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ABSTRACT

The power stroke of mastication has been traditionally divided into two parts, one which precedes centric occlusion, and the other which follows it -- "Phase I" and "Phase II" respectively. Recent studies of primate mastication have called into question the role of "Phase II" in food processing, as they have found little muscle activity or accompanying bone strain following centric occlusion. That said, many researchers today look to "Phase II" facets to relate diet to patterns of dental microwear. This suggests the need to reevaluate microwear patterns on "Phase I" facets. Here we use texture analysis to compare and contrast microwear on facets representing both phases in three primate species with differing diets (*Alouatta palliata*, *Cebus apella*, and *Lophocebus albigena*). Results reaffirm that microwear patterns on "Phase II" facets better distinguish taxa by diet than do those on "Phase I" facets. Further, differences in microwear textures between facet types for a given taxon may themselves reflect diet. Some possible explanations for differences in microwear textures between facet types are proposed.

INTRODUCTION

The power stroke of mastication involves the application of forces to food particles between the teeth. It has traditionally been divided into two intervals: "Phase I" and "Phase II", which immediately precede and follow centric occlusion respectively (Butler, 1952; Butler and Mills, 1959; Hiiemae and Kay, 1972; Kay and Hiiemae, 1974). Wear facets produced along the surfaces leading away from the crests as the teeth move upwards and lingually into centric occlusion were identified with "Phase I" of mastication. Wear facets produced in the tooth basins as the teeth come into full centric occlusion and then are moved parallel to the occluding surfaces were associated with "Phase II".

However, the importance of "Phase II' to chewing has since been called into question as, at least for some primates, minimal muscle activity and jaw bone strain occur following centric occlusion. This suggests that little food processing is done once the lower teeth begin to separate from the uppers (Hylander and Crompton, 1980; Wall et al., 2006). Nevertheless, it is precisely the "Phase II" facets that are usually used in primate dental microwear analysis. This stems from research conducted in the early 1980s when microwear was first compared between facet types. These studies demonstrated that "Phase I" and "Phase II" facets could have differing patterns of microwear, even on an individual tooth. Thus, control over sampling area on an occlusal surface was deemed key to interpreting results. These analyses also showed that the sizes and shapes of microwear features that dominated "Phase II" facets separated primates with differing diets in expected, predictable ways (Gordon, 1982; Teaford and Walker, 1984).

Observations that patterns of microwear features on "Phase II' facets distinguish primates with differing diets, but that minimal bone strain and muscle activity occur during "Phase II" of the power stroke present a conundrum. If the work of mastication is not being done during "Phase II", why are the facets associated with it considered to be the best for distinguishing microwear patterns caused by different diets? This paper reexamines the use of specific facets for primate microwear research in light of new understandings of the biomechanics of chewing and new approaches to the quantitative characterization and comparison of dental microwear. Results confirm that "Phase II" facets generally distinguish primates with differing diets better than "Phase I" facets. They also suggest that differences between facet types for a given taxon can themselves be of value for inferring diet from microwear textures.

MATERIALS AND METHODS

We examined microwear on "Phase I" and "Phase II" facets of the M_1s and M_2s of 36 individuals, consisting of *Alouatta palliata* ($n = 10$), *Cebus apella* ($n = 13$) and *Lophocebus albigena* ($n = 13$). *Alouatta palliata* is usually considered a tough food eater, consuming mostly leaves, stems, and fruit seeds and flesh. *Cebus apella* and *Lophocebus albigena* are soft-fruit eaters that fallback on hard, brittle foods such as nuts and palm fronds (Chalmers, 1968; Estrada, 1984; Estrada and Coates-Estrada, 1986; Lambert et al., 2004; Teaford, 1985). All specimens were wild-caught, with originals housed at the US National Museum of Natural History (*A. palliata* and *C. apella*) and in the Tappen Collection at the University of Minnesota Department of Anthropology (*L. albigena*).

High-resolution replicas were produced following standard microwear molding

and casting procedures (Grine, 1986), and surfaces were analyzed using published dental

microwear texture analysis protocols (see Scott et al., 2006; Ungar et al., 2008). "Phase

I" (5 or 7n) and "Phase II" (9, 10n or x) facets were scanned using a Sensofar Plµ white-

light scanning confocal profiler (Solarius Development Inc., Sunnyvale, CA) with a 100x

objective lens. Point clouds were generated for each surface examined with a lateral

sampling interval of 0.18 µm and a vertical resolution of 0.005 µm. Four adjoining fields

of view were scanned, for a total work area of 276 x 204 µm (Fig. 1). Scan data were

then normalized and leveled using Solarmap Universal software (Solarius Development

Inc., Sunnyvale, CA), and any identifiable defects, such as dust particles, were deleted

from the dataset prior to analysis.

The four adjoining scans of each specimen were analyzed using Toothfrax

(Surfract, www.surfract.com) and SFrax scale-sensitive fractal analysis (SSFA) software

packages. Scale-sensitive fractal analysis operates on the principle that the apparent

length of a profile from a rough surface, the apparent area of that surface, and its apparent

volume change with scale of observation. Surface textures that appear smooth at a course

scale can be rough at a finer scale. Scale-sensitive fractal analysis is valuable as it can be

applied to three-dimensional surfaces, allowing for length, area, and volume scale

analyses.

Six texture variables were analyzed for this study following previous analyses:

complexity (*Asfc*), anisotropy (*epLsar*), scale of maximum complexity (*Smc*), textural fill

volume (*Tfv*), and heterogeneity dividing each scan into 3x3 (*HAsfc$_9$*) and 9x9 (*HAsfc$_{81}$*)

rows and columns. These attributes are described in detail in Scott et al. (2006) and

Ungar et al. (2008) and summarized in Table 1.

Data were collected for individual fields, and median values for each variable

were calculated for each surface analyzed. These were rank-transformed to mitigate

violation of assumptions inherent in parametric statistical analyses (Conover and Iman,

1981). Data for the variables were compared among species and facet type using a two-

factor multivariate analysis of variance model, with taxon and facet type as the factors,

the individual texture attributes (*Asfc*, *Smc, epLsar*, *Tfv*, *HAsfc$_9$*, and *HAsfc$_{81}$*) as the

dependent variables, and values for each individual as the replicates. This model assesses

significance of variation among taxa, between facet types, and interactions between the

two factors in overall microwear surface textures. Factorial ANOVAs for each variable

(again, with taxon and facet type as the factors) were used to identify those attributes that

evinced significant variation between taxa, facet type, or an interaction between the two.

Multiple comparisons tests were then used to determine the sources of significant

variation. Given that these groups were chosen for the dietary (and expected microwear)

differences, Fisher's LSD *a priori* tests were used to compare species. Tukey's HSD *post*

hoc tests were also run to balance the risks of Type I and Type II errors (Cook and

Farewell, 1996).

RESULTS & DISCUSSION

The results are presented in Figures 1-2 and Tables 2-4. We found significant

variation between taxa and phases in overall microwear surface texture, as well as an

interaction between the two factors. The sources of these variations are identified in

individual ANOVAs for each variable. First, there was significant variation between taxa, but no interaction between taxon and facet type for complexity (*Asfc*) and scale of maximum complexity (*Smc*). In other words, the three taxa differed from one another in *Asfc* and *Smc*, and those differences were independent of whether "Phase I" or "Phase II" facets were examined. Significant variation was also found between taxa for textural fill volume (*Tfv*) and heterogeneity 9x9 (*HAsfc$_{81}$*) though a significant interaction between taxon and facet type for these two texture variables required separate consideration of taxa by facet type.

The facet types differed significantly from one another in complexity (*Asfc*) and anisotropy (*epLsar*) in similar ways for the three taxa considered. "Phase II" facets were both more complex and more anisotropic than were "Phase I" facets for the samples examined. Fill volume (*Tfv*) also showed significant variation between facet types; however, as with taxon, a significant interaction required further statistical analyses.

Significant interactions between factors necessitated separate comparisons of facet types by each taxon for *Tfv*, *HAsfc$_9$,* and *HAsfc$_{81}$*. Individual results indicated that *C. apella* and *L. albigena* both had higher *Tfv* values on their "Phase II' facets, and that *C. apella* had more heterogeneous "Phase II" microwear surface textures. Further, *A. palliata* demonstrated no significant differences in these three variables between facets. These differences between the facet types in complexity and anisotropy presumably reflect differences in tooth-food interactions before and after centric occlusion, and support earlier suggestions that facet types should not be mixed in microwear analyses (Gordon, 1982; Gordon & Walker, 1983).

The interactions are especially interesting because they suggest that different taxa have different patterns of variation between "Phase I" and "Phase II" microwear textures. Specifically, while the more folivorous *A. palliata* had no significant difference between "Phase I" and "Phase II" facets in *Tfv*, the two "hard-object" fallback species had higher *Tfv* values on Phase II facets. Further, *C. apella* had more heterogeneous "Phase II" texture features than did any of the other taxa.

Further statistical analysis of the significant interactions of taxon and phase suggests that "Phase II" facets better distinguish taxa by diet than do "Phase I" facets. "Phase I" facets do not distinguish taxa for *Tfv*, *HAsfc₉*, or *HAsfc₈₁*. Conversely, all three of these texture attributes did differ significantly between species on "Phase II" facets. Although this offers additional support for the use of "Phase II" facets in microwear studies, it still does not provide a biomechanical explanation for this trend. It begs the question "what is occurring during 'Phase II' of the power stroke that accounts for its reliability in dental microwear research?"

Several possible reasons can be suggested to explain why wear patterns on "Phase I" and "Phase II" surfaces differ. These differences may relate to the volume of food and associated abrasives interposed between surfaces as they contact one another. Alternatively, differences may relate to the angle of masticatory forces relative to the planes of the wear facets themselves. In the first case, the most sharply delineated facets of "Phase I" are most likely formed at a stage in the masticatory process when few food particles are interposed between the teeth. The prevalence of tooth-tooth contact occurring later in a masticatory cycle might obliterate or obscure wear features produced more specifically by the food or the grit adhering to it (*i.e.,* in the earlier puncture-

crushing stages of mastication). In contrast, "Phase II" facets occur in the trigonid and talonid basins and are produced, at least in part, at the end of a "Phase I" movement as food is compressed between relatively flat opposing surfaces.

Even in the later stages of a masticatory cycle, one might expect to find food particles and abrasives trapped in the trigonid and talonid basins to still have a role in producing microwear features. In the second case, "Phase I" facets are produced largely at a time when the anatomy of the teeth dictates when the most precise occlusion should occur. Because of the way the "Phase I" occlusal surfaces are arranged, the masticatory forces are concentrated at the leading edges of the surfaces and likely oriented at an acute angle to the surfaces. "Phase II" movement and the accompanying facets it produces are less rigidly constrained by the anatomy of the teeth. It would not be surprising to find more complexity and anisotropy on facets produced by a less precise part of the occlusal cycle (occlusion produced by forces more-or-less normal to the plane of the facets).

In summary, the use of dental microwear texture analysis in this study confirms that "Phase II" facets better distinguish primates by diet than "Phase I" facets. This study also suggests that distinct biomechanical events leading to differences in dental microwear occur during "Phase I" and "Phase II". Moreover, the variation among species in degree of difference between textures on the two facets suggests that comparisons of patterns of microwear across a tooth may yield even more information about diet than we can obtain using "Phase II" facets alone. Further studies including larger samples of primates with other diets will help us gain a better understanding of this phenomenon.

ACKNOWLEDGEMENTS

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FIGURE LEGENDS

Figure 1. Photosimulations of "Phase I" and "Phase II" surfaces generated from elevation data: A) *Alouatta palliata*, B) *Cebus apella,* C) *Lophocebus albigena*. Each image represents a surface 276 µm x 204 µm.

Figure 2. Dental microwear texture attributes by species and facet type. Species and variables are as indicated on x- and y-axes. Black and white bars indicate "Phase I" and "Phase II" facets respectively.

Table 1: Dental microwear texture variables, definitions, and examples.

Texture Variable	Definition	Example
Asfc	Complexity	Pits and scratches of different sizes overlaying one another would present a complex surface.
Smc	Scale of Maximum Complexity	A surface dominated by large pits with an absence of fine scratches might have a high *Smc*.
epLsar	Anisotropy	A surface dominated by scratches all running in the same direction would have a high *epLsar*.
Tfv	Textural Fill Volume	A surface dominated by deep features would have a high *Tfv*.
HAsfc	Heterogeneity	High heterogeneity indicates differing patterns of scratching and pitting across a microwear surface.

Table 2. Statistical Analyses. Overall comparisons.

A.   MANOVA results. Variables considered include *Asfc*, *epLsar, Smc, Tfv, HAsfc₉*, and *HAsfc₈₁*. This
analysis was conducted on ranked data.

Effect	Wilk's λ	*df*	*F*	*p*
Taxon	0.340	12, 122	7.276	0.000
Facet type	0.562	6, 61	7.912	0.000
Interaction	0.697	12, 122	2.009	0.029

B. Univariate test results.

Variable	Taxon		Phase		Interaction	
	df	*F*	*df*	*F*	*df*	*F*
Asfc	2	31.701*	1	7.338*	2	3.003
epLsar	2	2.263	1	4.333*	2	1.329
Smc	2	3.286*	1	1.095	2	0.744
Tfv	2	8.025*	1	22.447*	2	5.279*
HAsfc₉	2	0.820	1	2.679	2	4.363*
Hasfc₈₁	2	3.578*	1	3.182	2	4.242*

*$p < 0.05$

Table 3. Tests for differences between facet types by taxon, and between taxa by facet types.

A.　ANOVA results for differences between facet types by taxon.

Variable	*A. palliata*		*C. apella*		*L. albigena*	
	df	*F*	*df*	*F*	*df*	*F*
Tfv	1	0.021	1	7.526*	1	45.117*
HAsfc$_9$	1	0.092	1	15.522*	1	0.386
HAsfc$_{81}$	1	0.217	1	16.536*	1	0.384

B.　ANOVA results for differences between taxa by facet type.

Variable	Phase I		Phase II	
	df	*F*	*df*	*F*
Tfv	2	1.025	2	15.047*
HAsfc$_9$	2	0.828	2	3.966*
HAsfc$_{81}$	2	0.115	2	7.339*

*$p < 0.05$

Table 4. Pairwise comparisons

A.   *Asfc* (Independent of Phase)

	A. palliata	*C. apella*	*L. albigena*
A. palliata	-		
C. apella	33.325[a,b]	-	
L. albigena	27.113[a,b]	-6.212	-

B. *Smc* (Independent of Phase)

	A. palliata	*C. apella*	*L. albigena*
A. palliata	-		
C. apella	9.671	-	
L. albigena	15.460[a,b]	5.788	-

C. *Tfv* (Phase II)

	A. palliata	C. apella	L. albigena
A. palliata	-		
C. apella	28.504[a,b]	-	
L. albigena	29.696[a,b]	1.192	-

D. *HAsfc$_9$* (Phase II)

	A. palliata	*C. apella*	*L. albigena*
A. palliata	-		
C. apella	17.523	-	
L. albigena	-4.631	-22.154[a,b]	-

E. *HAsfc$_{81}$* (Phase II)

	A. palliata	*C. apella*	*L. albigena*
A. palliata	-		
C. apella	17.227[b]	-	
L. albigena	-12.081	-29.308 [a,b]	-

[a] Tukey's HSD test $p \leq 0.05$

[b] Fisher's LSD test $p \leq 0.05$