

12-16-1987

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Teaford, Mark F. (1987) "A Review of Dental Microwear and Diet in Modern Mammals," *Scanning Microscopy*: Vol. 2 : No. 2 , Article 48.

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A REVIEW OF DENTAL MICROWEAR AND DIET IN
MODERN MAMMALS

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(Received for publication May 26, 1987, and in revised form December 16, 1987)

Abstract

Recent work has shown that microscopic wear patterns on teeth may yield insights into variations in diet and tooth use in modern and prehistoric mammals. This paper presents a review of dental microwear and diet in modern mammals, plus a discussion of topics for further research. To date, incisor and molar microwear have been examined, although there are far fewer studies of the former. Facilitated by the use of high-resolution casts and scanning electron microscopy, analyses have ranged from: qualitative to quantitative, low magnification to high magnification, and experimental studies to comparative studies of museum collections. Results are encouraging and may lead to further insights into a variety of topics including food processing and dental microstructure.

Introduction

Over the past few years, many investigators have turned to scanning electron microscope analyses of dental microwear to document changes (and differences) in the oral behavior patterns of modern and prehistoric mammals. The logic behind these analyses is relatively straight-forward. Essentially, many abrasives can leave microscopic defects on teeth - even tooth-on-tooth wear can leave characteristic microscopic wear patterns (see Figure 1). It follows that analyses of variations in these wear patterns can provide a unique record of the oral behavior patterns that caused them. Nevertheless, interpretations of the results may be difficult because there is no general theory of wear - thus the effects of different abrasives and the ways in which they are applied to teeth must be determined empirically.

The precise origin of these analyses is difficult to trace because investigators have frequently made comments about the potential usefulness of microscopic scratches on teeth in interpretations of jaw movement and tooth use (e.g., Butler 1952, 1972, 1973, Mills 1955, 1963, 1967). However, a reasonable candidate for the first step towards today's dental microwear analyses is a brief paper published by Dahlberg and Kinzey (1962). Based on light/optical microscope analyses of a sample of modern and prehistoric human teeth, they suggested that careful inspection of variations in microscopic dental wear patterns could shed light on dietary differences within and between species.

After these initial suggestions, however, nothing was published for over ten years until LeJeune and Baron (1973), Walker (1976), and Wallace (1974) showed that the orientation of microscopic striations on teeth could be used to infer differences in jaw movement and tooth use in different populations. The study by Walker was particularly noteworthy, because it combined microwear

Key Words: Scanning Electron Microscopy, Teeth, Enamel, Diet, Incisors, Molars, Abrasion

analyses with observations of feeding behavior to show that differences in incisor microwear could be related to differences in leaf-stripping behavior in cercopithecoid primates. Still, these analyses involved the use of the light microscope and were limited by the range of magnifications and depth of focus of that instrument.

Two things happened during the 1960's and 1970's that were of critical importance to the development of current analyses of dental microwear. The first was the development of the scanning electron microscope and the demonstration by Boyde (1964, 1967, 1970, 1971) of the immense potential of the SEM for future analyses of dental structure. The second involved the development of high-resolution casting techniques (Barnes 1978, Pameijer 1978, Pameijer and Stallard 1972, Pfefferkorn and Boyde 1974) which allowed investigators to use replicas in place of original specimens. This made possible longitudinal studies of tooth wear and analyses of valuable museum material that was heretofore unavailable for such purposes.

With these techniques, investigators began to look seriously at dental microwear and its relationship to diet. Given the range of work on modern and fossil animals, and for the sake of brevity, this paper will concentrate on the work on modern mammals. Incisor microwear is dealt with separately from that of molars because these teeth are used in different ways.

Incisor Microwear and "Diet"

In one respect, incisor microwear is extremely difficult to interpret, for, located at the front of the mouth, the incisors are put to many uses, and mastication is generally not one of them (see Brace 1962, Molnar 1972, and Schour and Sarnat 1942 for interesting examples of incisor use in humans). Even if we could rule out the effects of various behaviors such as grooming (see Rose, et al. 1981), the best we could hope for would be a record of ingestion that might be one step removed from a record of diet. Such information might seem to be of little use from an anthropocentric viewpoint, since humans now use tools, not incisors, to prepare most of their food. However, for other mammals, variations in ingestive behavior are extremely important. Thus, while a variety of factors could produce wear on the incisors, careful study might distinguish the types of wear that typify each factor. By so doing, the multiple uses for which an incisor was used might be detectable from the microwear. What we have so far is but a glimpse of the potential of these analyses.

Ryan (1981) was the first to use the SEM for this purpose. Working at very low magnifications (35X), he created photographic montages of entire occlusal surfaces. He then compared the orientation, density, and form of microwear features in Gorilla, Pan, and Papio, three primates that he felt were useful for comparison with fossil hominids. The results were interpreted in terms of published accounts of incisal food preparation in the three species, and the bulk of the microwear differences were tied to interspecific differences in either the amount of extraneous grit on food items or the way in which the animals used their incisors in stripping leaves from branches.

Given the magnitude of the differences documented by Ryan, and by Walker in 1976, Teaford (1983) decided to see if finer microwear distinctions could be made. Two species of langurs were examined: Presbytis rubicunda and Presbytis cristata. While both species had traditionally been viewed as leaf-eaters, more recent behavioral work (Davies 1984) had shown that P.rubicunda spent a significant portion of its feeding time (approximately 29%) eating the seeds of legumes not eaten by P.cristata. Since P.rubicunda uses its incisors to open the legume pods, and since P.rubicunda has a pronounced underbite (or underjet), while P.cristata has variable incisal occlusion, it was felt that the wear on the incisors might prove interesting. Low magnification surveys of the incisors of younger individuals suggested that these species were indeed using their incisors differently (see figure 2). At higher magnifications (500X), it became apparent that most scratches on the enamel ran in a labio-lingual direction. However, statistical analyses showed that the species with the underbite had significantly higher proportions of scratches running in the labio-lingual direction. This, in conjunction with the differences in gross incisor wear, reaffirmed that P.rubicunda was using its incisors differently than P.cristata and that the underbite in P.rubicunda is not merely an insignificant trait put to variable use as it is in humans.

More recently, Kelley (1986) has completed a survey of incisor microwear in 10 primate species with different diets. Working at magnifications of 50-100X, he described the patterns of incisor microwear visible on samples of 4-7 individuals of each species and compared those patterns between primate folivores and frugivores. The main difference was that the frugivores showed heavier microwear, and in particular, more striations, on their incisors.

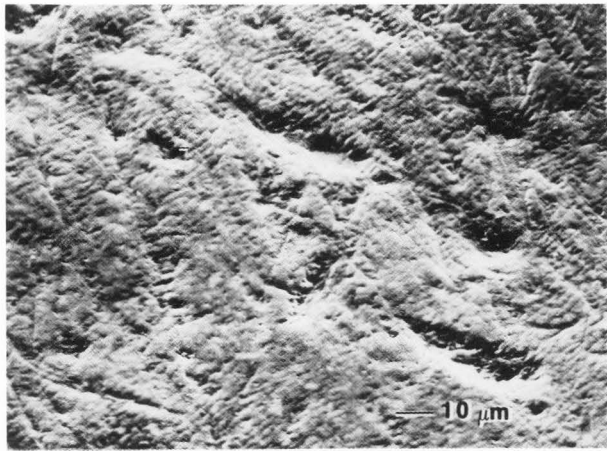


Figure 1. LM₁ of a laboratory vervet monkey. This animal is known to grind its teeth quite frequently. Note prism relief throughout the micrograph.

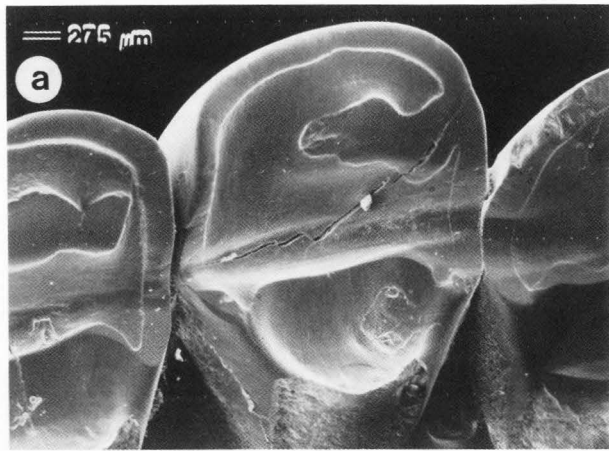


Figure 2. Mandibular incisors of two species of langurs.

a = Presbytis rubicunda (species with underbite).

b = Presbytis cristata (individual with edge-to-edge incisal occlusion).

Note pronounced step worn into lingual surface of top specimen.

Molar Microwear and Diet

Kelley related this to either increased incisal preparation of food, or more abrasives in (or associated with) the diet. He also noted some interesting exceptions (e.g., unexpectedly heavy incisor microwear in Colobus badius), and suggested that "diets within any major dietary category are not uniform, and perhaps not even similar, with respect to food procurement tasks and/or the physical properties of dietary items and food substrates" (Kelley, 1986:239).

In addition to these studies of museum material, there is one longitudinal study of laboratory primates in progress (Teaford and Oyen 1986a, b). In that study, 10 vervets are being raised on a diet of monkey chow and fruit, while 5 vervets are being raised on a softer diet of water-softened monkey chow and pureed fruit. Differences in gross incisor wear between the two groups are already apparent (see figure 3). At first glance, these differences may seem to be surprising because the animals on the softer diet are showing more pronounced wear on their incisors. However, the different wear patterns are readily explainable in terms of the ingestive behaviors used by the animals in the two diet groups - i.e., the animals on the softer diet routinely use their incisors to scrape soft food off their fingers, while the animals on the hard diet only use their incisors occasionally to bite through monkey chow biscuits. Microwear analyses are just beginning, but perplexing differences between incisal edges and labial surfaces are already apparent (see Figure 4).

As indicated above, investigators have often found it easier to make inferences about diet based on analyses of molar wear (rather than incisor wear) because mammalian molars are generally used for chewing rather than for ingestion, grooming, etc. (see Taylor 1963 for an interesting exception in humans). Studies of molar microwear have been of two types: those concerned with the inference of jaw movements from wear patterns (e.g., Gordon 1984a, b, c, Gordon 1984, Kay 1977, 1981, Kay and Hiiemae 1974, Ryan 1979a, b, c, Teaford and Byrd 1987, Teaford and Walker 1983a, b, Walker 1984, Young and Robson 1987), and those concerned with the inference of diet. The latter will be emphasized in the following discussion.

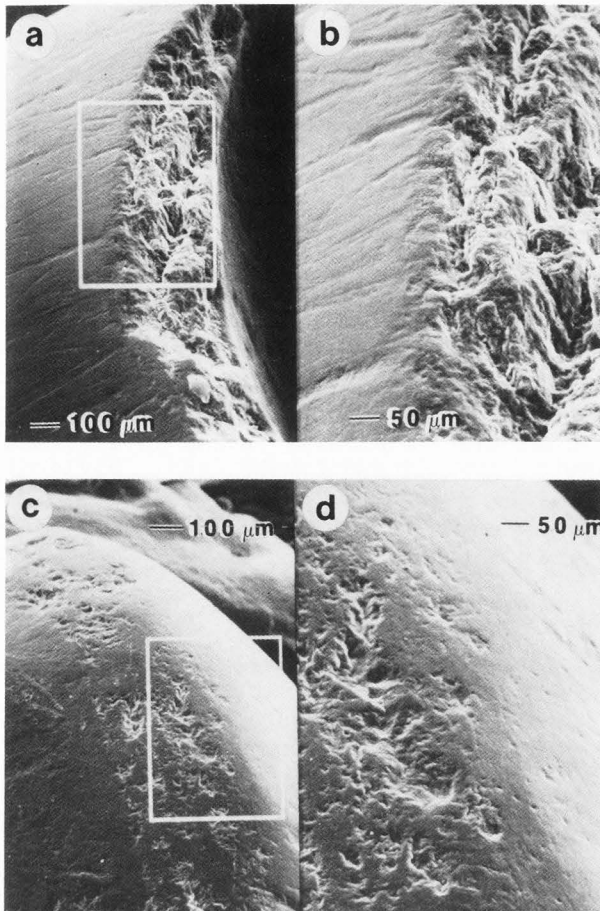


Figure 3. Mandibular incisors of vervet monkeys raised on different diets. a & b = animal raised on hard diet c & d = animal raised on soft diet

In 1978, two papers rekindled interest in molar microwear analyses. Walker et al. (1978) showed that seasonal changes in diet in one species of hyrax (*Procavia johnstoni*) were accompanied by marked changes in molar microwear - i.e., the months spent browsing produced a fine polishing on the molar enamel and the subsequent time grazing scratched the enamel quite heavily. Analyses of fecal pellets from *P. johnstoni* and a control species, *Heterohyrax brucei*, showed that opaline phytoliths were the most likely cause of the heavy scratching on the teeth of the grazing animals.

Rensberger (1978) documented differences in molar microwear between six genera of modern rodents known to have different diets. This paper is especially noteworthy because it not only described patterns of wear but also "systems" of wear for each genus. In other words, it tried to correlate specific patterns of wear with specific causes of wear, and in so doing, it

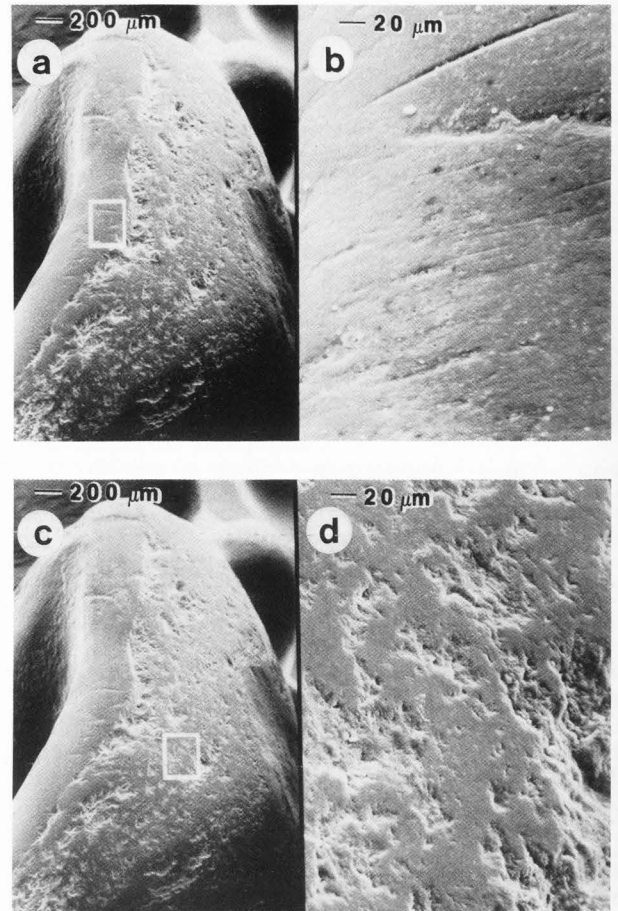


Figure 4. Maxillary central incisor of laboratory vervet monkey. Note preponderance of scratches on incisal edge (in a & b) and preponderance of pits on labial surface (in c & d).

provided the first glimpse of the complexity of tooth-food-tooth interactions in chewing.

These papers were followed by a number of others that showed that qualitative differences in molar microwear could be related to a number of dietary/behavioral differences - e.g., browsing vs. grazing (Walker 1981), forest vs. open-country herbivory (Walker 1980), wear with food vs. wear without food (Teaford and Walker 1983a, b), and feeding on vertebrates vs. invertebrates (Taylor and Hannam, 1987). The magnitude of the differences documented in these studies was very encouraging. If the differences were this great, could finer dietary distinctions be made? Or, given the speed and magnitude of the seasonal changes in wear documented by Walker et al. (1978), would seasonal or annual changes in diet wreak havoc with microwear analyses of species with

variable diets? Clearly, more work was necessary. To date, that work has come from two different perspectives - i.e., experimental laboratory work and quantitative analyses of museum material.

Experimental Laboratory Work

The easiest way to sort through the complexities of tooth wear would seem to be through controlled, laboratory studies - either using laboratory animals raised on known diets, or experimental models of tooth wear using materials with known properties subjected to strictly-controlled abrasive (or non-abrasive) environments. Both have been used, but with mixed results.

Initial experimental studies (Puech and Prone 1979, Ryan 1979a, b, c) were encouraging because they suggested that the size and shape of microwear features were related to the size and shape of the abrasive particles that caused them. However, the results come from simple experiments where abrasives were ground against teeth (or vice versa), and generalizations to dental microwear in living animals are difficult - especially in using striation morphology to determine directions of jaw movement (see Gordon 1984a, b, Gordon 1984, Kay 1981, Ryan 1979a, b, c, Teaford and Walker 1983b, and Walker 1984 for further discussions).

Peters (1982) followed this work by testing the effects of individual food items on human teeth in an INSTRON compression testing machine. More specifically, isolated third molars were placed on a rigid, flat surface, and food items (attached to the crosshead of the INSTRON tester) were then forced onto the teeth. The object of the study was to see if different food items yielded different microwear patterns. As it turned out, some did and some didn't. For example, Peters found that grit on wild onion bulbs yielded fine scratches on the teeth while dicotyledonous seed coats did not. Since the scratches produced by grit were similar to those thought to be caused by opal phytoliths in the study by Walker et al. (1978), Peters concluded that "microscratch morphology alone may not provide a reliable indication of dietary food type" (Peters, 1982:299). It should be noted that many of the tests in this study were run with only one to five repetitions. Those that were run with more repetitions (i.e., 10-50) can still represent only a few bites of food at best since each bite of food is generally chewed 10-20 times before being swallowed. Since every bite of food might not yield microwear, these small samples pose problems for interpretations of the significance of

these results. More importantly, hard objects are never punctured between a flat surface and a third molar in hominid mouths. Initial puncturing of large objects will inevitably occur more anteriorly along the tooth row between opposing cusp tips, or cusp tips and basins (Lucas and Luke 1984). As Osborn and Lumsden (1978) and Lucas (1979, 1982) have demonstrated, the geometry of the opposing structures is important for both food retention (between teeth) and food breakage. It follows that a necessary addition to Peters' experiment is the use of opposing teeth so that the food item is broken between the teeth. Finally, the focus of Peters' study is still on isolated food items. Since diets vary from day to day, the relative importance of isolated food items in the creation of overall patterns of molar microwear is still not known. Thus, while there are some extremely interesting revelations in this study (e.g., grit on soft foods can indeed scratch enamel), more sweeping conclusions concerning the usefulness of microwear analyses in dietary interpretations must await additional experiments.

Citing the need for strict dietary control in microwear analyses using live animals, Covert and Kay (1981) ran a short-term study using opossums fed different diets. Three opossums were fed cat food, five were fed a mixture of cat food plus 15% plant fibre, and 4 were fed a mixture of cat food plus 15% chitin. After 90 days, no molar microwear differences were visible between the three groups. One of the individuals in the first group was fed a mixture of cat food and 10% pumice for the last 30 days of the study, and that individual did show a pattern of heavy scratches similar to that described by Walker et al. (1978) for grass-eating hyraxes (*Procavia johnstoni*). Given the other results of this study, Covert and Kay were skeptical of the general usefulness of dental microwear analyses in dietary interpretations.

This prompted criticism by Gordon and Walker (1983) and a reply by Kay and Covert (1983). The bulk of this argument centered around the methods used by Covert and Kay in their original paper. Excluding questions of qualitative vs. quantitative analyses and the effects of isolated food items vs. entire diets, the most important question seems to be the following, "was this a realistic test of the relationship between dietary changes and changes in dental microwear?" Unfortunately, the answer is probably "no". The main problem concerns the way in which opossums chew cat food - essentially they do not (Hiimae et al. 1978). Each lump of cat food is passed from the front of the mouth to the back

of the mouth relatively quickly with little or no chewing. Thus, as Gordon and Walker (1983) noted, any abrasives added to the food may not have been between the teeth long enough to have a noticeable effect. Moreover, since cat food is very soft, the chewing that did take place probably resulted in tooth-tooth contact anyway - so the bulk of the macroscopic wear observed by Covert and Kay may have been caused by tooth-on-tooth wear rather than tooth-food-tooth wear. In light of these difficulties, the lack of baseline replicas (i.e., those prepared before the diet was changed at the start of the study) is of critical importance for establishing the amount and types of wear observed in these animals (Gordon and Walker 1983).

To avoid some of these problems and yet retain control over diet in living animals, Teaford and Oyen (1986a, b) have begun a long-term study of tooth wear in two laboratory populations of vervets. As noted previously, only the hardness of food items is varied between diet groups. Results will be a long time coming, but already three things are suggested by preliminary analyses of the mandibular first molars: (1) it is hard to find features in common between casts made six weeks apart - i.e., the turn-over in dental microwear is relatively rapid (see Figure 5); (2) the molar shearing facets of animals in both groups are very similar (see Figure 6) indicating that there are abrasives in both diets; but (3) the molar crushing facets are different, with the animals feeding on soft food showing significantly fewer features per field of view. This might be expected since the animals feeding on soft food would process little if any food that would need crushing. It is still encouraging, however, for it is the first hint that differences in microwear in living animals can be produced by changing the consistency of food items.

In sum, experimental studies of molar microwear have just begun. As a result, they have probably raised more questions than they have answered. Some investigators (e.g., Kay 1984, Kay and Covert 1984) have used results of initial studies to claim that microwear will not be very useful in future dietary interpretations. Perhaps it is better to simply reserve judgement until more data are available.

Quantitative Analyses of Museum Material

Another group of investigators has taken a different approach to the subject, looking at molar microwear in a variety of modern populations using museum collections. In the process, they have introduced a series of quantitative analyses that may help to sort through

the intricacies of future findings.

The pioneering work was done by Gordon (1982, 1984b,c), who suggested a number of precautions that must be observed if future investigators are to make dietary inferences based on interspecific comparisons. Using a museum collection of chimpanzee material, she made a variety of measurements on a number of facets on M1 through M3. Measurements of microscopic wear features were computed from SEM micrographs taken at 125X. Her results suggested that molar position, facet type, and individual age could all have effects on microwear, as there were essentially two "gradients" of microwear changes detectable within her sample: (1) in going from M₁ to M₃, scratch length, pit diameter, and the relative frequency of scratches decreased, and (2) in going from shearing facets to crushing facets (on the same tooth), total feature density and the relative frequency of pits increased. These gradients seemed to be tied to variations in occlusal mechanics at different points along the tooth row. For instance, the incidence of pitting versus scratching could be seen as a reflection of relative amounts of compression and shear during occlusion. Since the amount of compression and shear during occlusion varies at different points on a tooth, and at different points along the tooth row, microwear might be expected to vary due to these biomechanical differences. Finally, since most of these differences were not obvious to the eye, Gordon (1984b) concluded that statistical analyses of large samples were necessary to sort through the subtleties of microwear differences.

As Gordon (1982) has correctly emphasized, this work was based on analyses of 8 individuals of one species from a museum collection, thus conclusions concerning age- and sex-related differences in microwear must be viewed with a great deal of caution. Furthermore, we do not know the effects of drastically different tooth morphologies on Gordon's results. Nonetheless, independent analyses of other primate species (Teaford 1985, 1986, Teaford and Oyen 1986a, b, Teaford and Walker 1984) have reaffirmed Gordon's observations concerning interfacet differences in dental microwear, and until further data suggest otherwise, investigators should make every effort to at least control for tooth number and facet type in interspecific comparisons.

In 1984, Teaford and Walker presented the first quantitative interspecific comparisons of dental microwear. Seven species of modern primates were selected to test for possible differences between primate

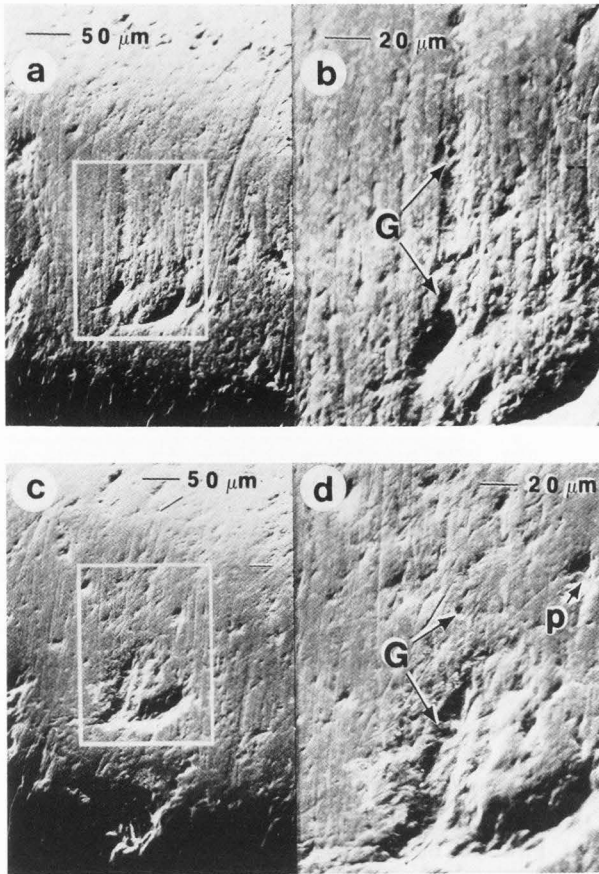


Figure 5. LM₁ of vervet monkey raised on soft diet.

a & b = Epoxy cast made from dental impression taken on October 12, 1985.
 c & d = Epoxy cast made from dental impression taken on November 22, 1985.
 Note modification of the large gouge (labeled "G") and a new, large pit (labeled "P" in the bottom micrograph).

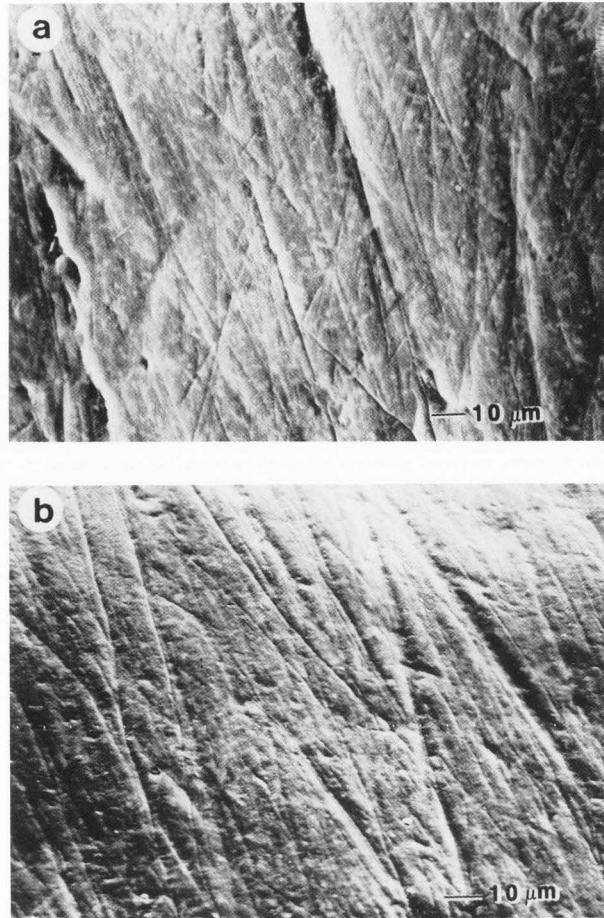


Figure 6. Shearing facets on LM₁'s of vervet monkeys raised on different diets.
 a = Facet 3 of vervet raised on hard diet.
 b = Facet 3 of vervet raised on soft diet.

hard-object feeders and leaf-eaters. In view of Gordon's work, and to speed up the analysis, a shearing facet and a crushing facet were examined on M2 for each specimen. Since small scratches had proven difficult for Gordon to measure at magnifications of 125X, Teaford and Walker used higher magnifications (500X). This insured that all microwear features within a given micrograph were measured. Wherever possible, two micrographs were taken for each facet. Every feature within each micrograph was measured, and the ratio of the length to the width of each feature was used to categorize each feature as either a pit or a scratch. Chi-square analyses were used to test for intraspecific and interspecific differences in the distribution of pits and scratches. Results included the only test of microwear differences in upper

vs. lower teeth (indistinguishable for *Colobus guereza*). More importantly, primate hard-object feeders could be distinguished from primate leaf-eaters. The molars of hard-object feeders were characterized by high proportions of pits, while those of leaf-eaters were characterized by fine scratching (see Figure 7). A species with a more variable diet (*Pan troglodytes*) was then added to the analysis as was the fossil primate, *Sivapithecus*. Both were intermediate in terms of wear patterns and significantly different from leaf-eaters and hard-object feeders. Wear patterns for *Pan* and *Sivapithecus* could not be distinguished.

This study is encouraging but not without problems. The biggest is that it overlooks individual variation in dental microwear. Through the chi-square analyses, individual microwear features

are effectively treated as independent events. Since microwear features on a given tooth are liable to be more highly correlated with each other than with features on the teeth of other individuals, the chi-square analyses are probably inappropriate. The way around this is to treat the proportion of pits (or scratches) for each individual as a data value in a multiple comparison test (Zar, 1974:156-157). Since proportions are not normally distributed, the arcsine transformation should be used beforehand (Zar, 1974:185-186). Comparisons should thus involve a series of transformed mean values (from each individual) for each species. If this is done for our data, the differences between hard-object feeders, leaf-eaters, and the combination of Sivapithecus and Pan troglodytes are still highly significant ($p < 0.001$). Results for individual interspecific comparisons, however, become harder to interpret because the proportions of pits and scratches for Sivapithecus and Pan troglodytes cannot be distinguished from those for Pongo pygmaeus. Given the highly significant results for the combined comparisons, perhaps these difficulties are more a reflection of small sample sizes as no sample is larger than 10 individuals. Closer examination of the features classified as pits is also necessary since subsequent work (Teaford 1985) has shown that the use of a 10:1 length:width ratio to categorize features as pits and scratches results in high proportions of short scratches being categorized as pits. Table 1 presents summary data for those modern species examined to date using a 4:1 length:width ratio as the cut-off between pits and scratches.

To test for differences between more closely-related species, Teaford (1985, 1986) looked at molar microwear in different species of Cebus and Colobus monkeys. Results showed that the average size of pits, and variation in the proportion of pits, could also differ between species (see Table 1). Teaford suggested that this might reflect dietary differences between the species. Of course, at this point, there is no way of establishing the precise cause of the observed differences in microwear. They may be due to differences in food or extraneous grit on food items. The key point is that these differences are direct evidence of environmental effects on teeth.

To examine the effect of seasonal variations in diet on microwear, Teaford and Robinson (1987) have begun a study of Cebus nigrivittatus using material collected by the Smithsonian Venezuelan Project (Handley 1976). Since the associated information with these collections is excellent, collection

dates and locations are readily obtainable for individual specimens. Preliminary results indicate that seasonal changes in microwear are small, but detectable (see Table 1). These seasonal differences may make certain comparisons difficult. For example, they may mask interesting differences between specimens collected from different ecological zones (see Table 1). However, they are not of the order of magnitude to interfere with interspecific comparisons such as those between Cebus apella and Cebus nigrivittatus (Teaford 1985) (see Table 1).

Discussion

So where do we stand in terms of dental microwear and dietary interpretations? Essentially, the analyses have just begun, yet they have already shown us some intriguing possibilities for future research. More importantly, it is now apparent that a number of critical questions need to be answered before the full import of dental microwear analyses can be realized. How do food items, and grit on food items wear enamel and dentin?

To date, the bulk of this work has centered on the process of abrasion, and even there (as noted by Lucas 1979 and Luke and Lucas 1983), investigators have had rather naive ideas about the abrasive effects of different materials on teeth. For instance, contrary to popular belief, relatively soft materials can abrade enamel (Boyde 1984). Moreover, factors other than gross measures of hardness of food items may have to be considered in determining which materials can or cannot scratch enamel and dentin (Grine 1981, Lucas 1979). For example, even though

Figure 7. Crushing facets (facet 9) on M2 of various primates.

- 7a = Cebus apella
- 7b = Alouatta palliata
- 7c = Cercocebus albigena
- 7d = Colobus quereza
- 7e = Pongo pygmaeus
- 7f = Gorilla gorilla
- 7g = Pan troglodytes
- 7h = Sivapithecus indicus

Cebus apella, Cercocebus albigena, and Pongo pygmaeus are all species known to eat hard objects, while Alouatta palliata, Colobus quereza, and Gorilla gorilla do not eat hard objects and have traditionally been regarded as leaf-eaters. Pan troglodytes is known to have a variable diet. Sivapithecus indicus is a Miocene primate originally thought to be a hard object feeder. Based on its dental microwear, it was probably not a classic hard object feeder like Cebus apella.

Dental Microwear in Modern Mammals

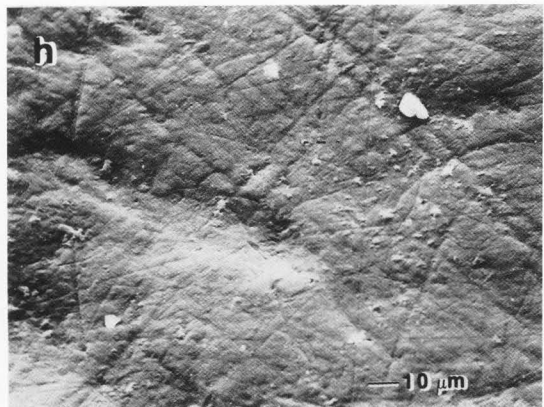
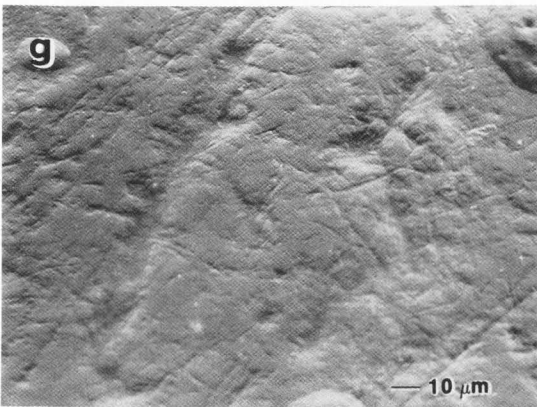
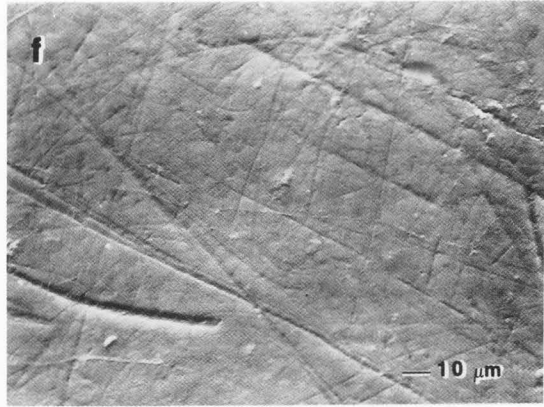
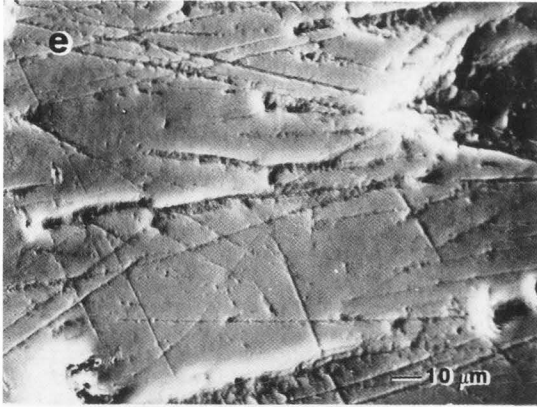
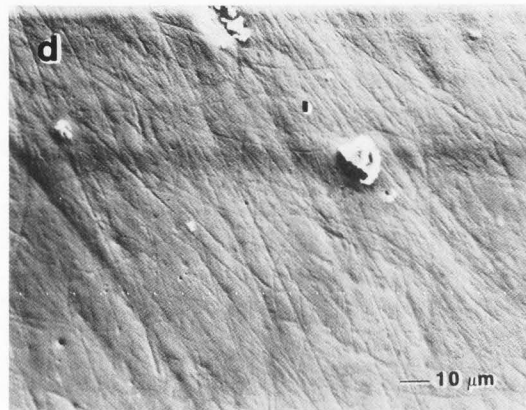
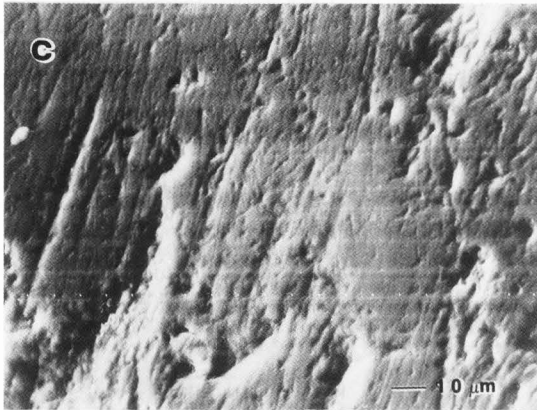
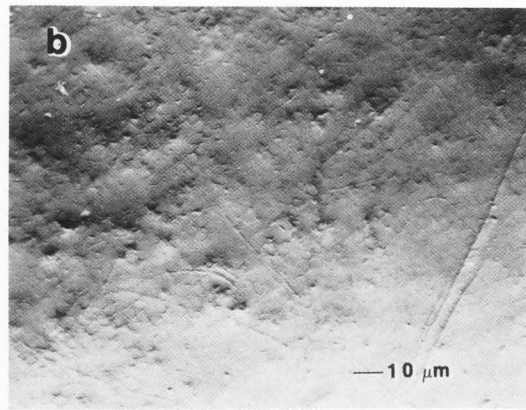


Table 1

Measurements of Dental Microwear for Various Primate Species

Species (N)	% Pits (mean±sd)	Pit Width (in microns) (mean±sd)	Scratch Width (in microns) (mean±sd)
<u>Cercocebus albigena</u> (10)	55.2 ± 12.4	9.9 ± 3.2	3.9 ± 1.2
<u>Cebus apella</u> (10)	45.1 ± 16.2	8.4 ± 1.5	2.9 ± 0.8
<u>Pongo pygmaeus</u> (10)	42.5 ± 19.1	7.1 ± 1.7	2.8 ± 0.4
<u>Pan troglodytes</u> (10)	24.2 ± 14.2	6.9 ± 2.6	2.6 ± 0.7
<u>Sivapithecus indicus</u> (6)	35.2 ± 8.8	5.5 ± 1.7	1.9 ± 0.5
<u>Alouatta palliata</u> (10)	9.7 ± 18.6	9.2 ± 6.6	2.1 ± 1.1
<u>Gorilla gorilla</u> (10)	3.4 ± 4.0	6.0 ± 4.1	1.4 ± 0.4
<u>Colobus quereza</u> (10)	9.7 ± 4.3	5.6 ± 2.5	1.2 ± 0.2
<u>Colobus badius</u> (10)	12.6 ± 14.0	6.1 ± 2.8	1.3 ± 0.3
<u>Cebus capucinus</u> (10)	11.7 ± 5.1	5.1 ± 1.7	1.5 ± 0.2
* <u>Cebus nigrivittatus</u> (10)	16.2 ± 7.4	8.6 ± 1.8	0.8 ± 0.1
<hr/>			
** <u>Cebus nigrivittatus</u>			
dry tropical woodland (13)	13.2 ± 7.5	6.6 ± 2.1	0.9 ± 0.1
humid premontane forest (13)	18.9 ± 8.3	7.7 ± 1.9	1.0 ± 0.2
humid tropical forest (36)	15.4 ± 6.6	8.3 ± 2.1	1.0 ± 0.2
<hr/>			
(within sample from dry tropical woodland)			
Oct./Nov. 1965 (6)	13.2 ± 7.7	7.6 ± 1.9	0.8 ± 0.1
June 1968 (3)	20.0 ± 3.0	7.8 ± 1.3	1.0 ± 0.1
Sept. 1968 (3)	4.9 ± 1.2	4.1 ± 0.8	0.8 ± 0.1

*specimens from Teaford (1985)

** specimens from Teaford and Robinson (1987)

All measurements are computed from SEM micrographs of facet 9 on M2 using a 4:1 ratio of feature length to feature width as a cut-off between pits and scratches. Means and standard deviations are computed from mean values for individuals.

still-born guinea pigs show significant wear, but no scratches, on their teeth (Teaford and Walker 1983b), can microscopic pieces of enamel still scratch enamel surfaces in different situations? In addition to chips of enamel, what other materials might abrade enamel? Thus far, suggestions in the literature have included opaline

phytoliths (Walker et al. 1978), cellulose and lignin (Walker et al. 1978), and grit adhering to soft foods (Peters 1982). At this point, however, none of these potential "abrasives" has been rigorously tested against enamel, and the relative contributions of food particles, versus extraneous grit on food, to overall patterns of microscopic

wear are unknown.

More importantly, abrasion isn't the only form of wear affecting the dentition. Other processes may be just as important, and none of these can be expected to work in isolation. For instance, certain food items (e.g., acidic beverages) have been shown to have a pronounced erosive effect on teeth (Eccles and Jenkins 1974, Imfeld 1983, Linkosalo and Markkanen 1985, Sognaes et al. 1972). Regurgitation may also lead to severe dental erosion (Hellstrom 1977, Hurst et al. 1977, Smith and Knight 1984). The potential rate of erosion in these situations may be as high as one micron per minute (Davis and Winter 1977a,b), and in clinical studies, rates of one micron per week have been measured (Xhonga et al. 1972). When one considers the fact that exposure to dietary acid may also lead to accelerated abrasion of enamel (Davis and Winter 1980), the need for work on the erosion of teeth becomes all the more apparent. In essence, we have over-simplified the entire wear process by over-emphasizing the effects of abrasion on teeth. Perhaps some of our current microwear puzzles will be solved through consideration of a variety of wear processes. For instance, in the case of "folivorous" primates, why do howler monkeys and colobus monkeys exhibit similar patterns, but different amounts, of molar microwear? Is the high proportion of fruit in the diet of the howler monkeys changing microwear patterns through acid etching? Are the howler monkeys undergoing more tooth-tooth contact as a result of eating soft foods (see below)? Are the colobus monkeys eating more mature leaves that are perhaps tougher or dustier? Such questions may, in turn, force field ecologists to collect new data, since most chemical analyses of potential food items (e.g., Glander 1982, Rosenthal and Janzen 1979, and Waterman 1984) concentrate on the presence or absence of nutrients and secondary compounds, such as tannins, with little or no mention of acidity per se.

How does enamel structure influence wear patterns?

Despite pioneering work by Boyde (1964, 1969, 1976), most investigators are only just beginning to appreciate the complexity of dental microstructure (see Boyde and Martin 1984 for a recent review of variations in primate dental microstructure). Can differences in tooth microstructure be responsible for interspecific (or even intraspecific) differences in dental microwear? We already know that differences in microstructure can be related to wear patterns at the gross morphological level in ungulates (Fortelius 1985, Rensberger and von Koenigswald 1980), rodents

(Koenigswald 1982, Rensberger 1978) and primates (Walker 1984). What about wear patterns at the microscopic level? As Boyde (1976) has noted, the intricacies of enamel structure will certainly influence the physical properties of enamel, thus one might expect dental microstructure to have an influence on dental microwear patterns (Boyde and Martin 1984). However, at this point, all we have in the literature are two suggestions of possibilities: (1) Gordon (1984b) has suggested that age differences in dental microwear may be tied to differences in hardness between surface and subsurface enamel, and (2) Teaford and Walker (1983b) and Gordon (1984) have noted that minute cracks along scratches may form preferentially between enamel prisms yielding information about the direction of movements producing the scratches. Clearly, at this point much more information is needed. An obvious starting point is to examine microwear in animals with similar diets but different enamel structure and compare that with dental microwear in animals with different diets and similar enamel structure. Thus far, consistent microwear results from studies of museum material suggest that variations in dental microstructure will complicate microwear interpretations but not overwhelm them. Only further information will tell.

How do teeth really process foods?

At first glance, this last question may seem naively unnecessary in a review of dental microwear and diet. After all, a great deal of work has shown that there are some remarkable similarities in mammalian mastication (see Hiiemae 1978 or Hiiemae and Crompton 1985 for recent reviews). In addition, studies of molar wear facets (e.g., Butler 1952, 1972, 1973, Crompton 1971, Crompton and Hiiemae 1970, Kay and Hiiemae 1974, Kay 1977) have led to a fairly good understanding of the intricacies of molar occlusion in a variety of mammals. Nonetheless, there are additional subtleties of jaw movement and tooth use that must be understood if we are to answer some of the questions facing dental microwear analyses.

It is now generally accepted that masticatory sequences include both puncture crushing and chewing cycles and that both of these cycles involve opening and closing movements which can be divided into two phases apiece (fast close, slow close, slow open, and fast open) (Hiiemae and Crompton 1985). Puncture crushing cycles occur early in the masticatory sequence and involve an initial "tenderization" of food through tooth-food-tooth contact (Crompton and Hiiemae 1970), while chewing cycles occur later in the sequence, after the food has

been softened, and may, or may not, involve tooth-tooth contact (Hiemae and Kay 1973) (see below). The relative lengths of these cycles and their opening and closing phases have been shown to vary with the size, shape, and consistency of the food items being processed (Crompton and Hiemae 1969b, Hiemae 1976, Hiemae and Crompton 1971, Hiemae and Kay 1973, Hylander et al. 1987, Lucas et al. 1986, Thexton et al. 1980). Thus, mammalian jaw movements in mastication have been shown to be remarkably predictable, and certain basic patterns are evident in laboratory studies. So why look at them in any more detail?

First, additional questions need to be answered. For instance, does the incidence of puncture crushing vary significantly between closely-related species with different diets? One might suspect that it would, but thus far, all we have are comparisons between extremely different species (Hiemae 1976). More importantly, what are the effects of puncture crushing and chewing on teeth? Here we are drawn into a close examination of the intricacies of jaw movement during portions of the masticatory sequence. Once there, it becomes apparent that the relationship between subtle variations in masticatory movement and tooth wear patterns is not as clear as one might expect. Some of this confusion is due to methodological difficulties, for it is extremely difficult to track tooth-food-tooth movements (in mastication) as the teeth approach intercusp range. However, some of the confusion can also be tied to the perplexing "evolution" of molar wear facet analyses.

Initial studies of primitive mammals (e.g., Crompton 1971, Crompton and Hiemae 1969a, 1970) pointed to a clear contrast between molar wear facets formed at the tips of cusps and those formed on the slopes of cusps. The former were thought to be formed during puncture crushing, while the latter were formed during chewing. This distinction was carried into analyses of primate molar wear facets, where it was tied to different wear processes, i.e., tip facets were thought to be formed through "abrasion," or tooth-food-tooth wear, while slope facets were formed by "attrition," or tooth-tooth wear (Hiemae and Kay 1973, Kay 1977, Kay and Hiemae 1974).

In contrast to primitive mammals, however, primates were thought to have incorporated the initial stages of jaw opening (slow open) into the power stroke of chewing (Hiemae and Kay 1973, Hiemae 1976, Kay and Hiemae 1974). Thus, the power stroke in primates was said to involve two steps: the movement from

tooth-food-tooth contact into centric occlusion (called "Phase I"), and the movement from centric occlusion out of occlusal contact ("Phase II"). With the recognition of these two "phases" of the power stroke came a change in perspective regarding molar wear facet formation. In essence, slope facets became the center of attention. They were numbered in great detail and categorized as either Phase I (shearing) facets or Phase II (grinding) facets (Kay 1977, 1978, Kay and Hiemae 1974, Maier 1977, 1984). More importantly, this emphasis of slope facets (at the expense of tip facets) created a number of problems for subsequent dental microwear analyses.

First, it effectively left puncture crushing out of subsequent discussions of molar wear facet formation. Admittedly, puncture crushing was occasionally mentioned in discussions of tooth use (e.g., Grine 1981, Seligsohn and Szalay 1978); but the actual formation of facets was still treated in terms of Phases I and II. Since Phase I "is probably the only functional phase in puncture crushing" (Hiemae and Kay 1973:40), and yet puncture crushing is "characterized by the failure of the teeth to approach the intercusp range" (Hiemae and Kay 1973:51), the implication of this Phase I/Phase II emphasis was clear: facets of interest were formed during the power stroke of chewing rather than during the power stroke of puncture crushing.

Yet, puncture crushing comprises over 50% of a masticatory sequence in certain situations (Crompton and Hiemae 1969b, Hiemae and Crompton 1971). How could it be ignored in discussions of molar wear facet formation? This bias may ultimately be traced to the young chronological age of the specimens used in most analyses of primate molar wear facets (e.g., Kay 1977, 1978, Kay and Hiemae 1974). As Crompton and Hiemae (1970) noted in their study of *Didelphis*, at advanced stages of wear, some molars may be turned into flat "tables" that are only suitable for puncture crushing. Unfortunately, while investigators noted that puncture crushing leads to cusp tip blunting and dentin exposure (Hiemae and Kay 1973, Kay and Hiemae 1974), descriptions of molar wear still concentrated on Phase I and Phase II facets of relatively young individuals. Gordon (1982) did note that cusp tip facets show microwear patterns intermediate between those on Phase I and Phase II facets, but there has been no mention of how molar wear facets change during the progression from light to heavy wear. What happens to puncture crushing/cusp tip facets with wear? Do they merely coalesce with Phase II facets? If so, they may tell us something about intrafacet microwear

differences (see below). Taking this one step further, perhaps some of Gordon's (1984b) age-related differences in dental microwear are tied to (or complicated by) age-related changes in dental function as older teeth are used more for puncture crushing and less for cutting or shearing.

A second problem arising from the emphasis of chewing over puncture crushing concerns the exact method of formation of molar wear patterns. In other words, as suggested by initial contrasts between "abrasion" and "attrition" (e.g., Kay 1977), are there really significant tooth-tooth contacts during the chewing of certain foods, or does chewing "involve only tooth-food-tooth contact" (Hiemae and Kay, 1973:34)? At one level, investigators have noted that maximum intercuspation may be reached relatively quickly during the mastication of soft or brittle foods (Hiemae 1976, 1978, Hiemae and Crompton 1971, Hylander et al. 1987, Thexton et al. 1980). Moreover, maximum bone strain may occur at maximum intercuspation during the chewing of soft foods or when a swallow occurs (Hylander et al. 1987).

At a microscopic level, however, are tooth-tooth contacts occurring during such sequences; or, is there still a "thin film of food and associated material" (Hiemae and Kay, 1973:53) between the teeth? Contrasts between wear in the absence of food and wear in the presence of food (Teaford and Walker 1983a, b) indicate that these may be important questions for future interpretations of dental microwear variations. Microwear evidence from nonhuman primates suggests that, in certain situations, significant tooth-tooth contacts may be occurring. For example, molar occlusal surfaces of Cercocebus albigena frequently look like those of laboratory primates that are known bruxists (compare Figures 1 & 7). In processing hard objects, is Cercocebus experiencing more tooth-tooth contact?

A third, and final, problem for dental microwear analyses concerns another topic that has been masked by the emphasis of Phase I versus Phase II facets - i.e., intrafacet variations in microscopic wear patterns. From the outset (Kay and Hiemae 1974), investigators have recognized that the two-phase power stroke used by primates required certain occlusal areas (e.g., the basins of lower molars) to serve a "dual function": crushing at the end of Phase I and grinding during Phase II. Still, the facets formed in these areas were categorized as either Phase I or Phase II facets, implying a degree of homogeneity (and homology) that is probably misleading for dental microwear interpretations. In other words, since

"pits and striations may simply represent opposite poles of a continuum characterized by varying degrees of compression and shear during occlusion" (Gordon 1982:210), one might expect areas that are used for crushing and grinding to show a mixture of microwear features. Recent work suggests that many of the features on Phase II facets are probably formed at the end of Phase I of chewing (Hylander et al. 1987, Teaford 1985) or during puncture crushing (Teaford 1985). More importantly, changes in the patterns of microwear features should also be expected as one moves from molar cusp tips into basins - i.e., as one moves from crushing, to grinding, to crushing areas. Gordon's (1982) demonstration of microwear differences between cusp tip facets and Phase II facets is intriguing in this light. Is it the first step in the development of intrafacet differences in dental microwear? The gross morphological analyses presented by Janis (1984) suggest that it may be the case, but no other work has been published on the topic.

Conclusion

We have every reason to be optimistic about the prospects of using dental microwear analyses in dietary interpretations. Even at this early stage, a variety of analyses have raised questions that were heretofore out of our reach. However, the amount of work that needs to be done is enormous. At the present time, microwear analyses are progressing on modern ungulates (Solounias, pers. comm.), carnivores (Van Valkenburgh, pers. comm.), viverrids (Biknevicius, pers. comm.), and various human populations (Gordon 1986), but we still need more experimental and museum work on an even larger range of modern mammals. We need to expand upon existing techniques and to develop new techniques too (e.g., will computerized image analysis speed-up the entire process?). Only with a combination of approaches will we obtain clear answers to our questions concerning diet and dental microwear.

Acknowledgments

In a review paper such as this, it is impossible to thank all of the people who have helped at every step along the way. However, the author wishes to offer special thanks to the following people: (1) to Alan Boyde, Fred Grine, Sheila Jones, and Lawrence Martin - for asking the author to participate in the session "Scientific Investigation of Vertebrate Mineralized Tissue" at the 1986 SEM Meetings; (2) to Mikael Fortelius, Kathleen Gordon, Karen Hiemae, Sheila

Jones, and Peter Lucas - for excellent comments on the manuscript; (3) to Alan Walker and Dean Oyen for fruitful discussions throughout the preparation of the manuscript; (4) to Alan Walker for taking SEM micrographs #7f, 7g, 7h, (5) to Jim Cheverud for persistent statistical prodding concerning the methods of microwear analysis, and (6) to Om Johari and his staff for their patience and help during the lengthy revisions of the manuscript. The author also wishes to thank Richard Thorington for allowing access to specimens in his care at the Smithsonian Institution. This work was supported by NIH grants R23 DE07182 and F32 DE05312.

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Discussion with Reviewers

M. Fortelius: Studies have concentrated on mammals with relatively slow tooth wear. Much faster wear rates do exist. In voles, for example, the entire height of the evergrowing molars is replaced within a month or two. Maybe such fast-wearing teeth would be useful for experimental work?

Author: At this point, any legitimate experimental work would be useful! Animals with rapidly-wearing teeth might be particularly useful in studies of induced changes in jaw movement (e.g., Teaford and Byrd 1987), or if they could be "coaxed" into consuming food items with drastically different physical properties. However, wild populations of such animals might show one uninteresting correlate of rapid tooth wear - i.e., a relatively homogeneous microwear pattern consisting of nothing but fine scratches caused by the abrasives in the diet.

S. Jones: Could the author please explain how pits are counted in fields of complex topography? For instance, how many pits are there in the field illustrated in Figure 7a?

Author: This is one of the most difficult problems facing investigators in this sort of work. It may also pose significant problems for future attempts at image analyses of SEM micrographs.

At the present time, there aren't nearly as many guidelines as there should be - mainly because we still have very little information concerning the formation and obliteration of individual microwear features. Since one piece of abrasive can cause more than one microwear feature (e.g., a pit at the end of a gouge as in Teaford and Walker's (1983b) figure 8), and since pits tend to have irregular edges, walls, and floors,

it is perhaps best to be as conservative as possible. In other words, features sharing common edges or boundaries are usually counted as one - unless one feature is obviously overlying the other as evidenced by scratches sandwiched between them. In figure 7a, the micrograph of Cebus apella has approximately 18 pits of various sizes.

S. Jones: Is the length of a scratch related to the food being processed or is it only a feature of the individual facet?

Author: To date, the only evidence for either alternative has been Kathleen Gordon's discovery (1982) that scratch lengths are longer on facets that are routinely subjected to more shearing (as compared with facets subjected to more compression). Other than that, we have so little information that it's probably too early to decide between the two alternatives. We may even be ignoring other factors which could be important. For instance, how might the overall rate of wear affect scratch length? If the same abrasives were rubbed against similar tooth surfaces (in various directions) for drastically different lengths of time, the more heavily abraded surface might give the appearance of having shorter scratches because individual scratches would be extremely difficult to follow.

S. Jones: In primates, is there intersexual variation in (a) the depth of scratches, or (b) the length of scratches, related to body size, muscle strength, or chewing cycle variation?

K. Gordon: In my study of chimpanzee molar microwear, I found a little evidence for intersexual differences in scratch length - although the results are somewhat paradoxical. Females had significantly shorter scratch lengths than did males. I anticipated the reverse, given theories that large male canine size might limit the amount of lateral excursion. Perhaps we are seeing body size differences expressed here instead.

Author: At this point, quantitative analyses of dental microwear are so time-consuming that there are very few samples large enough to yield insights into sexual differences. In our sample of 62 individuals of Cebus nigrivittatus (Teaford and Robinson 1987), there are no obvious sexual differences in pit width, scratch width, or proportion of pits & scratches. But then, Cebus nigrivittatus is not as sexually dimorphic as certain other primates (e.g., Papio, Gorilla), so these microwear results are not too surprising.

K. Gordon: I would like to make a comment in answer to the queries raised in this paper concerning the role of puncture crushing in microwear pattern formation. One fact which Teaford alludes to is the possibility of functional differences in the use of young versus old teeth, which in most species will show considerable morphological alteration due to wear. Microwear studies have focused on young teeth for two reasons: the assumption that unworn morphology represents the ideal functional state, and also to have significant amounts of enamel to analyze. There are, in fact, radical differences between young and old chimp teeth in gross morphology due to wear, and old chimp teeth (like those in Didelphis) are probably most suited to puncture crushing or grinding rather than shearing since all shearing surfaces and crests have been lost. Based on occlusal analyses of aged individuals, I would say that functionally, cusp tip facets do not so much coalesce with Phase II facets as obliterate them altogether, but the microwear correlates of this process are as yet unstudied. The possibility of such functional components in age-related changes, as well as microstructural ones, is quite likely.

Author: Thank you for your comments.