Technical note: dental microwear textures of "Phase I" and "Phase II" facets

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<th>Journal:</th>
<th><em>American Journal of Physical Anthropology</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Manuscript ID:</td>
<td>draft</td>
</tr>
<tr>
<td>Wiley - Manuscript type:</td>
<td>Technical Note</td>
</tr>
<tr>
<td>Date Submitted by the Author:</td>
<td>n/a</td>
</tr>
</tbody>
</table>
| Complete List of Authors: | Krueger, Kristin; University of Arkansas, Department of Anthropology  
Scott, Jessica; University of Arkansas, Department of Anthropology;  
University of Arkansas, Environmental Dynamics  
Kay, Richard; Duke University, Biological Anthropology and Anatomy  
Ungar, Peter; University of Arkansas, Anthropology |
| Key Words: | Microwear, Mastication, Primate, Diet |
Technical Note: Dental microwear textures of “Phase I” and “Phase II” facets

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Number of text pages: 12
Number of figures:  2
Number of tables:  4

Grant sponsor: US National Science Foundation. Grant number: BCS 0315157
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 M₁s and M₂s 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 ($A_{scf}$), anisotropy ($epLsar$), scale of maximum complexity ($Smc$), textural fill volume ($TfV$), and heterogeneity dividing each scan into 3x3 ($HA_{scf9}$) and 9x9 ($HA_{scf81}$).
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, HAsfc9, and HAsfc81) 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 \textit{a priori} tests were used to compare species. Tukey’s HSD \textit{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 (HAsfc9) 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, HAsfc9, and HAsfc81. 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 $T_{fv}$, the two “hard-object” fallback species had higher $T_{fv}$ 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 $T_{fv}$, $HAsfc_{9}$, or $HAsfc_{81}$. 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

We are grateful to Mark Teaford for help collecting dental impressions used in this study, and Robert Scott, for generating the “Phase II” microwear data, which was first published in Scott et al. (2006) and Ungar et al. (2008). We also thank curators at the US National Museum of Natural History, and Martha Tappen for their permission to study specimens in their care. This study was funded by the US National Science Foundation (BCS 0315157).
LITERATURE CITED


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.

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

<table>
<thead>
<tr>
<th>Effect</th>
<th>Wilk’s λ</th>
<th>df</th>
<th>F</th>
<th>p</th>
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</thead>
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<tr>
<td>Taxon</td>
<td>0.340</td>
<td>12, 122</td>
<td>7.276</td>
<td>0.000</td>
</tr>
<tr>
<td>Facet type</td>
<td>0.562</td>
<td>6, 61</td>
<td>7.912</td>
<td>0.000</td>
</tr>
<tr>
<td>Interaction</td>
<td>0.697</td>
<td>12, 122</td>
<td>2.009</td>
<td>0.029</td>
</tr>
</tbody>
</table>

B. Univariate test results.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Taxon</th>
<th>Phase</th>
<th>Interaction</th>
<th>df</th>
<th>F</th>
</tr>
</thead>
<tbody>
<tr>
<td>Asfc</td>
<td></td>
<td></td>
<td></td>
<td>2</td>
<td>31.701*</td>
</tr>
<tr>
<td>epLsar</td>
<td></td>
<td></td>
<td></td>
<td>2</td>
<td>2.263</td>
</tr>
<tr>
<td>Smc</td>
<td></td>
<td></td>
<td></td>
<td>2</td>
<td>3.286*</td>
</tr>
<tr>
<td>Tfv</td>
<td></td>
<td></td>
<td></td>
<td>2</td>
<td>8.025*</td>
</tr>
<tr>
<td>HAsfc9</td>
<td></td>
<td></td>
<td></td>
<td>2</td>
<td>0.820</td>
</tr>
<tr>
<td>HAsfc81</td>
<td></td>
<td></td>
<td></td>
<td>2</td>
<td>3.578*</td>
</tr>
</tbody>
</table>

*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.

<table>
<thead>
<tr>
<th>Variable</th>
<th>A. palliata</th>
<th>C. apella</th>
<th>L. albigena</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>df</td>
<td>F</td>
<td>df</td>
</tr>
<tr>
<td>Tfv</td>
<td>1</td>
<td>0.021</td>
<td>1</td>
</tr>
<tr>
<td>HAsfc9</td>
<td>1</td>
<td>0.092</td>
<td>1</td>
</tr>
<tr>
<td>HAsfc81</td>
<td>1</td>
<td>0.217</td>
<td>1</td>
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B. ANOVA results for differences between taxa by facet type.

<table>
<thead>
<tr>
<th>Variable</th>
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<th>Phase II</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>df</td>
<td>F</td>
</tr>
<tr>
<td>Tfv</td>
<td>2</td>
<td>1.025</td>
</tr>
<tr>
<td>HAsfc9</td>
<td>2</td>
<td>0.828</td>
</tr>
<tr>
<td>HAsfc81</td>
<td>2</td>
<td>0.115</td>
</tr>
</tbody>
</table>

*p < 0.05
Table 4. Pairwise comparisons

A. \textit{Asfc} (Independent of Phase)

\begin{tabular}{ccc}
 & \textit{A. palliata} & \textit{C. apella} & \textit{L. albigena} \\
\hline \\
\textit{A. palliata} & - & 33.325_{a,b} & - \\
\textit{C. apella} & 27.113_{a,b} & -6.212 & - \\
\end{tabular}

B. \textit{Smc} (Independent of Phase)

\begin{tabular}{ccc}
 & \textit{A. palliata} & \textit{C. apella} & \textit{L. albigena} \\
\hline \\
\textit{A. palliata} & - & 9.671 & - \\
\textit{C. apella} & 15.460_{a,b} & 5.788 & - \\
\textit{L. albigena} & - & - & - \\
\end{tabular}

C. \textit{Tfv} (Phase II)

\begin{tabular}{ccc}
 & \textit{A. palliata} & \textit{C. apella} & \textit{L. albigena} \\
\hline \\
\textit{A. palliata} & - & 28.504_{a,b} & - \\
\textit{C. apella} & 29.696_{a,b} & 1.192 & - \\
\textit{L. albigena} & - & - & - \\
\end{tabular}

D. \textit{HAsfc}_9 (Phase II)

\begin{tabular}{ccc}
 & \textit{A. palliata} & \textit{C. apella} & \textit{L. albigena} \\
\hline \\
\textit{A. palliata} & - & 17.523 & - \\
\textit{C. apella} & -4.631 & -22.154_{a,b} & - \\
\textit{L. albigena} & - & - & - \\
\end{tabular}

E. \textit{HAsfc}_{81} (Phase II)

\begin{tabular}{ccc}
 & \textit{A. palliata} & \textit{C. apella} & \textit{L. albigena} \\
\hline \\
\textit{A. palliata} & - & 17.227_{b} & - \\
\textit{C. apella} & -12.081 & -29.308_{a,b} & - \\
\textit{L. albigena} & - & - & - \\
\end{tabular}

\textsuperscript{a} Tukey’s HSD test \( p \leq 0.05 \)

\textsuperscript{b} Fisher’s LSD test \( p \leq 0.05 \)