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A REVIEW OF METHODOLOGY AND QUANTIFICATION IN DENTAL MICROWEAR ANALYSIS

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Abstract

Dental microwear analysis is a method of inferring oral events (primarily food processing and aspects of masticatory biomechanics) from microscopic abrasion patterns retained on the enamel surfaces of teeth. Although some qualitative pattern differences may be easily distinguishable, most of the significant results produced thus far have derived from quantified studies of SEM images of occlusal enamel. It often goes unnoticed by readers of microwear reports who are not themselves specialists that microwear analysis is essentially a statistical method, not a visual one. In this review of current techniques and methods, several problems in current approaches are detailed. It is noted that feature definition can have significant effects on ultimate pattern differentiation. Sampling bias is also a major concern, as most microwear studies are carried out on samples which are very small. Compounding this are the effects of magnification level choices, and the effects of SEM instrumentation on feature visibility. Finally, the interpretation of pattern differences requires careful attention to comparisons of within-group and between-group variability.

Key Words: Scanning Electron Microscopy, Tooth Wear, Dental Abrasion, Dietary Reconstruction, Dental Biomechanics.

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Introduction

Translating visual information into quantitative data is a problem common in many fields of scientific research today. However, it is a problem which microwear specialists have been slow to solve. In the early days of microwear research, it was considered sufficient to assess microwear differences or similarities on the basis of visual inspection alone. As luck would have it, some of the first significant differences to be revealed, those between microwear patterns of grazing and browsing species (Walker 1980, 1981; Walker et al 1978), were indeed distinctive enough to distinguish in this manner. Other differences have been noted since which may also be amenable to qualitative differentiation alone (Rose & Harmon 1986). However, it is impossible to mentally store and access more than a few images at a time. Consequently, most workers have come to agree that microwear analysis can achieve its full potential only if it is objective and rigorously quantified.

The other major insight of the past decade of microwear studies is that there is as yet no easy or readily available way to achieve this level of objectivity. Quantitative microwear analysis, as it is currently carried out, requires an enormous input of labor to produce miniscule amounts of output. In the future there may be several ways of quantifying data more easily than present methods allow. A number of workers are exploring alternative methods of automated image analysis (Walker et al 1987) and other data abstractions such as optical diffraction and Fourier transforms (Kay 1987) which may revolutionize this field, and perhaps in the near future the methodology described herein will be obsolete. While future innovations in methods may permit us to answer many questions about microwear analysis which have so far been neglected because of the difficulty of collecting enough relevant data, there are nonetheless a few considerations of technique and method which should be addressed by all of us now, some of which will continue to be of concern even after we have grown beyond the limitations of our current technology.

In its current form, microwear analysis relies heavily on the scanning electron microscope for collection of basic data, and on computers and computerized digitizing tablets for the analysis of that data. The difficulties of obtaining accurate metrical information from single SEM photomicrographs are numerous, and have been addressed in various ways (Boyde 1969, 1970, 1972, 1973, 1974a,b, 1979). Stereopairs would be more accurate than single photographs, but to make and analyze stereopairs of the large number of surfaces usually treated in microwear analysis is prohibitive in terms of time and cost. Automated measuring systems attached directly to the SEM also provide better accuracy, but are impractical for most specialists who share SEM access with others and therefore must minimize the amount of time spent actually at the microscope. Therefore most researchers (Gordon 1982; Grine 1981, 1987, 1988; Teaford & Walker 1984, Teaford 1985, 1986) use the SEM to make photomicrographs of selected enamel areas, fully recognizing that the photographs represent an imperfect and somewhat biased sample of the real enamel surface damage. For instance, accuracy of measurements from photographs is severely affected by the tilt of the specimen or surface during recording, which most workers either attempt to control (as in Gordon 1980, Grine 1987), or eliminate by recording surfaces only when they are absolutely perpendicular to the axis of the electron beam (Teaford & Walker 1984). While stereophotogrammetric methods would be the most defensible solution to these difficulties, this technique has yet to be applied in microwear studies. Since these concerns have been detailed elsewhere, it is the goal of the present paper to consider other factors affecting the accuracy of microwear statistics which have not been mentioned previously in the literature.

Feature Definition

A "typical" microwear fabric is composed of many small depressions on the enamel surface in a variety of sizes, shapes, and orientations. Figure 1 shows a typical micrograph as it would be oriented on the digitizer pad, overlaid with the compass field for measuring feature orientation. Three different categories of features can be distinguished, which have been defined by this author as follows: Scratches are linear features with a discernible angle of orientation. A small subset of scratches which are sinuous and exhibit more than one angle of orientation are termed gouges. Pits are features having approximately equal length and breadth measurements (from 1:1 to 2:1), with no discernible axis of orientation. Raw metrical data on length, maximum breadth, and angle of orientation are recorded for each feature. From these, statistics can be derived on feature density, proportions of pits to scratches, average length and breadth of pits and scratches,and measures of angle concentration or dispersion.

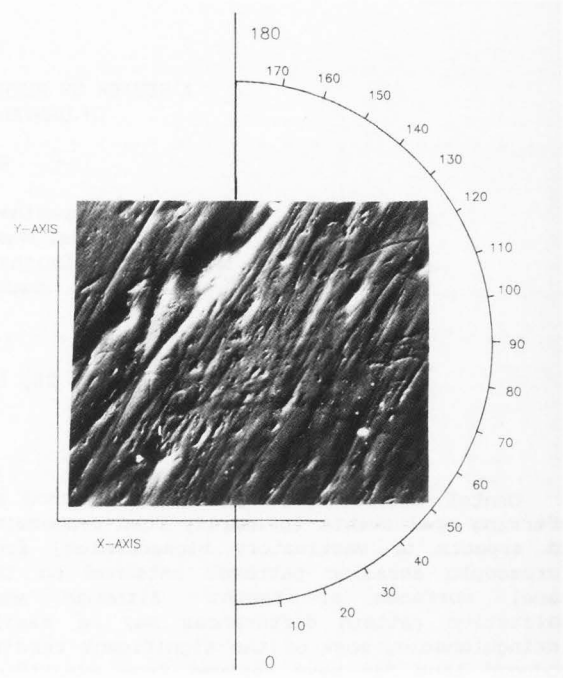


Figure 1: A typical micrograph placed within a 180-degree compass field for digitizing. The buccal edge of the tooth is to the right, the distal edge is superior.

One of the first problems to be noted was the difficulty sometimes encountered in assigning ambiguous features to separate categories. Previous work (Gordon 1980, 1982) has suggested that the recognized types of microscopic abrasion features are not intrinsically different, but are instead manifestations of differing degrees of shear and compression acting on the abrasive agents which produce microwear. According to this view, pits and scratches are found at opposite ends of a continuum of surface wear phenomena, and the decision about where to divide a continuum is always arbitrary. Different researchers have and continue to use different division points. This is a fact worth keeping in mind when comparing results of one study with another. For instance, Teaford & Walker (1984) have used metrical thresholds to discriminate between pits and scratches, employing length:breadth ratios varying from 10:1 to 2:1, and have found that the ability to discriminate some pattern differences is affected by the ratio chosen. Grine (1988) has also noted this problem, and uses a ratio of 4:1 or below to categorize pits. In spite of the difficulties and general undesirability of using a categorical approach to these data, this procedure continues to be useful, because variations in the relative proportions of pits and scratches have proven to be significant discriminators between surfaces.

Sampling Bias

Microwear analysis must be an essentially statistical approach to acquiring information about oral behavior. Consequently, it is subject to all the biases and interpretive problems that affect any statistical procedure. In particular, there are several aspects of sampling techniques used to collect microwear data which may significantly alter results. The most obvious of these concerns is the issue of sample size. All the published studies in this field - including the author's - have been based on very small samples. No study has so far reported on more than 10 individuals per population analyzed. There is one primary explanation for this: even small microwear samples generate enormous amounts of data. For instance, during previous work on a sample of chimpanzees (Gordon 1980, 1982) data was collected on over 20,000 separate microwear features. However, this apparently impressive sample was gathered from only 104 different wear facets, which in turn came from only 22 molar teeth of a grand total of 8 individual animals. There is a critical need to increase sample sizes of reference populations used in microwear studies, but until more automated techniques are available, sample sizes are likely to remain low.

Magnification level as a sampling strategy

One of the major advantages of SEM technology is the wide range of magnification levels available to the operator, up to 50,000X or higher, on an average microscope. However, it is not often appreciated by non-specialists that the choice of a particular magnification level itself constitutes a sampling strategy. What is visible at 50X, 500X and 1000X are not just different views of the same surface, but are essentially different samples from the same population. In microwear research today, there are two commonly used levels of magnification, "low" (generally 150X-200X) and "high" (in the range from 300X to 500X). Both levels, in fact, are quite low by general microscopy standards, but the differences between them are significant for microwear analysis, and each level has unique advantages and disadvantages relative to the other. For example, low magnification photomicrographs cover more surface area of a given facet, which minimizes the risk of missing important features or variations. Also, due to the larger surface area, scratches are more likely to be complete within the micrograph boundaries, with a smaller percentage (about 10%) truncated on one or both ends by the edge of the micrograph field of view. This results in more accurate measured scratch lengths. The main disadvantage of low magnification work is that very small features may not be visible, and very small dimensions, even when visible at 150X, often cannot be measured accurately at that level. In practice, even a high-resolution digitizing pad cannot consistently measure dimensions under 3 microns on a 150X micrograph. This can seriously affect accurate assessments of the numbers and size ranges of very small pits, as well as the breadths of fine scratches.

The principal advantage of higher magnification levels is the enhanced ability to resolve and measure small dimensions such as feature breadth. However, such a sampling technique also tends to reduce the amount of data collected. In hominoid primates, there may be as many as 300-400 measurable features in a single 150X micrograph, but only 100 or fewer of these may be visible on a single micrograph at 500X. In the short-term, working at higher magnification may result in quicker analyses, although the advantage is based solely upon a reduction in the amount of data processed. In addition, data on measured scratch length will be highly skewed, due to the higher percentage of scratches truncated by the micrograph edge. This figure may approach as much as 20% of the total, with many scratches truncated at both ends. But the most significant disadvantage of high magnification analysis is the enormous potential for sampling bias. A single photomicrograph taken at 500X covers only 0.03 mm^2 of surface area. Even if this amount is doubled by adding a second micrograph to the sample (as in Teaford and Walker 1984), the total area sampled is only 0.06 mm^2, as compared to the nearly 0.4 mm^2 area found on a single micrograph taken at 150X.

To illustrate the range of statistical differences presented by differing levels of magnification, a series of three micrographs of the same surface, taken at 150X, 500X, and 1000X, was digitized and analyzed (Figures 2a-c). Table 1 compares the results of the statistical analysis. Distributions of feature types (scratches and pits) were similar at 150X and 500X, but the distribution at 1000X was significantly different (X^2, $p < 0.005$) from either of the lower magnification levels. As expected, scratch orientation data did not change greatly from one level to another, but most other feature dimensions were significantly affected by magnification level (Student's t, $p < 0.05$, or lower). Only one pair of values, scratch breadth at 500X and 1000X, showed insignificant differences when evaluated by t tests.

Since choices must be made, there is a real need to come to some agreement about the standards to be used in microwear analysis. By adopting a single level of magnification, we inevitably sacrifice accuracy in one parameter or another. Alternatively, one may collect and analyze data at both levels of magnification, but this would double the work load, and further slow down progress in the field. A more pragmatic approach, first proposed by Grine (1987, 1988) is to photograph at low magnification (200X), and then enlarge the photograph to about 500X for digitizing. This permits more accurate measurements of small features, without sacrificing the amount of surface area covered.

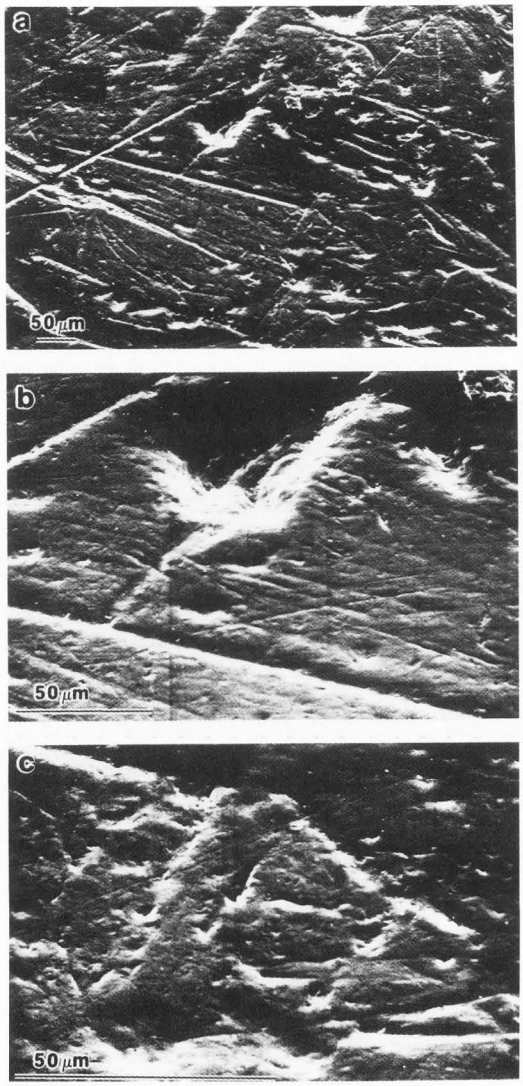


Figure 2: Micrographs of a single occlusal enamel surface (*Sivapithecus*, YPM 13825, right lower M3, facet 9), recorded at (a) 150X, (b) 500X, and (c) 1000X.

Table 1. Effects of Magnification Level on Microwear Analysis

	150X	500X	1000X
Total Features N (%)	383 (100) *	114 (100) *	106 (100)
Scratches	239 (62.4) **	79 (69.3) **	36 (33.3)
Pits	144 (37.6)	35 (30.7)	70 (66.7)
Area Digitized (mm^2)	0.354	0.029	0.008
Feature Density ($/mm^2$)			
Total N	1082	3931	13250
Scratches	675	2724	4500
Pits	407	1207	8750
Dimensions (microns)			
Scr Len x	89.2	35.6	23.0
s	73.6	29.8	25.3
range	12.2-438.5	6.5-171.8	3.1-111.0
V	82.5	83.7	107.3
Scr Brd x	6.3	3.0 +	2.3 +
s	4.4	3.8	2.1
range	3.2-38.7	1.0-26.0	0.7-10.1
V	69.8	126.7	91.3
Pit MaxD x	13.7	5.7	2.6
s	11.5	5.7	2.8
range	3.6-84.3	1.2-28.9	1.1-23.2
V	83.9	100	107.7
Pit MinD x	9.9	3.7	1.9
s	8.0	2.9	1.9
range	3.2-58.7	1.2-14.7	0.8-14.8
V	80.8	78.4	100
Truncated Features	42 (11.1%)	22 (19.3%)	14 (13.3%)
Scratch Orientation (deg)			
x	83.6 #	81.9 #	89.3 #
s	33.3	29.1	34.4
range	4.2-177.3	22.6-172.7	25.2-165.8
V	39.8	35.5	38.5

*, **, +, # - Differences between these values not significant. All other values significant at $p < 0.05$, or less.

Effects of instrumentation on feature visibility

Collector geometry may also play a significant role in structuring the nature of the sample recorded on SEM micrographs. Features on the surface which are aligned parallel to the axis between the electron collector and the specimen (generally this approximates the Y-axis of the specimen stage) will tend to appear less distinct than those found in other orientations. This is due to the fact that electrons from both margins of a groove will reach the collector in approximately equal numbers. Thus there will be little differential contrast between the two edges. Grooves intersecting the specimen-collector axis will tend to be more visible because of the differential in contrast between the two margins. The edge facing the collector will show up brightly, because more electrons will reach the collector, while the edge facing away from the collector will send fewer electrons to the collector, resulting in a darker image and greater contrast between the two edges. Multiple collectors, or at least two, set at right angles to each other, or an annular detector, would eliminate the effects of orientation on feature detection. However, since most SEM's (including the six with which this author has worked) are rarely equipped with such devices, some estimation of the degree of error induced by this limitation seems necessary.

As a preliminary assessment of the magnitude of collector bias on micro-wear data, this author analyzed a pair of photomicrographs taken of the same enamel surface, with a Cambridge Stereoscan 100 equipped with a single detector. One photograph was recorded in the standard orientation, while the second was taken after rotating the specimen 90 degrees (Figures 3a,b). If collector bias is a significant

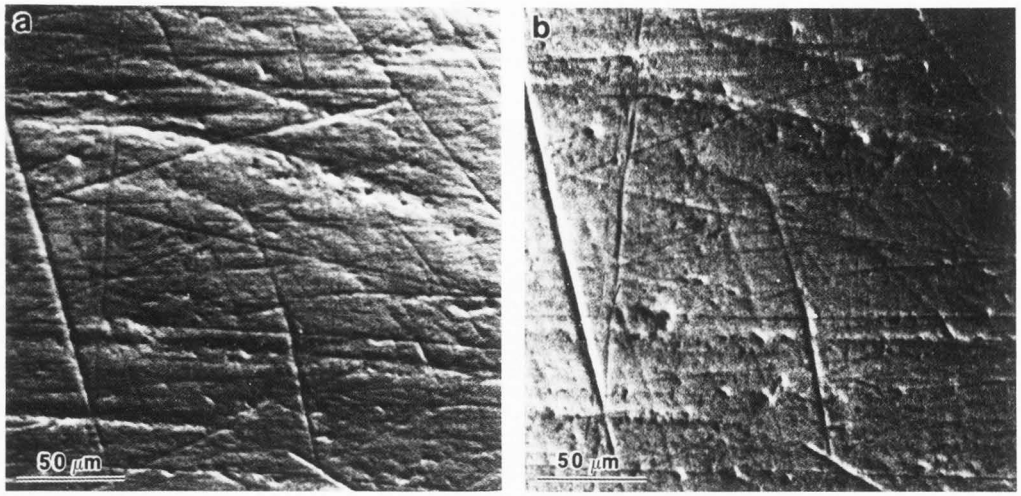


Figure 3: Two micrographs of the same surface recorded at approximately 300X. (a) specimen in "standard" orientation - buccal edge to the right. (b) specimen in "rotated" orientation - after shifting 90 degrees. In (b), the photograph has been returned to "standard" orientation.

problem, it should affect the microwear analysis in the following ways: for the standard image, the collector-specimen axis is mesiodistal, and bias should therefore act against the perception of scratches in relatively mesiodistal orientations (e.g., those between 0^{o} - 45^{o} and 135^{o} - 180^{o} in the compass field; see Fig. 1). The rotated image (which is returned to standard orientation for digitizing and analysis) should be most accurate between 0^{o} - 45^{o} and 135^{o} - 180^{o}, but should show deficits in the range of 46^{o} - 134^{o}, this corresponding to the specimen-collector axis during recording.

Results of the metrical analysis of the two images are given in Table 2. Differences between the two images are apparent in both the number of features perceived, and in the dimensions of features digitized. Dimensional differences are significant for scratch breadth, and the range of measured breadth is also different. Standard image scratches are on average wider, and the maximum measured breadth is double that found on the rotated image. Analysis of the feature counts showed that four exceptionally broad scratches on the standard image (Fig. 3a) were either not included in the rotated sample (Fig. 3b), or if present were digitized at much smaller maximum breadths. Whether this is a result of collector bias, image quality, or operator error, or some combination of these is unclear. A larger sample of such image pairs will have to be analyzed to clarify this issue.

Although the ratio of scratches to pits is similar for both images, the total number of features recorded is lower in the rotated image than in the standard view, resulting in different density estimates. This may be the result of collector bias acting primarily against the numerically largest subset of scratches (those in buccolingual orientations), resulting in a relatively greater impoverishment of the data set. The breakdown by orientation fields reveals that the hypothesis about differential effects of collector bias on different portions of the compass field appears to be confirmed. That is, on the standard image (Fig. 3a), there are fewer scratches recorded

Table 2. Comparison of Microwear Analysis of Surfaces in Standard and Rotated Orientations.

		Standard (Fig. 3a)		Rotated (Fig. 3b)	
Actual magnification of digitized photo enlargement		318X		343X	
Area surveyed (mm^2)		0.19		0.25	
Feature Summary:					
Scratches (N)		133	63.9%	101	68.2%
Pits		75	36.1	47	31.8
Total features		208	100.0	148	100.0
Dimensions (microns)		Length	Breadth	Length	Breadth
Scratches:	x	180.0	6.0+	181.7	4.8+
	s	138.8	4.5	143.5	2.9
	range	10.6-791.1	1.5-33.4	13.9-823.5	1.5-16.2
	V	77.1	75.0	78.9	60.4
Pits:		Max D	Min D	Max D	Min D
	x	9.1	6.6*	10.2	8.4*
	s	4.6	4.1	6.2	5.3
	range	3.6-25.4	2.5-23.9	4.1-30.4	3.2-29.7
	V	50.5	62.1	60.8	63.1
Orientation (degrees)					
Scratch N		133		101	
Angle x		74°**		86°**	
s		29		45	
range		8 - 177		3 - 179	
V		39.2		52.3	
By Fields:					
0 - 45 + 135-180°	(N)	27 (20.3%)		41 (40.6%)	
46 - 134°		106 (79.7%)		60 (59.4%)	

\+ t = 2.4419, DF = 232; 0.02 > p > 0.01
* t = 2.0160, DF = 120; 0.05 > p > 0.02
** t = 2.3785, DF = 232; 0.02 > p > 0.01

which fall along the specimen-collector axis (0^{o} - 45^{o} + 135^{o} - 180^{o}) than there appear to be on the rotated image (Fig. 3b), (27 versus 41 scratches, respectively). Similarly, in rotated orientation (Fig. 3b), there are fewer scratches found in buccolingual orientations (46^{o} - 134^{o}, corresponding to the collector-specimen axis during photorecording) than appear on the standard image (Fig. 3a), (60 versus 106 scratches, respectively).

Statistical differences between scratch orientation data follow from this bias. Mean angle values were significantly different, and the amount of dispersion of scratches through 180 degrees is also different. One estimate of this is the standard deviation, which is higher for the rotated image. This reflects the greater representation of scratches at the compass extremes than is true of the standard image. However, since such standard statistical measures are not truly appropriate for angular data (see Gordon 1984a for a discussion), a nonstatistical test of distribution pattern (Shipman 1981) has been applied to these data. These results (Fig. 4) show that the orientation differences are important. The standard image would be interpreted as a uniaxial pattern, based on its distribution of scratches with a single major peak corresponding to the buccolingual direction of the power stroke of mastication. However, the rotated version most closely approximates a random model of scratch dispersion, with only a weak peak in the buccolingual axis.

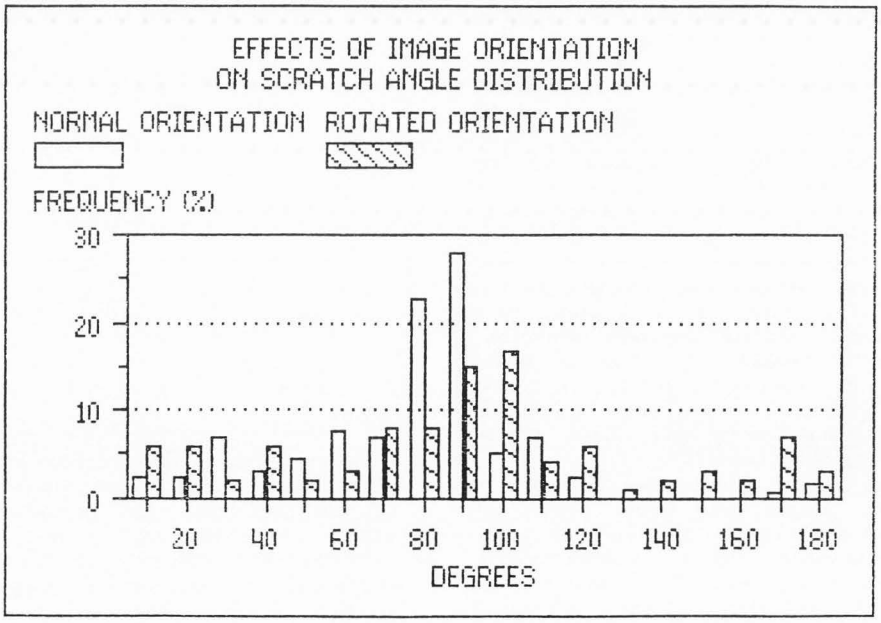
The ultimate effect of using SEM photomicrographs taken in standard orientation with only one collector is to eliminate or underestimate the already rare scratches in non-buccolingual orientations, thereby reducing the apparent dispersion of scratches in 180 degrees. This may lead to a false impression of relatively tighter occlusal guidance of tooth contact pathways, and will underestimate the amount of variability in tooth contact orientations. In view of this, previously published accounts which have signalled unexpectedly high degrees of apparently random or variable occlusal contact pathways (Gordon 1984b) or those which have shown significant species differences in occlusal guidance (Grine 1987) should be taken as minimum estimates of the actual amount of randomness in chewing movements.

Because this experiment is based only on a single specimen, these results are clearly suggestive, rather than definitive. More work will be required to confirm this preliminary study, to explore the effects of collector bias on work already completed, and to determine what steps should be taken in the future to resolve this problem.

Pattern Variability and Statistical Significance

The final point to consider here is the question of variability. The author would like first to review the kinds of variability which can be found within populations where dietary variation is not thought to be present (though it is always a theoretical possibility when dealing with the relative unknowns of museum

Figure 4: Histogram of scratch orientation frequency comparing results of standard image with those of the rotated image. The rotated orientation distribution most closely approximates a random pattern, while the standard distribution is clearly uniaxial.



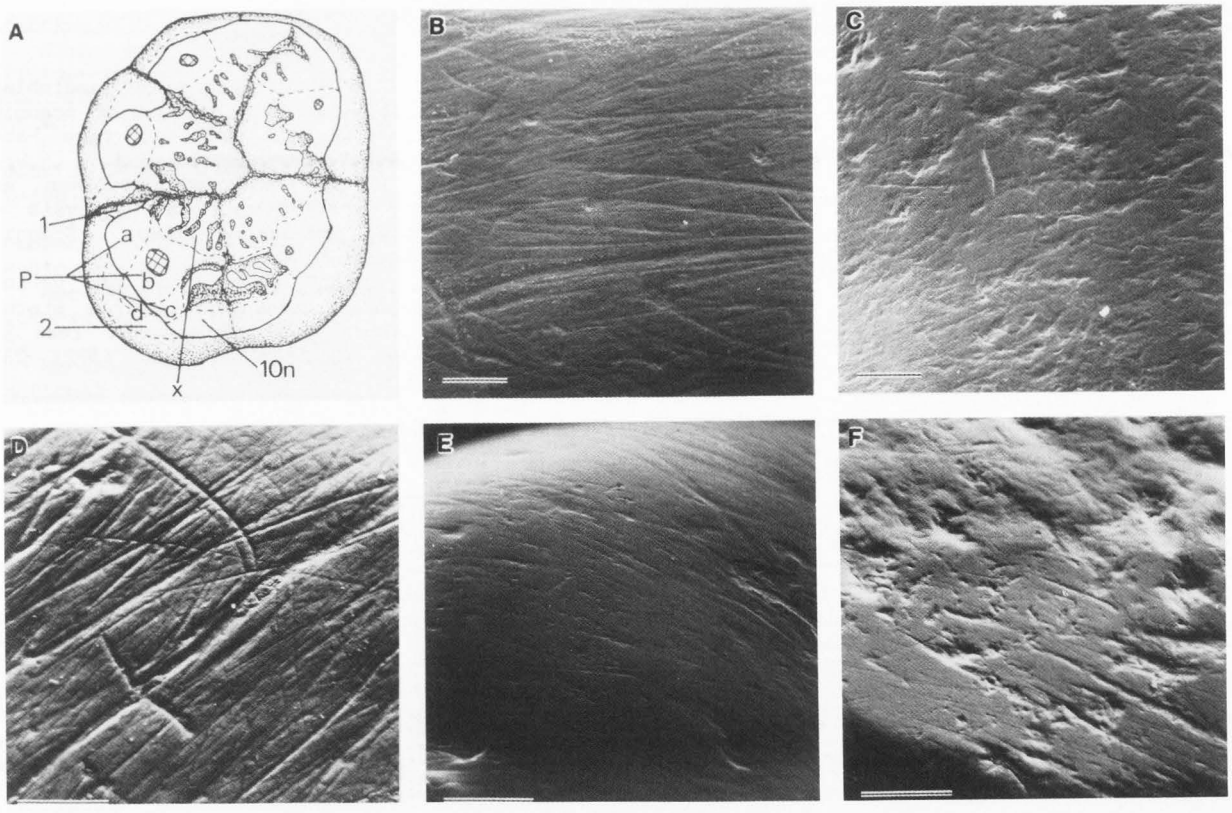
samples). Secondly, some guidelines are suggested for deciding how much microwear difference between populations is necessary to permit the conclusion of significant dietary differences.

Variability in microwear appearance can be enormous, both within dentitions and even on the surface of a single tooth crown, as previous work has shown (Gordon 1982, 1984c). The two primary variables which seem most closely associated with the distribution of microwear variants on molars are position on the tooth in the molar series, and facet or wear surface type. Figure 5 shows the range of microwear patterns which can be found within a single chimpanzee molar series.

Previous explanations for these variations have centered around the functional anatomy of the jaws and the geometry of chewing (Gordon 1982). Molar teeth of most mammals exhibit complex surface topography, expressed as an array of facets or surfaces which interact in various ways with those on the opposing teeth. These functions have been defined as shearing, puncture-crushing, and grinding (Crompton and Hiiemae 1970; Hiiemae and Kay 1972). It was suggested that the variations in microwear patterns found on functionally different facets (Figs. 5 D-F) might be the result of different amounts of shear and compression acting on the enamel surface. For example, shearing surfaces slide past one another, which promotes high relative movement ("shear") between the surfaces but not much compression or load. However, crushing and grinding surfaces shear relatively little, but experience greater compressive loads. Similar variations relative to the center of jaw rotation about the condyle may explain the differences noted between homologous surfaces on different molars within the same jaw (Figs. 5B, C). Distance from the active side condyle will influence the length of the arc through which a tooth moves during chewing, as well as the amount of load or compression it undergoes. Differences in such forces are thought to contribute to variations in scratch length and feature breadth.

Other factors may prove to be involved in intraspecific variations as well, such as changing orientations of enamel prisms relative to the wear plane (Rensberger and von Koenigswald 1980). It is also possible that ultra-structural differences between the enamel of different species (Boyde and Martin 1982,

Figure 5: Microwear variability to be found within a single dentition. (A) occlusal diagram of facets on chimpanzee molar (lower right first molar); (B) cusp tip facet (site Pb) on M1; (C) same site on M3 of same dentition; (D) Phase I shearing facet 2, M2; (E) cusp tip facet (Pa), M2; (F) Phase II grinding facet 10n, M2. Scale bar = 100 um. Reprinted with permission of the Journal of Dental Research.



1984; Martin 1985) may contribute to some of the interspecific microwear differences which have been previously attributed to diet, although work by Teaford and Walker (1984) found no differences in microwear pattern between species with similar diets, but dissimilar enamel prism patterns. Whatever the ultimate explanation, various studies (Gordon 1982; Grine 1987; Teaford and Walker 1984) have made it clear that when comparing results from different groups, microwear analyses must, at a minimum, control for tooth position, facet type, and probably wear angle or stage as well, in order to factor out microwear variability that occurs naturally as a result of biomechanics or ultrastructure, and that has nothing to do with the goal of these studies, which is the detection of dietary variation.

In addition to attempting to control for non-dietary sources of variation in microwear, it is essential to analyze data in such a way that it is possible to determine how much individuals within a target or reference population vary from the mean derived from the total sample. This requires that data be analyzed individual by individual, and that a group or grand mean then be constructed from the mean values for all individuals in the sample. It is specifically not useful to pool data from 10 different individuals, and consider the 3000 scratches so obtained to constitute a single sample, with an N of 3000 (as in Teaford and Walker 1984, for example). In biological terms this is meaningless, and furthermore, when data are analyzed in this way, it becomes impossible to reconstruct the degree to which individuals depart from the mean. Instead, one has only information about how much scratches or pits depart from the mean, a piece of information of a very different character, and one that is not nearly as valuable in making decisions about how well (or how poorly) microwear summaries may be said to describe populations.

To date, all the quantitative analyses which have been published have dealt with microwear variations on a parameter by parameter basis, using primarily univariate comparisons of data. Attempts to analyze more than one variable at a time, such as the reduction of feature size and shape to a length:breadth ratio as used by Teaford and Walker (1984), have been few and not altogether successful. It is time to apply multivariate approaches to this volume of data. A given species or population can be characterized by a vector of parameters, which would usually be the groups' means for particular traits such as scratch length or pit diameter, but these values might also be standard deviations or coefficients of variation of traits, where the population variability with regard to a specific trait (parameter) seems significant in itself. Only by making use of all the available information simultaneously can we make progress toward the goal of getting reasonable and repeatable results which truly define population differences.

The last point to consider is how are we to assess the significance of whatever differences we might find between populations, by whatever means we use? It seems clear that given the small sample sizes we are presently capable of handling, and the natural variability of microwear within homogeneous populations, our assessments of what constitutes a real difference between populations must take into account the amount of variability within each of the populations in question. In other words, the question we must ask of our analyses is whether the between-group variance is greater than the within-group variance. Consequently, analysis of variance (in some form) is the technique of choice here, as for example in Teaford (1985). Until microwear data are analyzed in ways which address this concern, we should all make a practice of being skeptical of everyone's conclusions, even (or especially) our own.

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Discussion with Reviewers

F.E. Grine: My principal concern is with the statistics used to compare scratch orientation between different magnifications, and between micrographs at different orientations. I do not believe that mean orientation and a simple t-test is appropriate, as these are data that should be analyzed in terms of their distributions (e.g., X^2 or Kolmogorov-Smirnov tests seem more appropriate).

Author: I agree with Dr. Grine that the statistical evaluation of orientation is best done with tests other than means and t-tests, as I stated in the paper itself. A non-statistical method of comparing the orientation distributions was also presented. I would like to explore the use of the Kolmogorov-Smirnov test with data such as these. Unfortunately, that proved impossible in this instance because the original data set used here was destroyed in a computer malfunction subsequent to the original submission of the manuscript.

F.E. Grine: Also I am a little concerned that the 'normal' orientation micrograph is of so much better quality than the 'rotated' micrograph, and I wonder whether the differences that are reported for them do not pertain to the difference in their quality rather than to a difference in the microwear fabrics that they picked up.

M. Teaford: In regard to feature detection, the results of other comparisons made in Table 2 (such as number and size of features) may also be reflecting the differing quality of the two images, because Fig. 3b is definitely a poorer image.

Author: While I agree that the quality of the two images shown in Figs. 3a and 3b is not as similar as I would wish for the purposes of comparison, I nonetheless feel confident that the essential differences in quantitative results are not merely a function of image quality, but rather of orientation relative to the collector. Similar comparisons still in progress seem to show the same kinds of differences, indicating that the preliminary results obtained here are unlikely to be due solely to micrograph quality.