

# Dental Microwear in Anubis and Hybrid Baboons (*Papio hamadryas*, *Sensu Lato*) Living in Awash National Park, Ethiopia

Pia Nystrom,<sup>1\*</sup> Jane E. Phillips-Conroy,<sup>2</sup> and Clifford J. Jolly<sup>3</sup>

<sup>1</sup>Department of Archaeology, Sheffield University, Sheffield S1 4ET, UK

<sup>2</sup>Department of Anatomy and Neurobiology, Washington University School of Medicine, St. Louis, Missouri 63110

<sup>3</sup>Department of Anthropology, New York University, New York, New York 10003

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**ABSTRACT** We describe dental microwear in baboons (*Papio hamadryas sensu lato*) from the anubis-hamadryas hybrid zone of Awash National Park, Ethiopia, outline its variation with sex and age, and attempt to relate the observed microwear pattern to environment and diet. Casts of the maxillary second molar of 52 adult and subadult individuals of both sexes were examined with a scanning electron microscope at  $\times 500$ . Digitized micrographs were taken at a consistent location on facet 9, and microwear was recorded with an image analysis software package. Univariate and multivariate statistics were used to investigate the shape, size, and density of microwear features. The overall pattern of microwear exhibits an unusual combination of high feature density, with numerous small pits and relatively wide striations, and a high

correlation between width of pits and striations across individuals. We interpret this pattern as predominantly the consequence of abrasion by relatively small-caliber environmental grit when accidentally ingested with tough foods such as dried seeds and fruits, as expected in a terrestrial omnivore living in a dusty habitat. Statistical analysis revealed no significant differences between groups defined by sex, age, or troop membership, a result consistent with qualitative observations of feeding habits in this population, and which lends no support to the hypothesis that the longer jaws of adult males should result in longer striations. A trend towards greater feature density in females, however, might be due to limited sexual dimorphism, and merits further investigation. *Am J Phys Anthropol* 125:279–291, 2004. © 2004 Wiley-Liss, Inc.

In the process of mastication, the occlusal surfaces of teeth acquire microscopic damage, known collectively as microwear, that persists until obliterated by abrasion or by contact with the opposing occlusal surface. Variation in microwear pattern (described by the density, size, and shape of microwear features) has been ascribed to a variety of factors. The mechanical properties of the diet itself are usually considered the most influential factor, but other variables have been shown or theorized to be important. These include the amount, size, and shape of exogenous abrasives ingested with food (Daegling and Grine, 1999; Teaford and Glander, 1991, 1996), biomechanical differences correlated with gnathic morphology (Gordon, 1982), and the microstructure of dental enamel (Maas, 1991). In spite of complications arising from nondietary factors, distinctive microwear patterns have been linked to each of the major food types commonly eaten by primates (Teaford, 1994; Daegling and Grine, 1999; Rose and Ungar, 1998 and references therein; Teaford et al., 1996) and, with due caution, have been used to reconstruct the feeding habits of fossil primates immediately before their demise (e.g., Teaford, 1993; Teaford et al., 1996; King et al., 1999).

Although the validity of the approach has been amply demonstrated and widely accepted, reconstructions of past diets must still depend on a limited comparative sample of extant primate populations in which both microwear and diet immediately before sampling were documented, and in which intrapopulational variation by sex and age is represented. The present study aims to augment the comparative dataset by describing and interpreting dental microwear patterns and their variation by sex and age in a population of wild baboons (*Papio hamadryas sensu lato* (s.l.)). We compare microwear patterns seen in this population with those reported for other anthropoid primates, attempt to

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\*Correspondence to: Pia Nystrom, Department of Archaeology and Prehistory, Sheffield University, Northgate House, West Street, Sheffield S1 4ET, UK. E-mail: p.nystrom@sheffield.ac.uk

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interpret them in terms of their diet and habitat, and use our results to test some predictions drawn from previous work on primate dental microwear.

### MATERIALS AND METHODS

Fifty-two subadult and adult baboons (*Papio hamadryas*, s.l.), ranging from approximately 60–183 months in age, were selected from 159 individuals live-trapped in the Awash National Park, Ethiopia, between July 4–August 11, 1998. Subjects ranged in external phenotype from anubis to intermediate anubis-hamadryas hybrids (Phillips-Conroy and Jolly, 1986). Three social groups were sampled. Group H (hybrids) inhabited the canyon region below the Awash Falls, and Group D (anubis) lived in the floodplain area above the Falls. Members of these groups comprised the main study sample. Four members of Group G (anubis), whose range included the Falls area and adjoining canyon, were captured and processed when they unexpectedly arrived at Group H's trap site. Group G animals were used to examine the potential influence of baiting with corn, but were not included in statistical analyses of intrapopulation variation by age or sex.

The home ranges of all groups (Jacobs and Schloeder, 1993; Nagel, 1973; Nystrom, 1992) included mainly thornbush with *Acacia senegal*, *A. mellifera*, *A. nubica*, and *Grewia* spp., and savanna grassland with scattered *Acacia tortilis*, *Dobera glabra*, and *Balanites aegyptiaca* trees, but Group D also had access to more extensive areas of evergreen riverine woodland, seasonal watercourses, and productive floodplain with fruit-bearing trees and shrubs such as *Ficus sycamorus*, *Celtis* sp., *Cordia* sp., *Tamarindus indica*, *Zizyphus* spp., *Berchemia* sp., *Acacia tortilis*, *A. brevispica*, *A. seyal*, and *A. clavigera*, while the canyon habitat of Group H was more rocky, with sparser, more xeric vegetation. Group G's range spanned both habitats.

The natural diet of the baboons immediately before trapping was reconstructed from systematic information collected in the area in 1988–1989 (Nystrom, 1992), as well as qualitative observations (by P.N.) during the present study period. Baboons of Groups H and D were baited for trapping with approximately 2 kg of dried corn (maize: *Zea mays*) kernels per day per group of ~65 to ~120 animals. Corn feeding prior to trapping lasted 19 days for Group H and 10 days for Group D. Group G was not deliberately fed corn during the study period, although it had been baited and trapped 3 years before. The four animals trapped from this group, which ate only a little corn on their day of capture, therefore serendipitously provided a control group for the effects of corn feeding.

Examination and dental molding were carried out under ketamine sedation (Phillips-Conroy et al., 1991). Each individual was allocated to one of three dental age stages, defined by molar wear. In stage I, third molars were unerupted, and there was slight to obvious dentine exposure on the cusp tips of the

TABLE 1. Group, sex, and age group affinities for animals used in statistical analyses of Intrapopulation variation by age and sex<sup>1</sup>

Location	Group	Sex	Age group			Total
			I	II	III	
Above Falls	D	Male	5	12	3	20
		Female	1	2	0	3
Below Falls	H	Male	4	4	1	9
		Female	9	3	4	16
Awash	All	Male	9	16	4	29
		Female	10	5	4	19

<sup>1</sup> For definition of age groups see text.

first molars and no or slight exposure on the second molars. In stage II, the third molars were erupted, with obvious dentine exposure on the second molar cusps and no or slight dentine exposure on the third molar cusps. In stage III, exposed dentine was confluent between at least two cusps on the first molars, and there was extensive dentine exposure on the second molars, with obvious dentine exposure on the third.

A high-resolution dental impression of the left maxillary molar teeth was then taken (Table 1). Cleaning followed the method of Teaford and Oyen (1989a), except that lack of electricity in the field barred the use of the recommended oral cleaning device. The maxillary postcanine teeth on the left side were rinsed thoroughly with filtered water. The occlusal surface of the teeth was then washed with denture cleaning liquid (Boots®, active ingredients: sodium perborate and trisodium phosphate) by gently dabbing a cotton swab onto the surface to remove saliva and any organic film adherent to the tooth surface. This was followed by a further rinse with filtered water. The occlusal surface of the teeth was dried with 100% ethanol applied with a cotton swab. The resultant micrographs showed no evidence of residual adherent film or moisture.

We made at least two dental impressions from each animal using a hydrophobic polyvinylsiloxane silicone-based impression material (President Jet, Light Body®, Coltène) in a previously made tray (President Putty®, Coltène). The filled tray was placed on the occlusal surface of the teeth and held firmly in place for 1–2 min, allowing the low-viscosity silicone-based material to set into a solid but still flexible mold. Once set, the mold was removed from the teeth, and stored in an airtight plastic bag.

In the laboratory, the mold of facet 9 (Kay, 1977) from the left second maxillary molar was excised from each specimen with a sharp scalpel blade, in order to reduce scanning electron microscope (SEM) image distortion due to angulation of tooth surfaces (Gordon, 1982). To eliminate the problem of surface distortion, the depth of the excised piece was greater than the surface area, providing strength and stability for the well (President Putty®, Coltène) into which the araldite mixture (Araldite MY 753, hardener HY 956, Ciba-Geigy) was poured. The resulting high-resolution Araldite replica was placed on an

aluminum SEM stub, and held in place using a high conductivity paint (Electrodag 1415M). It was then sputter-coated with a 20- $\mu\text{m}$  layer of gold palladium and examined with a high-resolution digital SEM (Philips XL30), fitted with a TETRA backscatter electron detector. Accelerating voltage was set at 5 kV, and the beam spot was set at 3.0. A working distance between 13–19 mm was used. The specimen was oriented so that the intersection between the two furrows forming the distal and medial border was aligned parallel to the x-axis of the screen. Since only facet 9 was replicated, and it was close to horizontal, tilting was unnecessary. All images were taken close to the base of facet 9, and recorded at  $\times 500$  magnification. A single digitized image ( $702 \times 484$  pixels) measuring approximately  $0.031 \text{ mm}^2$  of surface was collected from each tooth.

A semiautomated image analysis system (Microware Version 3.0<sub>Beta</sub>; Ungar, 1997) was used to count and measure the microwear features from the digitized images, using a resolution of  $0.333 \mu\text{m}$  per pixel (DPI = 152). The width and length of each feature were measured and recorded, and each feature was identified as a pit (width to length ratio of  $1 < 4$ ) or a striation. The total number of features (= feature density), percent pits, percent small pits ( $< 4 \mu\text{m}$  width), mean pit width, mean pit length, mean striation width, mean striation length, mean length of small striations (length  $< 10$  times width), and mean length of large striations (length  $> 10$  times width) were calculated.

The data were first tested against the assumptions of multivariate analysis (e.g., normal distribution). Though no cases were considered multivariate outliers, all variables, except percent pits and percent small pits, showed high values for kurtosis (i.e., a broad spread) when examining sex and age groups independently. These variables were transformed using natural logs which alleviated the kurtosis (Tabachnick and Fidell, 1996).

To explore the effects of location, age, and sex on dental microwear patterns, multivariate analysis of variance (MANOVA) tests were performed. Four dependent variables were used for the three-factor MANOVA (feature density, percent pits, percent small pits, and mean striation length). Other dependent variables were excluded because they showed significant correlation and added to collinearity. Wilks' lambda was used to determine significant effects. One-way analysis of variance (ANOVA) tests were used to assess significant differences of each independent variable under different conditions (location, sex, and age). To reject the hypothesis that all population means were equal, alpha was set to  $\leq 0.05$  (two-tailed). To minimize type I errors, a Scheffé correction for multiple comparisons was performed when comparing the three age groups. All statistical analyses utilized the SPSS 6.0 statistical package (Norušis, 1990).

For comparison with the Awash baboons, a set of comparative data was compiled from published studies of living and fossil anthropoid primates.

## RESULTS

Descriptive statistics for the Awash baboons are shown in Table 2 (and are compared with values from the comparative series in Table 6). Average feature density (per  $0.031 \text{ mm}^2$  of surface area) was  $124.2 \pm 42.3$ . Approximately half of the features ( $47.0 \pm 12.2\%$ ) were classified as pits. Of these, most ( $75.5 \pm 10.7\%$ ) were small pits ( $< 4 \mu\text{m}$  width). The prevalence of small pits is also expressed in the small mean width of all pits ( $3.35 \pm 0.59 \mu\text{m}$ ). Striations were on average  $2.5 \pm 0.4 \mu\text{m}$  wide and  $26.9 \pm 6.0 \mu\text{m}$  long. This microwear pattern is not precisely similar to any previously described (e.g., Teaford et al., 1996; see also Table 6). Its unusual features include the high overall density of features, combined with a high prevalence (mean = 47%) of pits, and a small average pit diameter ( $3.35 \pm 0.6 \mu\text{m}$ ) that is combined with a fairly high mean striation width, which are illustrated in Figures 3 and 4.

### Effects of prebaiting with corn

Comparing the four members of Group G (unbaited) with all 48 animals in the rest of the sample (baited), we found no significant difference in any microwear variable. T. Bergman (personal communication) provided information about the social rank of each individual in Group H, and its attendance at the baiting site, enabling us to estimate its relative corn consumption before sampling. No significant correlation was found between any microwear variable and the number of prebaiting days (Spearman's rho = 0.085–0.279), or estimated corn consumption (Spearman's rho = 0.115–0.336) for the pooled sample or for females alone. When males were examined alone, however, there was a significant rank correlation between feature density and estimated corn consumption (Spearman's rho =  $-0.883$ ,  $P = 0.008$ , two-tailed).

### Effects of sex, age and group membership

A three-factor MANOVA test was used to test for interaction between age, sex, and location on dental microfeatures. None of the main effects (sex, age, and location) or interactions between any of the combinations of the main effects (sex, age, and location; location and age; location and sex; age and sex) showed any significant differences (Table 3).

One-way ANOVA and nonparametric tests supported these findings. No comparison between groupings based on age, sex, or troop membership (Group D vs. H) showed a statistically significant difference for any microwear parameter, and in most cases the mean values for groupings were very similar in comparison to intragrouping variation. In a few cases, however, differences were large enough,

TABLE 2. Descriptive statistics for microwear frequencies and measurements (mean and SD)

Variables	Group total (n = 48)	Location			Sex		Age groups		
		Below Falls (n = 25)	Above Falls (n = 23)	Male (n = 29)	Female (n = 19)	I (n = 19)	II (n = 21)	III (n = 8)	
Total features	124.19 (±42.28)	131.90 (±41.20)	115.80 (±42.80)	114.40 (±36.40)	139.20 (±47.00)	126.05 (±51.84)	123.30 (±37.94)	122.00 (±31.02)	
Percent pits	47.00 (±12.23)	50.18 (±12.70)	43.60 (±10.90)	45.61 (±10.93)	49.13 (±14.03)	46.77 (±14.11)	44.99 (±10.44)	52.84 (±11.41)	
Percent small pits	75.51 (±10.73)	75.08 (±10.94)	75.97 (±10.71)	75.94 (±10.57)	74.84 (±11.21)	78.85 (±8.32)	75.19 (±10.77)	68.39 (±13.22)	
Mean pit width	3.35 (±0.59)	3.39 (±0.66)	3.31 (±0.51)	3.34 (±0.56)	3.36 (±0.65)	3.19 (±0.46)	3.35 (±0.57)	3.74 (±0.79)	
Mean pit length	6.93 (±1.02)	6.88 (±1.08)	6.98 (±0.97)	6.97 (±1.06)	6.86 (±0.97)	6.74 (±0.85)	7.13 (±1.10)	6.85 (±1.20)	
Mean striation width	2.46 (±0.40)	2.46 (±0.44)	2.46 (±0.36)	2.44 (±0.40)	2.48 (±0.41)	2.45 (±0.38)	2.45 (±0.43)	2.50 (±0.42)	
Mean striation length	26.86 (±6.00)	25.84 (±4.96)	27.97 (±6.90)	27.84 (±6.27)	25.37 (±5.38)	27.48 (±6.16)	26.35 (±6.74)	26.73 (±3.55)	
Mean small striation length	16.21 (±2.76)	16.13 (±3.06)	16.29 (±2.46)	16.02 (±2.83)	16.50 (±2.74)	15.81 (±2.65)	16.34 (±3.02)	16.96 (±2.48)	
Mean large striation length	41.33 (±9.45)	40.01 (±9.11)	42.77 (±9.81)	43.12 (±9.57)	38.60 (±8.81)	42.67 (±9.10)	40.36 (±10.30)	40.71 (±8.70)	

TABLE 3. Results from three-factor multivariate analysis of variance (MANOVA) showing interactions of main effects of location, sex, and age using Wilks' lambda to determine significance<sup>1</sup>

Main effects	Statistic	F	df	P
Location by age by sex	0.9406	0.537	4, 34	0.710
Location by age	0.7899	1.064	8, 68	0.399
Location by sex	0.9533	0.417	4, 34	0.795
Age by sex	0.7409	1.375	8, 68	0.223
Location	0.9243	0.697	4, 34	0.600
Sex	0.9630	0.327	4, 34	0.858
Age	0.9040	0.440	8, 68	0.893

<sup>1</sup> Dependent variables included feature density, percent pits, percent small pits, and mean striation length.

TABLE 4. One-way ANOVA results from sex comparisons (df 1, 46)

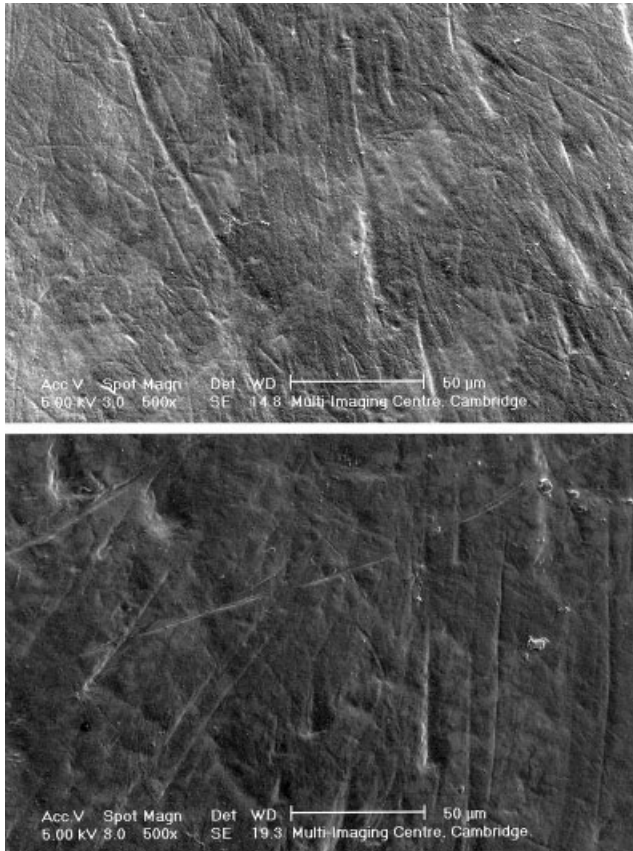
Variable	Sum of squares (between groups)	Sum of squares (within groups)	F	P
Feature density	0.384	4.307	4.105	0.049
Percent pits	142.610	6,891.260	0.952	0.334
Percent small pits	13.907	5,392.808	0.119	0.732
Pit width	0.0002	1.389	0.006	0.938
Pit length	0.127	48.685	0.120	0.730
Striation width	0.003	1.231	0.105	0.748
Striation length	0.092	2.020	2.097	0.154
Small striation length	0.037	5.507	0.312	0.579
Large striation length	0.140	2.176	2.963	0.092

and sufficiently close to statistical significance, to suggest that further investigation with larger samples would be warranted. Thus, the below-Falls group (H) showed a higher prevalence of pits (Group H, 50.2 ± 12.7%; Group D, 43.6 ± 10.9%; df, 1, 46; F = 3.7148, P = 0.060); overall feature density was higher on female teeth than on male teeth (male, 114.4 ± 36.4; female, 139.2 ± 47.0; df, 1, 46; F = 4.1047; P = 0.049; Table 4), and male teeth had longer large striations (male, 43.1 ± 9.6 μm; female, 38.6 ± 8.8 μm; df, 1, 46; F = 2.9626; P = 0.092; Table 4 and Fig. 1). Finally, when males and females were combined, the frequency of small pits was inversely related to age (Tables 2 and 5, Fig. 2) (Dental Age Group I, 78.9%; II, 75.2%; III, 68.4%; df, 2, 45; F = 2.912; P = 0.066, with Scheffé correction).

DISCUSSION

Awash microwear compared

Accumulating data from studies of natural primate populations, represented by museum material or live-trapped individuals, provide a sample against which to compare findings from the Awash baboons. Table 6 sets the Awash results in the context of other studies methodologically close enough to permit direct comparisons. Attempts to extract generalizations about microwear patterns in extant primates have employed two complementary strategies. The first groups primates into major dietary categories (omnivore, folivore, frugivore, gramini-vore, insectivore/faunivore, and so on) with subcat-



**Fig. 1.** Scanning electron micrographs show general difference between male (**top**) and female (**bottom**) microwear pattern.

egories, such as hard vs. soft fruit eater, expressing variation likely to be important for microwear. It then seeks microwear patterns that reliably distinguish the categories. The other approach starts from mechanical principles rather than correlation, and looks for microwear features that reflect physical properties (especially hardness, size, and toughness) of elements in the ingesta (both food and contaminants) and characteristics of the masticatory system.

Correlative studies confirmed the existence of consistent microwear patterns, most readily apparent in taxa with relatively extreme and predictable feeding habits. Mastication of leaves generates a preponderance of elongated features (striations), and the few short features (pits) produced tend to be small. Fruit-eating produces few striations; the characteristic features are pits, the size of which tends to increase in proportion to the toughness of the food, with the largest pits seen in animals that habitually eat fruits with hard seeds (Teaford, 1988; Teaford et al., 1996; Teaford and Walker, 1984). Softer (usually riper) fruits generate fewer microwear features, with a high percentage of small pits (Teaford and Oyen, 1989b; Teaford and Runestad, 1992). Like those seen in obligate faunivores (Strait, 1993), such pits may be formed not by interaction with the food

itself, but by forces developed during shearing tooth-tooth contact that cause “plucking” of enamel prisms (Gordon, 1982, 1988; Teaford and Runestad, 1992; Teaford and Walker, 1984; Walker, 1984).

The correlative approach by itself, however, leaves much microwear patterning unexplained. Some species supposed to belong to the same dietary group do not cluster closely, dietary clusters are linked by intermediates, and different samples of the same taxon may have very different microwear patterns, sometimes even falling into different dietary categories (cf. values for *Pongo pygmaeus* in Teaford, 1988 and in King et al., 1999). With few exceptions, every newly sampled population (including fossil forms) tends to show its own unique combination of mean values of variables such as density, feature size and shape, and frequency of pits vs. striations. Interindividual variation within population samples is also typically large, so that even when population means are apparently widely separated, statistical significance may be elusive.

All of this is hardly surprising if we recall that almost all microwear features are probably obliterated in a few weeks at most after formation (Teaford and Oyen, 1989b). Microwear patterns therefore track fine-grained dietary changes over relatively short timescales, and an instantaneously recorded, individual pattern can rarely be assumed to represent an individual's total diet, much less that of an entire population or species. One can be reasonably certain that individuals of *Colobus guereza* or *Ptilocolobus badius* would have eaten mostly tree leaves immediately before sampling, but problems arise with species whose diet varies opportunistically, seasonally, and/or locally among staple foods of very different mechanical properties, and among habitats with varying amounts of exogenous abrasives. To describe *Gorilla gorilla* as a folivore, for example, or *Pan troglodytes* as a frugivore, is useful as a device to explain the respective adaptive features of the African apes as whole species over evolutionary time, but can have very little predictive value for microwear patterns of individual gorillas or chimpanzees in a sample. Ideally, the feeding behavior of individuals to be sampled should have been monitored in the weeks leading up to sampling (e.g., Teaford and Glander, 1991).

The second (“materials science”) approach, which most of these authors also employ, avoids some of the problems of correlative studies, especially in interpreting patterns that have no close resemblance to any in the reference dataset. Though starting with clues derived from correlative studies, it uses basic principles to interpret the combination of microfeatures as observed in a specimen, or the mean values for a population sample, rather than attempting to match the population to preexisting dietary categories. Its starting point is an understanding of the way that microwear features are formed.

Unlike flakes and cracks, which may result from the impact of materials softer but tougher than

TABLE 5. One-way ANOVA results from age comparisons (df 2, 45)

Variable	Sum of squares (between groups)	Sum of squares (within groups)	F	P (with Scheffé correction)
Feature density	0.001	4.690	0.007	>0.995
Percent pits	358.789	6,675.081	1.209	>0.310
Percent small pits	619.517	4,787.198	2.912	>0.066
Pit width	0.127	1.263	2.255	>0.117
Pit length	0.003	0.978	0.642	>0.553
Striation width	0.004	1.230	0.075	>0.929
Striation length	0.023	2.089	0.244	>0.793
Small striation length	0.401	15.938	0.551	>0.599
Large striation length	0.114	12.534	0.204	>0.835

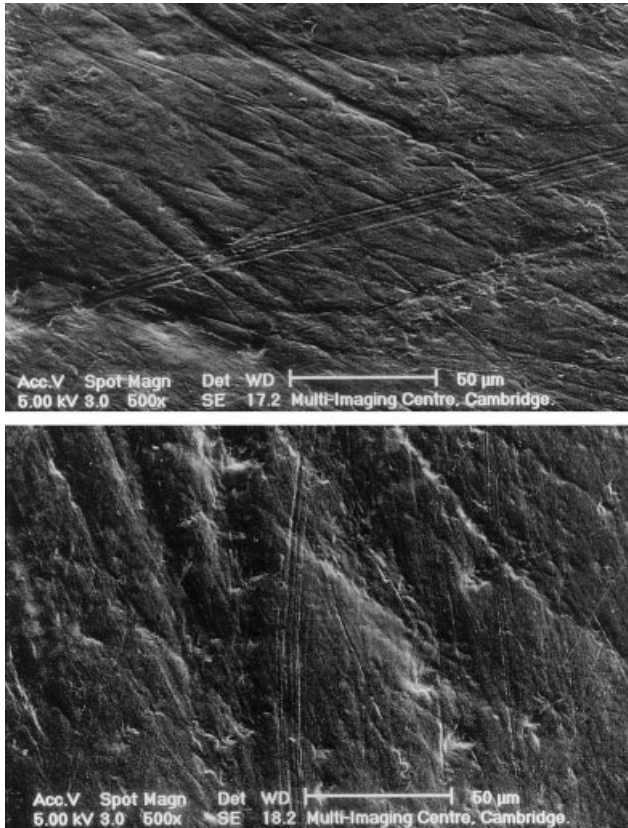


Fig. 2. Scanning electron micrographs show general difference in microwear pattern between younger (top) and older (bottom) individuals.

enamel, true microwear features are generated when a particle at least as hard as the enamel surface is forcefully dragged across or driven into it. Gordon (1984) proposed a model relating the size and depth of the resultant striations and pits to the strength of shear and compression forces acting on the enamel surface. In this model, surfaces exposed to low shear and compression show short, narrow striations and small, shallow pits, while high shear and compression result in long and wide striations. High compression and low shear result in large pits, while high shear and low compression result in long and narrow striations.

Only three materials that commonly interact with enamel surfaces in nature are recognized as hard enough to cause microwear: loose enamel plucked or

flaked by forceful contact with the opposing occlusal surface (Gordon, 1982, 1988; Teaford and Runestad, 1992; Walker, 1984); mineral inclusions (phytoliths) found in the cells of many plants (Ciochon et al., 1990; Piperno, 1988); and mineral particles, usually quartz (grains of siliceous sand, silt, or clay), that are ingested incidentally (Teaford, 1988; Ungar, 1994).

Of these, only phytoliths are regular constituents of the food itself. Silica phytoliths in the leaf tissues of some plant species, especially grasses (Poaceae) and sedges (Cyperaceae) (Lalueza Fox et al., 1996; Lucas and Teaford, 1995), produce a dense pattern of fine striations (Lalueza Fox et al., 1996; Ungar et al., 1995; Teaford, 1993) that may perhaps be considered the most unambiguous, "classic" microwear pattern. Among primates, this pattern is, as expected, seen in the specialist graminivore, *Theropithecus gelada*, and its extinct relative, *T. oswaldi* (Teaford, 1993). Even geladas, however, whose diet consists almost entirely of parts of grasses and other herbaceous plants (Iwamoto, 1993), exhibit pits as well as striations. As well as being few in number, the latter are much wider, on average, than striations in the same microfield (mean striation width = 18.6% of mean pit width in *T. gelada* and 24.4% in *T. oswaldi*; data from Teaford, 1993), and there is no relationship between pit and striation width, or between pit and striation incidence, across these two graminivorous *Theropithecus* species (data from Teaford, 1993). This apparent independence of pits and striations seems to point to distinct agents for each microwear type, and thus supports the attribution by Teaford (1993) of the pits in *Theropithecus* to occasional, accidental ingestion of grit, rather than to the phytoliths that generate striations.

If phytoliths were confined to grasses and sedges, and foods were entirely free of contamination by environmental dust and grit, feeding on leaves of other plants should produce occlusal surfaces polished by tooth-to-tooth grinding, but bearing few microwear features. In fact, leaf-eating primates such as *Alouatta palliata*, *Colobus guereza*, and *Ptilocolobus badius* exhibit as high a density of fine striations as the grazers (Teaford, 1993). Either their enamel is impacted by phytoliths in tissues of nonherbaceous plants (Cummings, 1992), or the striations are caused by exogenous abrasives chewed

TABLE 6. Summary of dental microwear features in anthropoid primates (means)<sup>1</sup>

Species or population	Label <sup>2</sup>	Diet	Density total	Density pits	Density striations	% pits	% striations	Pit width	Striation width	Relative striations <sup>3</sup>	References <sup>4</sup>
<i>Lophocebus albigena</i>	1	Hard fruits	42.2	23.3	18.9	55.2	44.8	9.9	3.9	39.4	3
<i>Cebus apella</i>	2	Hard fruits	70.7	31.9	38.8	45.1	54.9	8.4	2.9	34.5	2,3
<i>Pongo pygmaeus</i>	3	Mixed (incl. hard)	171.8	72.2	99.6	42.0	58.0	4.8	1.9	39.6	1
<i>C. nigrivittatus</i> , dry forest	4	Mixed, fruit	222.8	30.5	192.3	13.7	86.3	6.6	0.9	13.6	6
<i>C. nigrivittatus</i> , humid	None	Mixed, fruit	215.9	33.0	182.9	15.3	84.7	8.3	1.0	12.1	6
<i>C. nigrivittatus</i> , premontane	None	Mixed, fruit	187.8	35.5	152.3	18.9	81.1	7.7	1.0	13.0	6
<i>Pan troglodytes</i>	5	Mixed, fruit	114.4	45.4	69.0	39.7	60.3	5.6	2.5	44.6	1
Awash baboons	6	Mixed (hard)	124.19	58.4	65.8	47.0	53.0	3.4	2.5	73.5	5
<i>Alouatta palliata</i> (Costa Rica)	7	Leaves, some fruit	147.5	30.2	117.3	20.5	79.5	3.3	0.9	27.6	1
<i>Gorilla gorilla</i>	8	Leaves & fruit	99.2	32.9	66.3	33.2	66.8	4.7	2.7	57.5	3
<i>Colobus guereza</i>	9	Leaves	103.0	10.0	93.0	9.7	90.3	5.6	1.2	21.4	3
<i>Procolobus badius</i>	10	Leaves	85.0	10.7	74.3	12.6	87.4	6.1	1.3	21.3	3
<i>Theropithecus gelada</i>	11	Grass & herbs	94.2	9.1	85.1	9.7	90.3	4.3	0.8	18.6	4
+ <i>Griphopithecus</i>	12	? like <i>Pongo</i>	148.7	81.2	67.5	54.6	45.4	3.7	1.9	51.4	1
+ <i>Theropithecus oswaldi</i>	13	Grass & herbs	84.6	11.8	72.8	14.0	86.0	2.8	0.7	25.0	4
+ <i>Theropithecus brumpti</i>	14	? Grass & fruit	119.1	35.1	84.0	29.5	70.5	3.3	0.8	24.2	4
<i>Alouatta palliata</i> (Panama)	15	Leaves, some fruit	64.0	8.3	55.7	13.0	87.0				5

<sup>1</sup> All studies done at  $\times 500$  magnification. Pit widths and striation widths in microns.

<sup>2</sup> Label = numerical labels on symbols in Figures 3 and 4.

<sup>3</sup> Relative striations =  $100 \times$  mean striation width/mean pit width.

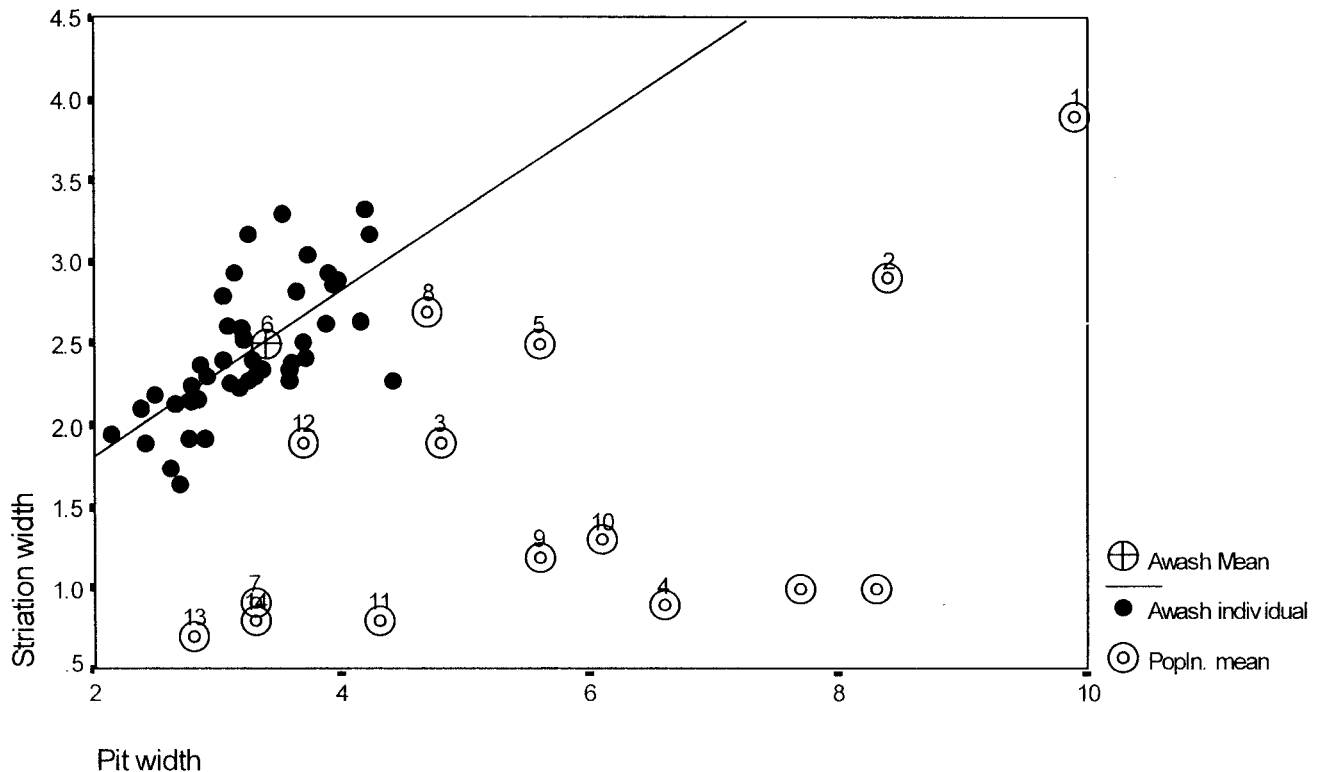
<sup>4</sup> References: 1, King et al., 1999; 2, Teaford, 1984; 3, Teaford, 1988; 4, Teaford, 1993; 5, Teaford and Glander, 1991; 6, Teaford and Robinson, 1989.

along with the herbage, or (most likely) both. The role of exogenous abrasives, in the form of wind-blown dust adhering to foliage, was strongly suggested by the contrast between feature densities in mantled howlers living in high rainforest (in Panama) and in forest remnants (in Costa Rica), respectively (Teaford and Glander, 1991, 1996; Teaford, 1993). In Costa Rican howlers, the mean number of pits was almost four times that seen in the rainforest animals, as expected if exogenous abrasives are the primary source of pits. However, the mean density of *striations* was also greater, by a factor of nearly two. This seems to confirm that narrow striations can be caused when shearing forces are applied, in mastication, to exogenous abrasives—perhaps fine dust particles in the same general size range as phytoliths.

The pits that are a distinctive feature of fruit-eaters' microwear patterns are presumably produced by compressive forces during the initial phase of mastication, in which softer tissues are crushed, and tougher ones cracked. Since even the most resistant tissues of tough fruits (e.g., seed coats and fruit rinds) are softer than dental enamel (Peters, 1982), the pits themselves must be produced either by tooth-to-tooth contact or by exogenous abrasive particles of sand or grit, which are presumably infrequent in the canopy of most rainforest habitats. The positive correlation between pit size and the toughness of food items commonly processed presumably appears because the greater compressive forces exerted in hard-object feeding drive adventitious grit particles deeper into the enamel surface, or cause forceful tooth-tooth contact when a resistant food object is cracked, or both. Among habitual hard-fruit feeders, which are admittedly few in the comparative sample (only three, even if the orangutan is included), the relationship of mean striation width to mean pit width is very consistent across a 2-fold range of striation widths (39.39%, 34.52%, and 39.58%, respectively, in *Lophocebus albigena*, *Cebus apella*, and *P. pygmaeus*; Pearson correlation coefficient = 0.97; data from Teaford, 1993; King et al., 1999).

This statistical relationship, which is not seen in other fruit-eaters or across the comparative sample as a whole (Fig. 3), perhaps suggests that the few striations seen in the hard-object feeders are produced by the same abrasive particles that cause pits (either grit or dislodged enamel chips, or both) as they are dragged across the enamel surface in the second phase of mastication.

Like baboons elsewhere (Altmann, 1998; Norton et al., 1987; Barton and Whiten, 1994), Awash baboons are eclectic omnivores that feed both on the ground and in trees. They derive the bulk of their diet from relatively few species, with most seasonal variation resulting from consumption of different plant parts. Leaf flush, grass shoots and seeds, flowers, and fruits are consumed when available, mainly during and immediately after the rains. In the dry



**Fig. 3.** Striation width plotted against pit width. Open symbols, means of population samples, numbered as shown in Table 6; solid symbols, individual Awash baboons. Linear regression is based on Awash individuals only.

season especially, the Awash baboons consume many mature seeds and sedge corms (Nystrom, 1992, and unpublished observations). Phytolith-rich grasses and sedges, leaves of trees, shrubs and herbs, fruits of various degrees of toughness, and exogenous abrasives are thus all potential microwear agents, and the challenge is to sort out their respective contributions to the distinctive pattern observed in our instantaneous sample of July 1998. In an experimental study on vervet monkeys (*Cercocebus aethiops*), Teaford and Oyen (1989b) found that most microwear features were obliterated within 7–10 days, with even faster obliteration in monkeys fed an especially abrasive diet. Judging from their feature density, the Awash baboons had a moderately abrasive diet, and we therefore estimate that the observed wear pattern was determined by behavior that occurred at most 2 weeks before capture. Within this interval, tree- and shrub-leaf flush and new grass were becoming available, but most of the baboons' diet (along with corn supplied as bait) comprised mature seeds (some of them very tough, e.g., those of the shrub *Acacia nubica*), flower buds, flowers, leaves from various *Acacia* species, tough, dried berries from *Grewia* bushes, and seeds from various herbs (e.g., *Tribulus terrestris*).

Exogenous abrasives such as grit and dust are likely to have been a major influence. In the Awash National Park, the dry season sees virtual elimination of herbaceous vegetation over much of the thornscrub and floodplain, exposing a topsoil of

clays, silts, and sands with a high concentration of crystalline quartz and olivine (Nystrom, 1992; Williams et al., 1977). Food items picked from the ground are likely to have adhering sand or dust particles, and a film of fine, wind-borne dust accumulates on vegetation, including the leaves, flowers, and fruits of trees, shrubs, and herbs eaten by the baboons.

The numerous pits seen in the Awash baboons are much smaller, on average, than those associated with forest-canopy hard-object feeding, as seen in *Cebus apella* and *Lophocebus albigena*, and are much more numerous, especially relative to striations, than in folivores and graminivores. Mastication of "soft" fruits and insects might cause the formation of small pits by tooth-to-tooth contact, but neither of these food types was prominent in the Awash baboons' diet, and in any case, the high density of such pits argues for an alternative, or additional, agent.

One possibility is tooth-to-tooth contact in contexts other than feeding. Baboons, especially adult males, audibly grind their teeth in tense or stressful situations, and such grinding can produce striations (Xhonga, 1977), increased density of pits, and extensive exposure of enamel prisms (Teaford, 1988). Among the Awash baboons, however, males failed to show the higher frequency of small pits which is expected if bruxing (much more commonly observed in males than females) were indeed an important cause of pit formation.

The comparatively high feature density seen in the Awash baboons suggests that abrasive agents, either dietary or exogenous, are involved in microwear formation (Teaford et al., 1996). Phytoliths were presumably present in the grass shoots eaten by the baboons, but most of the diet consisted of seeds, flowers, and leaves of dicots such as *Acacia* sp., which are relatively poor in phytoliths (Cumings, 1992; Lalueza-Fox et al., 1996; Mulholland and Rapp, 1992). Moreover, the microwear pattern in the Awash baboons is quite unlike that of the highly graminivorous gelada, *Theropithecus gelada* (Teaford, 1993), which includes few pits, but many striations finer than those characteristic of the Awash baboons. These considerations suggest that although phytoliths embedded in grass leaves might produce some small pits along with many striations (Teaford, 1993), they are unlikely to be an important agent in the formation of the Awash baboon pattern, which is dominated by small pits but shows comparatively few, and wide, striations.

Since phytoliths seem unlikely to have produced the small-pit-dominated pattern, an exogenous abrasive such as environmental grit may be suspected. Daegling and Grine (1999) attributed the high frequency of pits in a sample of chacma baboons (*Papio hamadryas ursinus*) to abrasive particles ingested during terrestrial foraging, especially grit adhering to plant parts (e.g., corms and bulbs) dug from the ground. The chacma baboons exhibited a frequency of pits (43.3%) very close to that seen in the Awash animals, but average pit width was three times as great in the chacmas. This striking difference may reflect a difference in size of the abrasive particles to which their molar surfaces were exposed. Abrasive particles in the ubiquitous dust of the dry-season Awash (perhaps finer on average than the grit particles that would be ingested from the ground with subterranean plant parts) may be the main cause of the many small pits distinctive of microwear in the Awash baboons.

Another distinctive feature of the Awash baboon pattern is that its small pits are combined with comparatively wide striations. Average striation width is 73% of average pit width, while in the comparative sample of populations (Table 6), average striations range between 12–57% of mean pit width. To some extent, this may be an artifact of technique, since the resolution used in the present study was not as fine as used in some others (e.g., Teaford, 1993; Teaford and Runestad, 1992; Ungar, 1994), and thus striation widths may have been slightly overestimated (P. Ungar, personal communication), but this seems an unlikely explanation for a difference of this magnitude.

In the comparative series, striations are wide in monkeys that are hard-object feeders, as discussed previously, and narrow in grazers and folivores. All the hominoid apes also show wide striations, but the taxon association cannot be separated from a confounding, equally plausible, body-mass effect. In

some prehistoric human populations, wide striations were shown to distinguish hunter-gathers from agriculturalists (Schmidt, 2001; Teaford, 1991), and it was suggested that they are due to a more abrasive diet with large amounts of sandy grit present on the foods consumed (Pastor, 1992, 1993; Teaford et al., 2001; Ungar and Spencer, 1999).

Maas (1991) suggested that striation width (unlike pit width, which is related to the size of abrasive particles interacting with the enamel) may reflect enamel microstructure rather than qualities of the ingesta. Baboons, like most monkeys, have a predominance of pattern 2 enamel, while hominoids have a predominance of pattern 3 enamel (Martin et al., 1988). Whether there is a significant difference in response to shear between the two patterns is unknown (Maas, 1991), although Ungar (1994) found no correlation between striation width and orientation and therefore suggested that striation width reflects abrasive particle size rather than enamel pattern.

The Awash data support the latter interpretation. Among *individuals* of the Awash series, there is a high and very significant correlation (Pearson's  $R = 0.67$ ,  $P < 0.001$ ,  $N = 44$ ) between average pit width and average striation width (Fig. 3), and a less strong but also significant correlation between density of pits and density of striations ( $R = 0.32$ ,  $P = 0.032$ ; Fig. 4). (Neither of these relationships is seen in the comparative series as a whole.) To us, this strongly suggests that in Awash baboons during the dry season (though not necessarily in other circumstances), striations and pits are both caused by the same agent. It seems most likely that in their case the cause of both pits and striations is exogenous abrasive particles ingested with food, pressed into the enamel surface, and dragged forcefully across it as tough items such as mature seeds of *Acacia nubica* and dried fruits of *Grewia* spp. are first crushed, and then ground between the molar surfaces. If this interpretation is correct, it is intriguing to speculate that under such circumstances the respective proportions of crushing and grinding strokes used in mastication of a particular food type could be related experimentally to the resultant pit/striation ratio, and this relationship might then be used more generally to infer the chewing habits of fossil forms.

#### Effect of corn prebaiting on dental microwear

Any inferences about the microwear patterns and diet of the Awash baboons must consider the possible effect of corn prebaiting. Like most grasses, the seed-coat of corn contains phytoliths, but the small amount of silica present (~0.01%; Lanning et al., 1980; Piperno, 1988) is unlikely to cause significant damage to dental enamel (Piperno, 1988). The toughness of the dried corn kernels was not measured, but it is probably comparable to dry *Grewia mollis* and *G. forbesii* berries, which were found experimentally (Peters, 1982) to break under peak loadings of 28–49 kg and 145–181 kg, respectively.

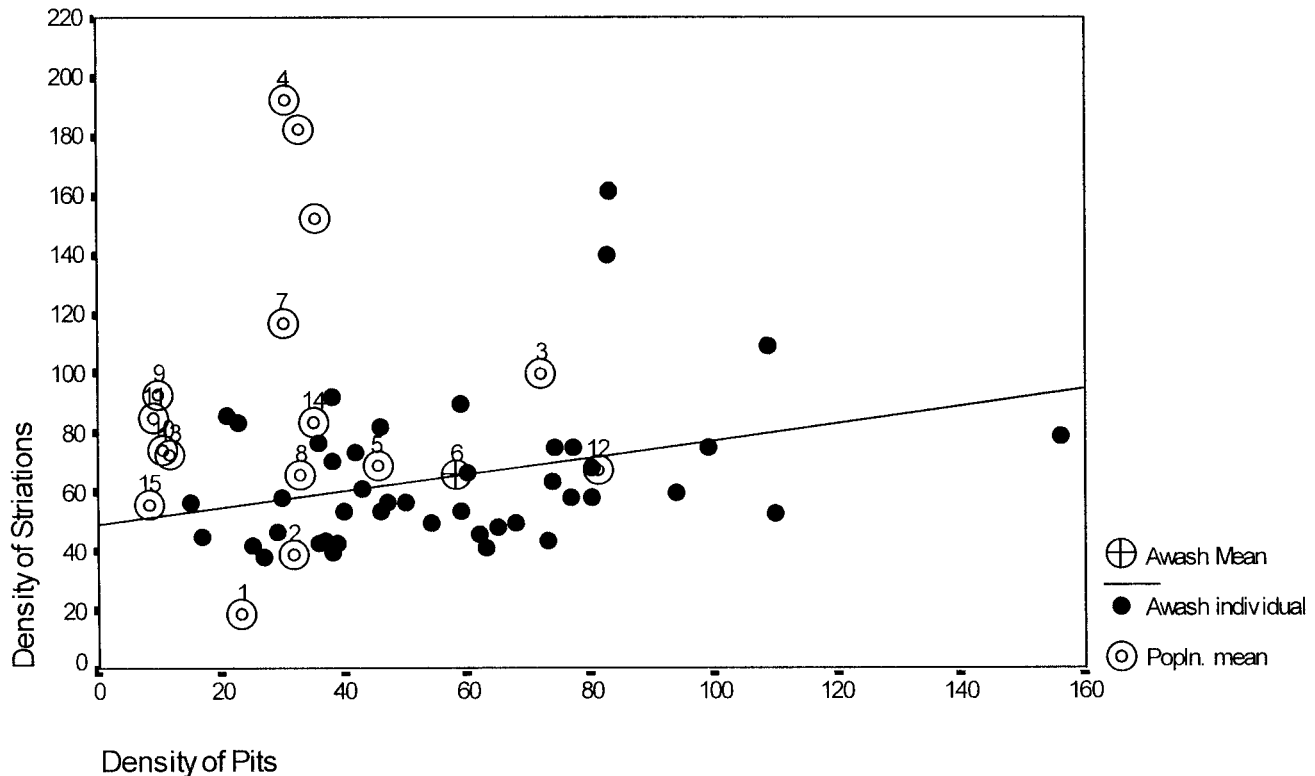


Fig. 4. Striation density plotted against pit density. Symbols and regression as in Figure 3.

Though the corn itself, like these natural foods of comparable toughness, probably caused no microwear directly, it would be a potent source of pits and striations if combined with abrasive dust and grit ingested as the baboons fed hurriedly in the tense and competitive milieu engendered by this highly concentrated and attractive food source.

It is, at first sight, surprising that, with the single exception of the negative correlation between feature density and estimated corn consumption in Group H males (which we cannot explain and are inclined to regard as a statistical aberration), we detected no influence of corn consumption on microwear patterns in the Awash baboons. One possible explanation is that the dried corn kernels, even if cracked and masticated together with gritty dust, caused no microwear at all, but this seems unlikely. Another explanation (which we prefer) is that corn consumption had no discernible effect because the microwear it engendered was indistinguishable from that produced by the similarly hard (and dusty) berries and seeds of trees and shrubs such as *Acacia nubica*, *Grewia* spp., *Zizyphus* spp., and *Celtis* spp. that were a major component of the baboons' natural diet. Thus the finding of no apparent corn effect could be seen as support for our speculation that feeding on seeds and berries, comparable in toughness to dried corn, and similarly contaminated with relatively small exogenous abrasive particles, was the major agent of the distinctive microwear pattern of the Awash baboons.

#### Location differences

Habitat differences, by influencing the amount of exogenous abrasives included in the diet, may cause differences in dental microwear pattern, even when diet remains the same (Teaford and Robinson, 1989; Ungar, 1994). In the present study, the habitats of the two target groups were in general very similar, but Group H spent more time in rocky and open areas with sparse vegetation than did Group D. It might be expected that Group H's environment would be associated with higher microwear feature density and a higher proportion of pits. The observed differences in these variables were in the expected direction, but failed to reach statistical significance. Evidently, if an effect is produced by the relatively minor differences between these adjacent habitats, it will take larger samples to detect them.

#### Sex- and age-associated variation

The Awash baboons are remarkable for their uniformity of microwear patterns across sex and age categories. With the few exceptions noted above, mean values for different age, sex, and troop categories were very similar, and the distances between them were slight compared to intracategory variation. This result differs from that of some previous studies, which found intrapopulational variation to correspond to observed differences in diet and/or food procurement practices associated with sex ("sexual dimorphism"), age, or social rank. For exam-

ple, Ungar (1994) found that male orangutans (*Pongo pygmaeus*) had significantly narrower striations than females, and suggested that they might ingest different-sized abrasive particles with their food because they forage at different levels in the forest.

Among the Awash baboons, animals of all ages and both sexes forage together on the same food patches, and all feed both on the ground and at all levels in savanna and woodland trees, a finding that accords with the lack of age- and sex-associated variation in their microwear. While our qualitative behavioral observations do not suggest the existence of gross sexual dimorphism or age-related dietary differences in this population, they do not rule out subtle effects such as those found by Post et al. (1980) in yellow baboons, where, as in Awash, adult males often displaced other animals from preferred foods, and were themselves interrupted less frequently while feeding. If such minor ecological differences do exist in the Awash, they appear to have little impact upon dental microwear patterns, although the sex-related trends noted in Results are in the predicted direction (the higher density of features in females, for instance, might be related to feeding on less desirable, more abrasive, foods, or eating more hastily in a competitive environment) and merit further investigation with larger samples.

Intra- and interspecific microwear differences are generally attributed to variation in food, exogenous abrasives, or both. Some variation, however, may reflect masticatory anatomy or dental microstructure. In chimpanzees (*Pan troglodytes*), for instance, the significantly shorter striations on female molars were attributed to the biomechanics of jaw motion. In this interpretation, male molars exhibit longer striations because they are located farther from the temporomandibular joint than their homologues in females, so that the arcs they travel during chewing cycles are more extensive (Gordon, 1982). In the Awash baboons, where this theory might predict markedly longer striations in adult males, owing to the considerable sexual dimorphism difference in jaw length, no such effect was found. Although male striations were on average longer, as predicted, mean striation lengths in the two sexes were extremely close.

Intratooth differences in enamel microstructure were also suggested as a cause of microwear variation, in this case correlated with dental age. In both human subjects and chimpanzees, the frequency of buccal tooth striations was significantly higher in subadults than adults, but remained constant in adulthood (Gordon, 1982; King et al., 1999; Pérez-Pérez et al., 1994). Gordon (1982, 1988) pointed out that in humans, enamel on crown tips is more dense than that deposited later in crown development (Moss and Moss-Salentijn, 1976; Karlstrom, 1931, cited in Gordon, 1982). This could produce age-associated differences in microwear patterns, with the less dense enamel showing more rapid abrasion and

obliteration of features (Gordon, 1982, 1988). No such effect was seen in the Awash baboons, where older and younger animals had almost identical feature densities, at least within the relatively narrow age range sampled.

#### **Paleontological and evolutionary implications**

Our interpretation of microwear in the Awash baboons emphasizes the role of exogenous abrasives in terrestrial, omnivorous catarrhine primates foraging in a semiarid, seasonally dusty habitat. This has a number of implications for interpreting dental and dietary evolution in baboons and other ecologically comparable catarrhines, including, we believe, some early hominins.

Most obviously, it suggests that in such animals, microwear parameters will largely reflect the size and prevalence of exogenous abrasive particles as well as the toughness or resistance of food items. Unless the diet includes a substantial component of phytolith-rich grasses and sedges, its microwear signature probably will not allow the population to be allocated to one of the traditional dietary categories. More pointedly, a microwear pattern comparable to a chimpanzee's, when observed in an australopith, signals "low grit" and "no grass-eating," rather than "frugivore" per se.

Although microwear has attracted anthropological interest primarily as a potential source of information about paleodiet, its ontogenetic role as a major component of dental deterioration also has evolutionary implications. Among anubis baboons of the Awash National Park population, for example, the oldest animals (especially those over 20 years old) have molars with little or no remaining occlusal enamel, and usually with one or more major breaks (Awash Baboon Research Project, unpublished data). While much of the gross damage, especially in the later stages, is presumably produced by spalling and chipping, it is surely abrasive microwear that steadily removes enamel (Phillips-Conroy et al., 2000) and exposes vulnerable dentine edges on the occlusal surface.

An evolutionary trend towards molars that are more microwear-resistant, by virtue of thicker enamel or enlarged occlusal area, or both, is seen in many catarrhine lineages. Hamadryas baboons, for example, have more molar area per unit body mass than do anubis baboons (Phillips-Conroy, 1978). Similarly, thicker molar enamel and larger molars are often included among the diagnostics of a stem hominin (Brunet et al., 2002), and a trend toward further molar enlargement is of course characteristic of "robust" australopiths. Such trends are common, and reasonably, related to shifts in dietary emphasis, e.g., from "soft fruit" to "hard seed" feeding. Adding exogenous abrasives to the ingesta, however, will produce more microwear, even if the diet remains constant. This suggests that environmental change towards greater seasonal aridity might itself select for microwear-resistant molars,

and should be considered as an alternative, or more likely, an ancillary explanation for such trends observed in fossil lineages.

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