particle size, shape, and chemistry could still affect texture pattern). This explains the decoupling of gross wear rate and microwear pattern [69, see below]. It also explains why diet-microwear pattern associations hold when comparing species representing a broad variety of mammalian taxa from a wide array of abrasive environments. From antelopes to zebras [70–72], bats to moles [73,74], pigs to sheep [75,76], marsupials to carnivorans [77,78], primates [64,79,80] and others, those species that eat hard foods tend to have more pitting, and those that eat tougher ones tend to have more scratches.

Most microwear research today focuses on whole surface textures rather than the shapes of individual features, but the distinction between tough- and hard-food feeders remains, whether we consider rabbits [81], bats [82], antelopes [83,84], bears [85], armadillos and sloths [86], dogs, hyenas, and cats [87–90], primates [91–93], or marsupials [94]. Mammals that more often consume hard, brittle foods tend to have higher average microwear surface texture complexity, whereas those that more often shear or slice tough items have more surface anisotropy. This is consistent with tough-food eaters having microwear surfaces dominated by uniform scratches running in a given direction, and hard-object feeders having pits of varying sizes and shapes.

In sum, given that teeth are guides for chewing, tooth shape affects angle of approach between opposing occlusal surfaces during mastication. Mammalian molars with long crests and

steep facets enable shearing, whereas blunt ones with less relief, rounded cusps, and capacious basins facilitate crushing. If shearing movements during “Phase II” result in anisotropic microwear textures dominated by long, parallel striations, whereas crushing during “Phase II” leads to complex textures dominated by pits, microwear texture could be affected by topography such that species with more sloping molars would tend to have more aligned striations whereas those with blunter cusps might have more pits. But what about variation in dental topography within species? Recall that, at least for primates, more worn molars tend to have lower average occlusal slope and relief than less worn ones; and this holds whether considering museum samples [31,37,43,54] or longitudinal series’ of individuals sampled repeatedly over time [49,52].

Could it be then that shape-related changes in occlusal topography affect microwear patterning within primate species? If so, mixed samples of variably worn teeth could introduce “noise” to the system when comparing microwear textures between species. Microwear studies have not to date been limited to like-worn specimens because samples available for many if not most mammalian species – especially fossil taxa – are simply not large enough to allow this. Nevertheless, it is important to assess possible effects of wear-related variation in topography on microwear in order to justify continued comparisons of variably worn samples and to better understand the process of microwear formation. In this study we compared dental topography and microwear texture attributes for a sample of variably worn capuchin monkeys, *Sapajus apella*, to determine whether pattern of microscopic wear covaries with, and is likely affected by, occlusal surface shape.

2. Materials and methods

This study involved both dental topographic analysis and dental microwear texture analysis of high-resolution replicas of *Sapajus apella* teeth.

2.1. Materials

The species chosen for this study, *Sapajus apella*, the brown capuchin, is a wide-ranging neotropical primate that inhabits a variety of forest types in the lower to middle Amazon. Studies of its feeding ecology in eastern Amazonia document a eurytopic species with a flexible diet, including approximately 53% fruit flesh, 29% seeds, 11% flowers, 6% leaves, and 1% roots during the wet season [95,96], with higher proportions of seeds and flowers [95] during the dry season. Brown capuchin molars are thickly enameled, and have large, symmetrical cusps with low relief and a wide talonid basin well suited for at least occasional consumption of mechanically challenging foods [97–100]. The molar teeth of these platyrrhines have been well studied, in part because of the long-standing suggestion that they might serve as a model for early hominin dental functional morphology [101].

We here report on an analysis of variably worn permanent upper second molars (M^2 s) of *Sapajus apella* ($n = 27$), all wild-caught in the Brazilian Amazon. Two of us, PSU and MFT,

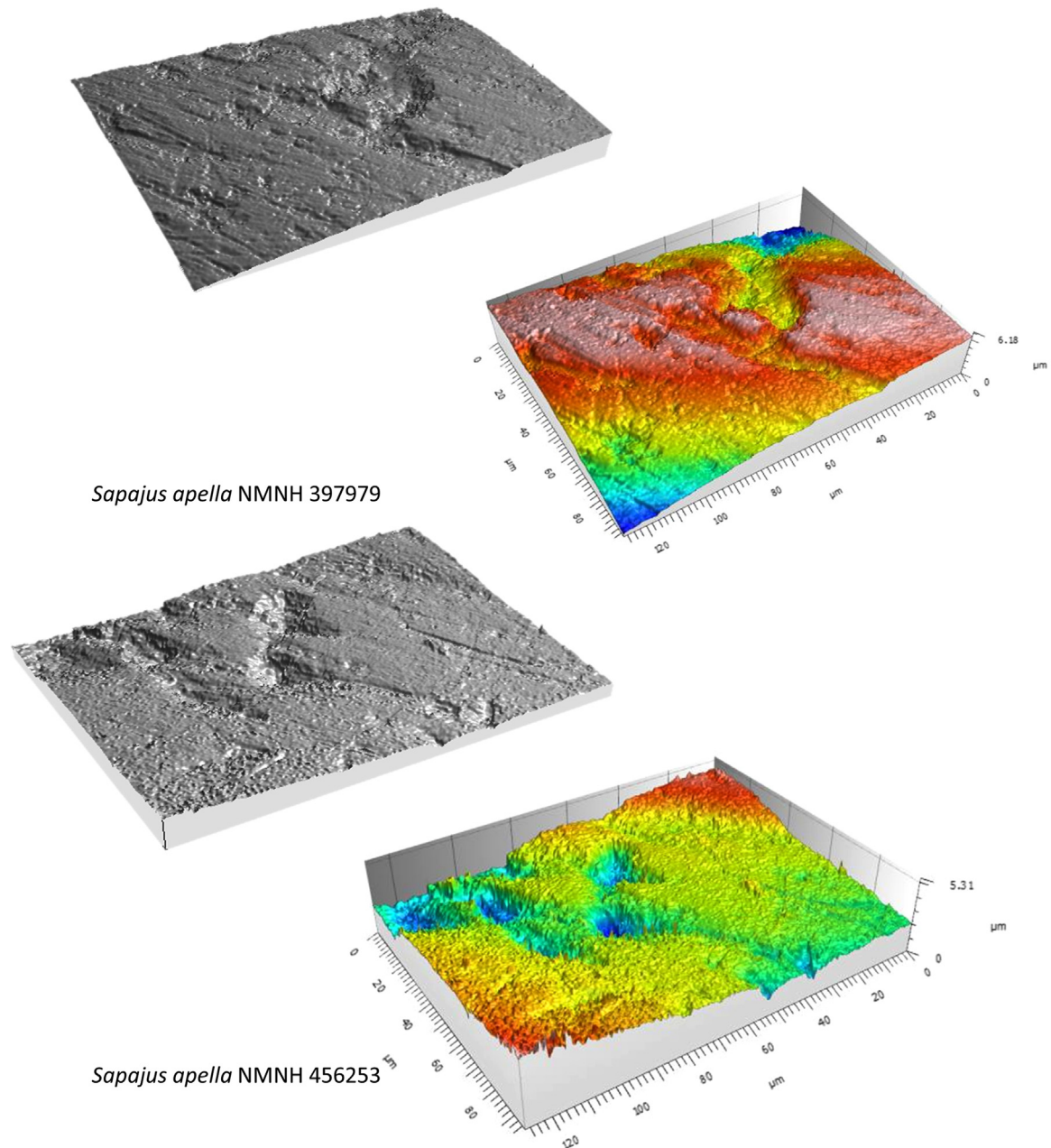


Fig. 1. Microwear images show photosimulations of two surfaces analyzed (each $127 \times 96 \mu\text{m}$), and color gradients to indicate depth of features on those surfaces.

made molds of the original teeth at the National Museum of Natural History in Washington DC. Specimens were cleaned with alcohol-soaked cotton swabs, then molds were taken using a polyvinylsiloxane dental impression material (President Jet Regular Body, Coltene-Whaledent Corp, Mawah, NJ). Two sets of high-resolution replicas were produced from each mold using Epotek 301 (Epoxy Technologies Inc, Billerica, MA) epoxy and hardener. The first set was used “as is” for microwear texture analysis, and the second set was coated with a thin layer of graphite (The B’Laster Corp, Valley View, OH) and Teflon (CRC Industries, Warminster, PA) to mitigate specimen translucency for topographic analysis [following 43].

2.2. Methods

2.2.1. Microwear

The microwear data were generated by ANW. All available specimens were screened for antemortem microwear following standard criteria [102,103] prior to analysis, and only those with suitable surfaces were included in the study. Data collection targeted the “Phase II” wear facet 9 of one M^2 per individual, following usual microwear protocols [104]. Point clouds were generated for each surface using a Plμ Neox scanning confocal profiler (Sensofar Corp, Barcelona, Spain) in white-light mode with a $100\times$ objective. Resulting digital elevation models

(DEMs) each represented a planimetric area of $127 \times 96 \mu\text{m}$, with a lateral (x,y) point spacing of $0.166 \mu\text{m}$, for a total of 442,170 z-values. The published vertical resolution of the instrument is $< 1 \text{ nm}$. Individual DEMs were then leveled using the least squares plane method, and manually edited to remove surface defects (e.g., dust specks, spikes) using MountainsMap v. 6.2 (Digital Surf Corp, Besançon, France). Examples are presented in Fig. 1.

Processed scans were analyzed using Toothfrax (SurFract Corp) scale-sensitive fractal analysis (SSFA) software. Three surface texture variables were considered: area-scale fractal complexity (A_{sf}), length-scale anisotropy of relief ($epLsar$), and textural fill volume (Tfv). These have all proven useful for distinguishing primate species with differing diets [92,93,105]

and, in combination, provide a robust surface characterization appropriate for assessing differences in texture associated with varying dental topography. Complexity is considered here as the slope of the steepest part of a curve fit to a plot of roughness, or relative area, over the range of scales at which it is measured (7200 to $0.02 \mu\text{m}^2$). Anisotropy is a measure of differences in relative lengths of depth profiles sampled at a scale of $1.8 \mu\text{m}$ in different orientations, with an interval of 5° . Fill volume is computed by filling a surface with large and small (10 and $2 \mu\text{m}$ on a side, respectively) square cuboids and calculating the difference. Detailed descriptions are published elsewhere [105], but these together provide a snapshot that distinguishes surfaces with differing microwear feature sizes, shapes, and orientations.

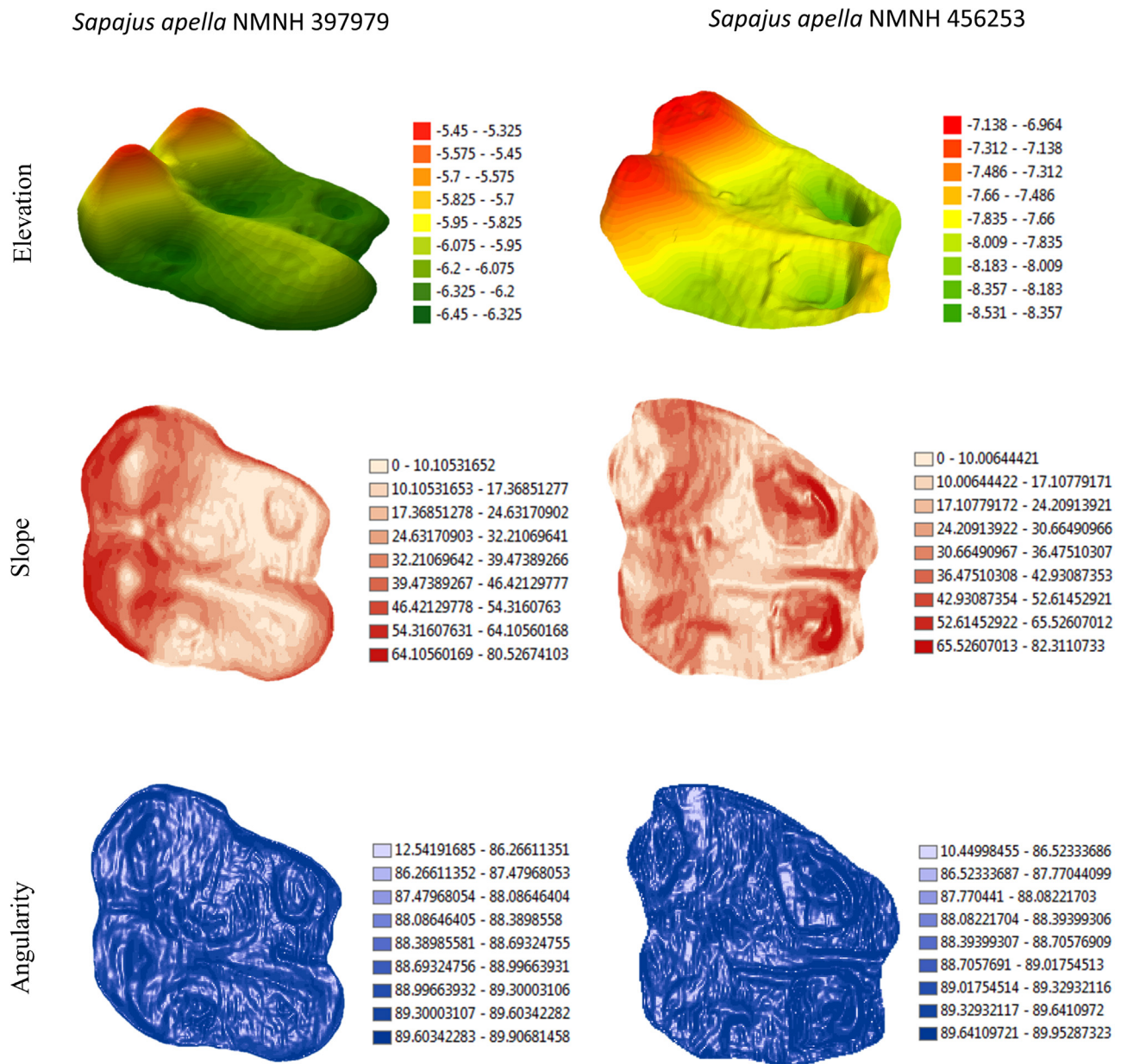


Fig. 2. Images from top to bottom show elevation of the tooth, slope, angularity with varying levels of the surface displayed by color gradient. NMNH 456253 is more worn than NMNH 397979.

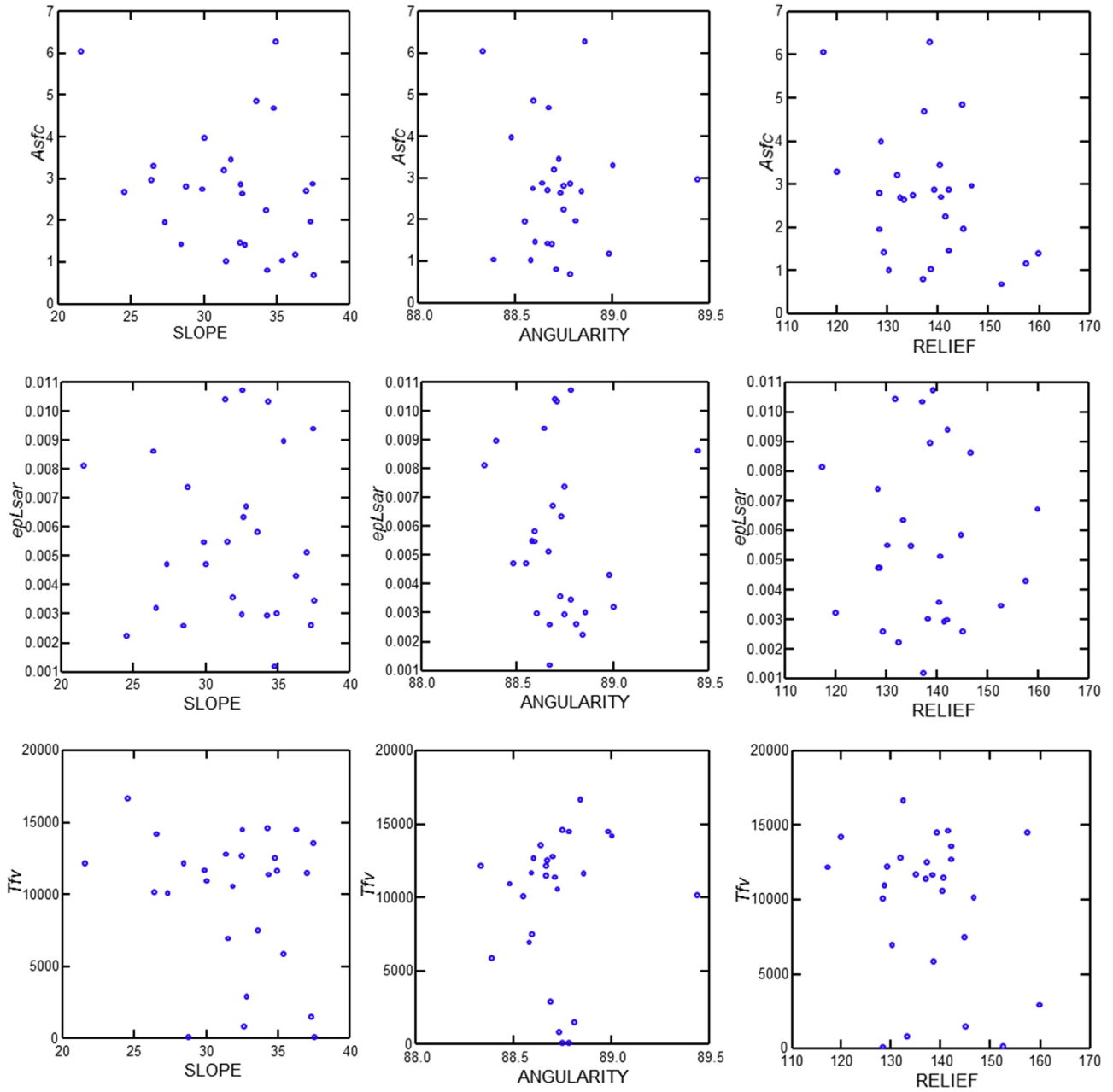


Fig. 3. Plots of dental microwear texture attributes against dental topography variables for the sample.

2.2.2. Topography

The dental topography data were collected by CLH. Digital elevation models were generated using a multi-sensor scanning machine (Xystrum Crop., Turino, Italy) with an integrated OTM3 laser head (Dr. Wolf & Beck GmbH, Wangen, Germany). The same specimens analyzed for microwear (in this case, replicas coated in graphite and Teflon, see above) were mounted on a horizontal plate with the occlusal plane as parallel to the plate as possible. A quasi-3D point cloud representing each occlusal surface was made with a lateral point spacing of 25 μm , resulting in a matrix of 1,600 z-values for each 1 mm^2 of planimetric surface, following the usual procedure for dental topographic analysis [31,43,106,107].

Table 1
Multiple regression analyses.

	SS	df	MS	F-ratio	p-value
<i>Asfc</i>					
Regression	155.778	3	51.926	0.806	0.504
Residual	1482.222	23	64.444		
<i>ePLsar</i>					
Regression	101.222	3	33.741	0.505	0.683
Residual	1536.777	23	66.816		
<i>Tfv</i>					
Regression	103.917	3	34.639	0.519	0.673
Residual	1534.083	23	66.699		

Table 2
Spearman's coefficient of ranked correlation.

	Slope	Angularity	Relief	Asfc	epLsar
Angularity	0.098				
Relief	0.670*	0.317*			
Asfc	-0.284	0.007	-0.261		
epLsar	-0.030	-0.234	-0.021	0.010	
Tfv	-0.151	0.181	-0.080	0.236	-0.202

* $p < 0.05$.

Point cloud data for each specimen were then converted to ASCII format using Digiline software (Xystrum Corp., Turino, Italy) and imported into ArcGIS 10.2 (ESRI Corp., Redlands, CA) for processing. A digital elevation model of each surface was interpolated using inverse distance weighting, and cropped to include only the occlusal table, defined as all elevations above the lowest point of the occlusal basin [107]. Examples are presented in Fig. 2.

Three topography variables were calculated for each DEM in ArcGIS: slope, angularity, and relief. Slope is the average change in elevation between adjacent points (the first derivative of elevation). Angularity is the average change in slope between adjacent points (the second derivative of elevation). Relief is the ratio of surface area calculated from triangular tiles fit to adjacent points divided by the underlying planimetric area. Each of these attributes has proven useful in distinguishing primate species that differ in diet, both in terms of food preferences and secondary, or fallback, elements [43,54,55]. These attributes in aggregate characterize functional aspects of surface topography, including both occlusal surface slope and jaggedness [37,108]. Moreover, while both slope and relief have been shown to decrease with wear (individual teeth get flatter), angularity has proven to be insensitive to change with time, holding steady until the point of dental senescence [49,109].

2.2.3. Statistical analyses

Two separate types of statistical analysis were conducted to compare the dental microwear texture and dental topography data: a multiple regression model to assess effects of topography on each texture attribute, and a Spearman's rank correlation coefficient matrix model to determine which pairs of texture and topography variables covary. For the multiple regression analyses, each of the dental microwear texture attributes (*Asfc*, *epLsar*, and *Tfv*) was individually tested as a dependent variable, and the three dental topography attributes (slope, angularity, and relief) were considered independent because the objective was to assess whether topography affects microwear. Data were rank-transformed prior to multiple regression analysis to mitigate violation of assumptions inherent to parametric tests [110].

3. Results

Results are illustrated in Fig. 3 and presented in Tables 1 and 2. First, none of the three multiple regression analyses showed significant variation. This suggests that none of the microwear

texture attributes (complexity, anisotropy, and fill volume) were affected in a consistent manner by variation in topography. There were also no significant associations between any of the texture-topography variable pairs. Indeed, the only significant associations in the Spearman's rank correlation coefficient matrix were between the topography variable pairs, relief and slope, and relief and angularity. This again suggests that, at least for the attributes considered here, dental microwear texture is independent of variation in occlusal table shape for this variably worn sample of *S. apella* M²s.

4. Discussion

Results presented here show no significant covariation between any microwear texture variable and occlusal slope, angularity, or relief for the M²s of *Sapajus apella*. That suggests that microwear textures are not affected in a consistent and predictable manner by variation in occlusal topography between individuals of this species. It further implies, by extension, that samples of specimens with flatter and steeper facets can be combined for interspecific comparisons without concern that within-species variation in occlusal topography will systematically confound diet signals.

4.1. Relationships between gross tooth wear and microwear

These results may also bear on considerations of relationships between gross tooth wear and microwear. Because hardness and stiffness of enamel can vary with depth in the crown, surface enamel of worn teeth may have different material properties than that of unworn ones. Changes in enamel properties across a tooth can relate to variation in microstructure and/or local chemistry (volume fractions of inorganic nanofibers and organic matrix, water content, etc.) [111–113]. Indeed, studies of some primates have shown that indentation hardness and Young's modulus can decrease from the initial occlusal surface to the enamel-dentin junction (EDJ), though this may not be so in all cases [114]. Still, if enamel properties do vary across a crown, then wear-related differences in microscale responses of enamel to chewing loads and food-borne abrasives could, in principle, affect microwear patterning and obfuscate diet signals.

Recent *in vitro* work by Karme et al. [69] has suggested that gross enamel wear rate depends largely on diet abrasiveness, but that such difference in dental tissue loss need not correspond with different microwear patterning. This effectively decouples gross wear and microwear. This is consistent with a recent study by Ramdarshan et al. [115] showing a lack of difference in microwear texture pattern across the wear gradient between M1 and M3 for a controlled sample of sheep.

The only study of which we are aware to consider direct associations between gross wear and microwear texture pattern in primates is Daegling et al.'s [116] analysis of fourteen *Cercocebus atys* individuals which, like *S. apella*, have the thickly enameled, relatively blunt molar teeth expected of a hard-object feeder. In that study, attrition was measured from digital photographs of both the P⁴ and M¹ as the proportion of

dentin exposed on the occlusal surface relative to crown. These data were compared by Spearman's rank-order correlation tests with four microwear texture attributes (including those considered in the current study) for both tooth types. Results indicated covariation for only one of eight tooth-texture attribute combinations, and even that was not significant at the experimentwise significance threshold. There is a hint that enamel microwear texture complexity might decrease slightly with increasing M^1 dentin exposure, though the observation runs counter to expectations if hardness declines toward the EDJ, and more wear means softer exposed enamel.

The data presented here are concordant with the lack of a consistent effect of gross wear on microwear patterning, given the firmly established relationships between surface topography and gross wear. Both slope and relief values are lower for more worn specimens of a given primate species, whether lemur, New World monkey, Old World monkey, or ape, and whether considering museum collections or longitudinal series' of individuals sampled repeatedly [31,37,49,52,54–56]. The fact that neither slope nor relief co-vary with microwear texture in *S. apella* therefore implies that gross wear likely does not either.

So what can we say, in the end, about the relationship between tooth shape and microwear patterning? Tooth shape clearly reflects dietary adaptation in primates. Folivores tend to have molars with longer crests and more sloping occlusal surfaces, whereas those of hard-object feeders tend to have shorter crests and less topographic relief. Likewise, folivorous primate species tend to have more anisotropic, heavily striated microwear surfaces, whereas those of hard-object feeders tend to be more complex and heavily pitted. This implies a rough association between microwear and topography *between* species with different tooth shapes and diets. Results presented here, on the other hand, suggest that there need not be an association between dental topography and microwear *within* species. This makes intuitive sense given that primates tend to retain consistent diets throughout life. Studies of other mammals have shown that tooth wear can lead to increased food intake or more time spent chewing to offset decreased chewing efficiency [117,118], but given a consistent diet, this would more likely affect gross tooth wear rate than microwear patterning per se, especially given the decoupling of macroscopic and microscopic patterns of wear.

It might also be noted that covariance between microwear textures and dental topography among taxa need not hold in all cases, particularly where species with similar tooth form have different diets. This is because morphology reflects selection on one's ancestors, whereas microwear reflects foods eaten in one's life. Food choice depends on a combination of factors, including not just occlusal form, but also availability and preference [119,120]. Liem's paradox provides one example [121]. A recent study of microwear textures of fossil mammals presents a case in point [122]. In this instance, three different tribes, Alcelaphini, Antilopini, and Hominini, with species in both South and eastern Africa showed microwear texture differences between regions despite similar occlusal morphologies. Patterns of differences between the regions varied by

taxon, suggesting that this is related to food choice rather than environment (e.g., grit load) per se. The differences between *Paranthropus* species is particularly noteworthy. While their cusps are similarly blunt, with low sloping surfaces and little topographic relief, neither have high microwear texture complexity, as would be predicted by molar form alone. In one case, texture complexity is consistent with fallback on hard, brittle foods and in the other, it is consistent with a sub-optimal solution for grinding tough vegetation [123,124]. This is consistent with the notion that occlusal morphology reflects food capabilities whereas microwear mirrors actual diet.

As a final note, this study raises some interesting questions that point us in several directions for future research. First, might the dual function of teeth as guides for chewing and tools for fracturing complicate interpretations of effects of occlusal topography on microwear texture pattern? Results presented here for *S. apella* M^2 s offer no evidence for this, given that neither slope/relief (presumed guide-related attributes) nor angularity (presumed tool-related attribute) co-vary with any microwear texture variable. Nevertheless, a consideration of other species with different molar morphologies, and inclusion of more topography and texture attributes would certainly be valuable to confirm or refute the lack of associations. Further, what about the effects of wear on angle of approach between opposing teeth? If microwear texture pattern indeed reflects approach angle, that angle evidently does not change with gross wear, despite the notion that occlusal form serves a guide for chewing. This requires further study. And what about the relationship between microwear and topography with extreme gross wear? This question may be moot for primate studies, though, as microwear is typically limited to enamel, but it could be of interest to consider teeth approaching senescence. Finally, there is the issue of scale when considering the relationships between masticatory kinematics and microwear texture pattern. How does gross-scale trajectory of approach between opposing teeth during chewing translate into contact angle between inclined wear facets and food/abrasive at microscales? Does this vary with different food/abrasive properties?

5. Conclusions

In conclusion, the evidence presented here indicates that wear-related changes in molar topography do not have a consistent, predictable effect on microwear texture pattern, at least for the M^2 s of *Sapajus apella*. This suggests that variably worn teeth may be considered together as samples for interspecific microwear comparisons without concern that topographic variation might swamp otherwise detectable differences related to diet.

Acknowledgments

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