

# Dental Topography and Molar Wear in *Alouatta palliata* From Costa Rica

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**ABSTRACT** Paleoprimatologists depend on relationships between form and function of teeth to reconstruct the diets of fossil species. Most of this work has been limited to studies of unworn teeth. A new approach, dental topographic analysis, allows the characterization and comparison of worn primate teeth. Variably worn museum specimens have been used to construct species-specific wear sequences so that measurements can be compared by wear stage among taxa with known differences in diet. This assumes that individuals in a species tend to wear their molar teeth in similar ways, a supposition that has yet to be tested. Here we evaluate this assumption with a longitudinal study of changes in tooth form over time in primates. Fourteen individual mantled howling monkeys (*Alouatta palliata*) were captured and then recaptured after 2, 4, and 7 years when possible at Hacienda La

Pacifica in Costa Rica between 1989–1999. Dental impressions were taken each time, and molar casts were produced and analyzed using dental topographic analysis. Results showed consistent decreases in crown slope and occlusal relief. In contrast, crown angularity, a measure of surface jaggedness, remained fairly constant except with extreme wear. There were no evident differences between specimens collected in different microhabitats. These results suggest that different individual mantled howling monkeys wear their teeth down in similar ways, evidently following a species-specific wear sequence. Dental topographic analysis may therefore be used to compare morphology among similarly worn individuals from different species. *Am J Phys Anthropol* 125:152–161, 2004.

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Researchers have been interested in the relationships between tooth form and function in primates for over a century (e.g., Owen, 1840–1845; Gregory, 1922). Much of this attention has focused on how molar morphology relates to known feeding adaptations (e.g., Kay, 1975, 1977, 1978; Kay and Hylander, 1978; Kinzey, 1978; Lucas, 1979; Maier, 1977, 1984; Rosenberger and Kinzey, 1976; Seligsohn, 1977). An understanding of this complex form-function relationship has led to important dietary inferences for many fossil species (Kay, 1977; Kay and Simons, 1980; Anthony and Kay, 1993; Strait, 1993; Williams and Covert, 1994; Ungar and Kay, 1995; Fleagle et al., 1996; Meldrum and Kay, 1997; Benefit, 2000).

Most studies of dental functional morphology have concentrated on unworn teeth. This approach is limiting because, without a clear understanding of how molar shape changes with wear, we cannot have a complete picture of the complex relationship between dental form and function. Natural selection should continue to act on tooth shape after the onset of wear, and in fact, should favor teeth that wear in a manner that keeps them mechanically efficient for fracturing foods. Studies of worn tooth form in extant primates are also important because worn teeth

usually dominate fossil assemblages. The ability to include worn specimens in studies of dental functional morphology would increase potential sample sizes and facilitate the reconstruction of diets for more species than possible if only unworn teeth can be used.

A new approach to the study of tooth form, dental topographic analysis, provides a method for characterizing and comparing variably worn primate teeth in three dimensions. This technique has already been used to examine molar form similarities and differences in variably worn museum specimens, suggesting that some aspects of shape change and

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that others remain constant with wear (Ungar and Williamson, 2000; Ungar and Kirera, 2003; Kirera and Ungar, 2003).

While this work suggests the potential of this approach, it has relied on different individuals to construct wear sequences. Other studies of morphological changes associated with tooth wear have also been based on analyses of museum specimens (Teaford, 1983; Janis, 1984; Benefit, 1987). Such studies made the assumption that different individuals in a species wear their molar teeth in similar ways, and so can be used to construct species-specific wear sequences. This assumption has yet to be tested because of the costs and logistical difficulties of studying living primates. Such a study is necessary, however, to determine whether different individuals may legitimately be used to reconstruct species wear sequences from fossil teeth, and ultimately to shed new light on the reconstruction of diet from worn teeth. In this study, we examine functionally relevant measures of molar tooth shape in wild-caught *Alouatta palliata* individuals over time.

Diet is generally recognized as “the single most important parameter underlying the behavioral and ecological differences among living primates” (Fleagle, 1999, p. 291). It follows that studies of diet in fossil species hold the potential to inform us of myriad aspects of the paleobiology of past primates. Teeth provide the most direct evidence available for diets of past mammals, as they are usually the only preserved part of the digestive system. They are also the most common elements found in primate fossil assemblages, providing the most reliable source of evidence.

Several researchers studied the relationships between tooth form and function in primates (e.g., Kay, 1973, 1975, 1978; Kay and Hylander, 1978; Rosenberger and Kinzey, 1976; Kinzey, 1978; Lucas, 1979; Maier, 1977, 1984; Benefit, 1987). The most commonly applied approach is that of Kay (1973, 1975), who reasoned that those primates subsisting primarily on leaves and insects have relatively long crests on their molar teeth, crests that are efficient for shearing and slicing. Conversely, frugivores, especially those that consume harder seeds, have blunter teeth with poorly developed crests to make them well-suited to crushing. These findings were subsequently tested in laboratory studies of primates (Walker and Murray, 1975; Sheine and Kay, 1977; Kay and Sheine, 1979), verifying that animals with relatively longer molar shearing crests were able to subdivide tough foods more finely.

Kay (1978, 1984) then developed a method for characterizing relative crest length as a residual from a regression line, comparing shearing crest length and mesiodistal occlusal table diameter for closely related taxa that fell within a given broad diet category. By plotting folivores on a regression line derived using only frugivore data, Kay (1978, 1984) was able to demonstrate that leaf-eaters have longer crests than would be expected of a fruit-eater.

Shearing quotients (SQs) are thus measures of relative shear, and have been effective in distinguishing folivores from frugivores, and among frugivores, hard-object specialists from softer fruit-eaters (e.g., Kay and Hylander, 1978; Anthony and Kay, 1993; Strait, 1993).

Shearing crests are measured as distances between cusp tips and the notches between cusps. Summed crest lengths include all mesiodistal crests (numbered 1–8) on each crown, and are compared with the straight-line distance between the mesial and distal edges of the occlusal table. Because two-dimensional (2D) relief of a line segment may be considered the difference between the actual length of that segment and the straight-line distance between its endpoints, SQs are essentially measures of relief. While this approach has proven invaluable for examining primate tooth form-function relationships, the technique works best for unworn teeth, as crest length values change with attrition, and quickly become impossible to measure as cusp tips are obliterated by wear (Teaford, 1981).

Unfortunately, studies that are restricted to unworn teeth give us an incomplete picture of dental functional morphology. The plain fact of the matter is that teeth begin to wear as soon as they come into occlusion, and there is no reason to assume that natural selection stops operating on dental morphology when the first facets appear on an occlusal surface. Not only should foods with different material properties select for teeth with different unworn occlusal morphologies (Kay, 1975; Lucas, 1979; Lucas and Teaford, 1994), but these foods should also select for teeth that maintain these differences with wear, or even change their shapes in different ways as they wear (Teaford, 1983; Kay, 1985). Restricting studies of extinct primate species to unworn teeth is also problematic because fossil assemblages tend to be dominated by worn specimens, and many taxa are not represented by sufficient unworn samples to measure shearing quotients or conduct statistical comparisons. What is needed is a new perspective on dental morphology: a method for “measuring” or characterizing occlusal relief and other functionally relevant aspects of molar morphology on variably worn crowns.

Several researchers have identified a new approach to the study of dental morphology, using three-dimensional (3D) point coordinates to model the surface of a tooth (Reed, 1997; Jernvall and Selänne, 1999; Zuccotti et al., 1998). These data are treated as landscapes, and analyzed using Geographic Information Systems (GIS) software. GIS software products are designed to assemble, store, manipulate, analyze, and display geographically referenced information in a single application. Several GIS tools have been developed for modeling and examining the surface of the Earth, but can just as easily be used to characterize and analyze the surface of a tooth. This approach has been called “dental topographic analysis” (Zuccotti et al., 1998).

Ungar and Williamson (2000) suggested that dental topographic analysis can be used not only on unworn molars, but also on worn teeth. This has spawned work comparing morphological differences in variably worn teeth within and between species (Ungar and Kirera, 2003; Kirera and Ungar, 2003). These studies have shown that more worn molars have flatter cusps and less surface relief on their occlusal tables than less worn specimens for both chimpanzees and gorillas. Further, gorillas have steeper sloped molar cusps and more occlusal relief at comparable stages of wear than do chimpanzees. Gorillas also have more angular or jagged cusp surfaces than chimpanzees, but angularity values do not differ within taxa between wear stages. The authors argued that, because slope, angularity, and surface relief differences between taxa are consistent in similarly worn specimens, variably worn fossil specimens can be included in functional analyses. The lack of change of angularity provides one of the first lines of evidence for the maintenance of a functional aspect of morphology despite wear.

These arguments depend, of course, on the existence of species-specific wear sequences. Because species have recognizable patterns of unworn molar morphology that presumably relate to dietary adaptations, we expect that they will likewise have recognizable patterns of worn tooth morphology and should, therefore, exhibit species-specific patterns of wear. Previous longitudinal studies of primate tooth wear were either limited by relatively crude methods of data collection (Teaford, 1991; Teaford and Glander, 1996) or focused solely on rates of tooth wear rather than the morphological ramifications of wear (Phillips-Conroy et al., 2000). This paper uses topographic analyses in a longitudinal study of wild-caught primates to determine whether tooth shape changes in a consistent manner with wear.

## MATERIALS AND METHODS

### Study animals

This study examines the morphology of worn mantled howling monkey teeth from Hacienda La Pacifica (Guanacaste Province, Costa Rica). *Alouatta palliata* has been studied at La Pacifica nearly continuously for the past three decades (Glander, 1978, 1981, 1992; Clarke and Glander, 1984; Teaford and Glander, 1991, 1996; Clarke and Zucker, 1994; Ungar et al., 1995; Zucker and Clarke, 1998; Clarke et al., 1998, 2002). One focus of this research has, since 1989, involved the collection of dental impressions for wear analysis.

The study described here focuses on tooth wear in individuals from four social groups at La Pacifica: 1, 7, 19, and 33 (Teaford and Glander, 1996). Groups 7 and 19 inhabit gallery forest lining the Corobici River, whereas groups 1 and 33 are found in drier forest patches preserved as windbreaks to prevent erosion of ranchland. Animals in these latter groups do not have access to the river, and thus live in a

microhabitat subject to more pronounced seasonal changes in resources (Glander, 1981; Teaford and Glander, 1996). In total, 14 individuals were used in this study (see Appendix). These individuals were repeatedly captured, and dental impressions were taken at 2, 4, and 7 years following the initial tooth moldings whenever possible. Given the vagaries of darting primates in the wild, however, not all animals could be captured during each field season.

### Specimen preparation

Animals were captured using the methods described by Glander et al. (1991). A CO<sub>2</sub>-powered gun was used to deliver a nonbarbed dart (Pneu-Dart™ System, Williamsport, PA) loaded with Telazol (Fort Dodge Laboratories, Fort Dodge, IA). The dosage of 25 mg per kilogram yielded rapid induction and immobilization, good muscle relaxation, a wide safety margin, and rapid recovery. Individuals were darted at distances up to 20 m. As very few trees at La Pacifica are taller than that, animals could be caught virtually anywhere at the site.

Dental impressions were taken following procedures described by Teaford and Glander (1991, 1996). Thus, 10–15 min before impressions were taken, each animal was given a small dose (0.05 mg per kilogram) of atropine, to reduce salivation and stabilize heart rate. The animal's teeth were then cleaned using 1) a toothbrush, 2) a water-pik, and 3) an acid gel (40% phosphoric acid) to cut organic films accumulated on the teeth, followed immediately by 4) the water-pik to remove the gel and any organic debris it had loosened, and then 5) 1–2 min of air-drying using a portable air compressor. Dental impressions were taken of the left mandibular tooth row, using a polyvinylsiloxane impression material (President Jet, Regular Body, Coltene-Whaledent, Mawah, NJ). As the animals had generally been darted at long range, there was no guarantee of exactly how much anesthesia each animal received. Thus, some animals began to recover from anesthesia during the impression sessions. Occasionally they were given small booster shots of anesthesia. At other times, that seemed inadvisable. As a result, some impressions included only partial tooth crowns, or crowns of only some of the teeth.

High-resolution casts were prepared following procedures described by Teaford and Oyen (1989) and Ungar and Kirera (2003). Araldite 501 (Ciba-Geigy, Tarrytown, NY) epoxy was poured into the vinyl molds collected in the field and centrifuged to remove bubbles that might obscure occlusal morphology. A pale gray pigment was added to the epoxy, and a thin layer of Magniflux Spotcheck SD-S2 Developer (Illinois Toolworks, Glenview, IL) was applied to the surfaces of hardened replicas to mitigate specimen translucency and prevent the laser from penetrating the surface.

Specimens were mounted on a rotating platform approximately as they would sit in the jaw. Precise orientation was accomplished with the aid of a bin-

ocular microscope, by rotating the platform around the mesiodistal and buccolingual axes using set-screws to maximize the occlusal surface visible in top view. Repeatability studies showed that most measurements taken on specimens oriented in this manner are precise to within less than 1% (Ungar et al., 2002).

### Data acquisition

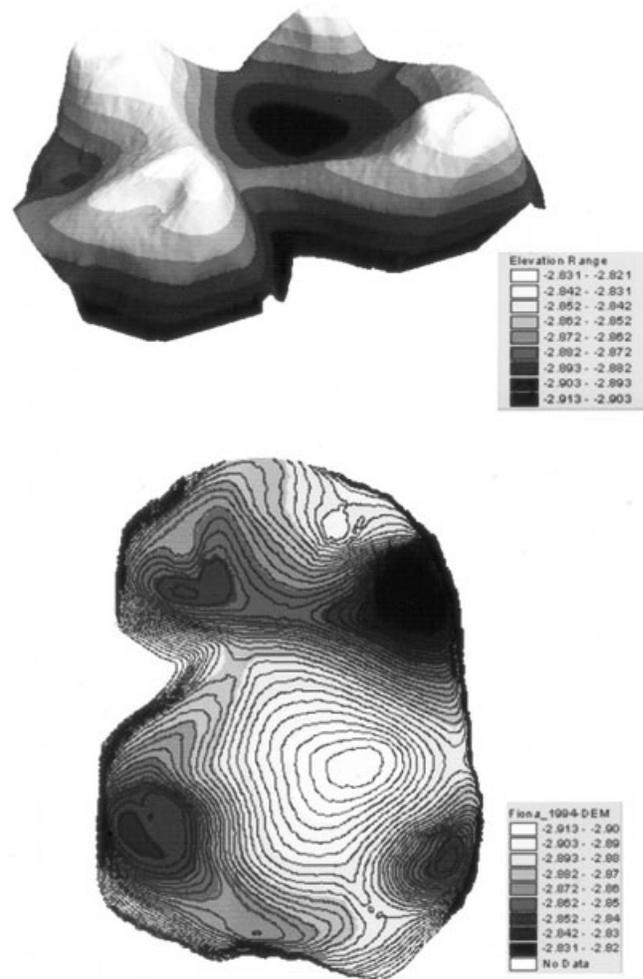
$M_2$  occlusal tables were then scanned at a resolution of 25.4  $\mu\text{m}$  in x-, y-, and z-axes using a modified Surveyor 500 laser scanner with an RPS 150 laser (Laser Design, Minneapolis, MN), following procedures described in detail elsewhere (Ungar and Williamson, 2000; Kirera and Ungar, 2003; Ungar and Kirera, 2003).  $M_2$ s were chosen following other studies of molar functional morphology (Kay, 1978; Ungar and Williamson, 2000). This resulted in an ASCII text file for each specimen at each sampled time interval, containing x, y, and z coordinates sampled at fixed distances along the surface.

These files were then opened as data tables in ArcView 3.2 (ESRI, Redlands, CA) with Spatial Analyst and 3D Analyst extensions, and a continuous surface was interpolated using inverse distance weighting (following Zuccotti et al., 1998). Surface interpolation was necessary, given missing data points resulting from the near-vertical drops associated with the steep edges of sharp cusps that characterize less worn *A. palliata* molars. These surfaces were then converted to 2D x, y matrices where each cell contains elevation z-values. These digital elevation models (DEMs) are used in dental topographic analysis to calculate surface attributes by comparing adjacent cell values.

Once a DEM was completed, it was cropped to include only the  $M_2$  occlusal table, defined as the surface above a horizontal plane intersecting the lowest point on the talonid basin when the tooth is oriented as described above (Ungar and Williamson, 2000). This approach assures comparability of specimens and eliminates the problem of surface overhang (more than one z-value for an x, y pair), such as may occur down the buccal and lingual sides of the tooth as the enamel cap approaches the cervix.

Average surface slope and angularity were calculated from each DEM. Slope is defined as the average change in elevation across the surface (first derivative of elevation), whereas angularity is the average change in slope across the surface (second derivative of elevation). Slope therefore refers to steepness of the surface, whereas angularity may be considered more a measure of surface roughness or jaggedness. The difference between slope and angularity is analogous to that between the sharpness and the serratedness of a knife blade (see Ungar and Kirera, 2003). Both slope and angularity variables are measured in degrees.

ArcView was then used to create a triangulated irregular network, a series of triangles connecting adjacent data points on the surface (Fig. 1). The



**Fig. 1.** Visual representation of data for Fiona  $M_2$ , 1994 capture date. Shaded relief sample image with superimposed contour lines (**top**) and triangulated irregular network in 3D view (**bottom**).

surface areas of these triangles were then tallied to generate a 3D surface area for the entire occlusal table. This value was then divided by the planimetric or 2D area of the DEM calculated from the x, y point data and multiplied by 100 to give a dimensionless index of occlusal relief. Occlusal relief in dental topographic analysis can be viewed as a 3D extension of more conventional shearing quotient studies, which also measure occlusal relief (Kirera and Ungar, 2003).

### Data analysis

Given missing values, non-normal distributions, and other limitations of the data set, signed ranks tests were used to assess changes in slope, angularity, and surface relief between initial capture and years 2, 4, and 7. The effect of environment was also examined because of differences in resources and possibly tooth-wearing abrasives in riverine and nonriverine microhabitats (Glander, 1981; Ungar et al., 1995; Teaford and Glander, 1996). Wilcoxon's

TABLE 1. Signed-ranks test results for individual comparisons

Interval	N	Slope		Relief		Angularity	
		$t_s$	P	$t_s$	P	$t_s$	P
2 years	11	25.0	0.0244	29.0	0.0068	9.0	0.4648
4 years	6	9.5	0.0625	5.5	0.3125	7.5	0.1563
7 years	8	18.0	0.0078	18.0	0.0078	18.0	0.0078

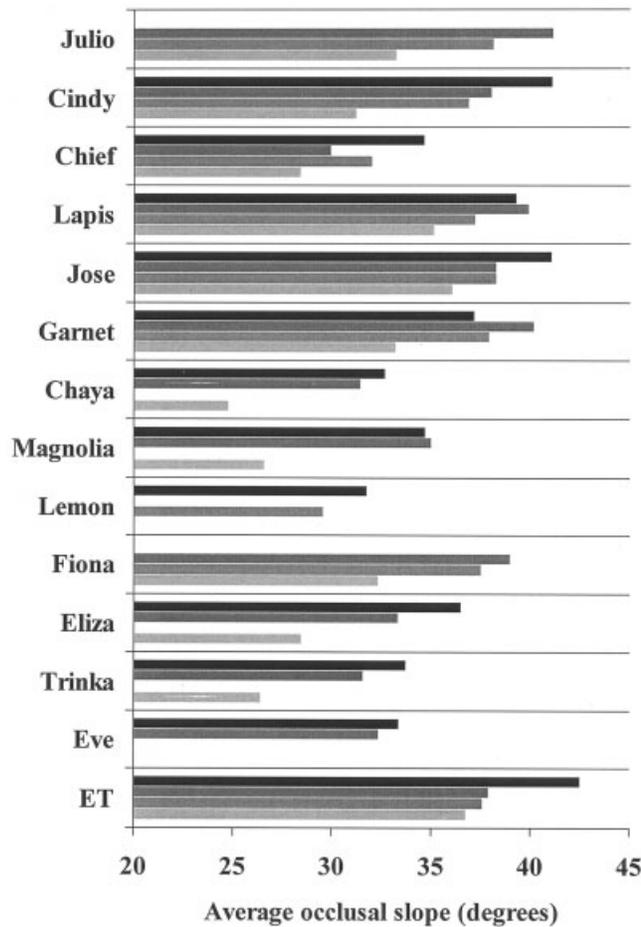


Fig. 2. Slope changes over time for individuals for initial capture (black), year 2 (dark gray), year 4 (lighter gray), and year 7 (lightest gray).

two-sample tests were used to compare river (7, 19) and nonriver (1, 33) groups for each variable.

**RESULTS**

**Individual monkey comparisons**

Raw data are presented in the Appendix. Results are summarized in Table 1 and Figures 2–4. Signed ranks test results indicate significant decreases in occlusal slope between the initial capture and years 2, 4, and 7 ( $P < 0.1$  at the one-tailed level). The marginal significance found between initial capture and year 4 is probably due to the relatively small sample available for year 4.

Results for surface relief were similar to those for slope, in that individuals showed a tendency for decreased occlusal relief over time. Differences were

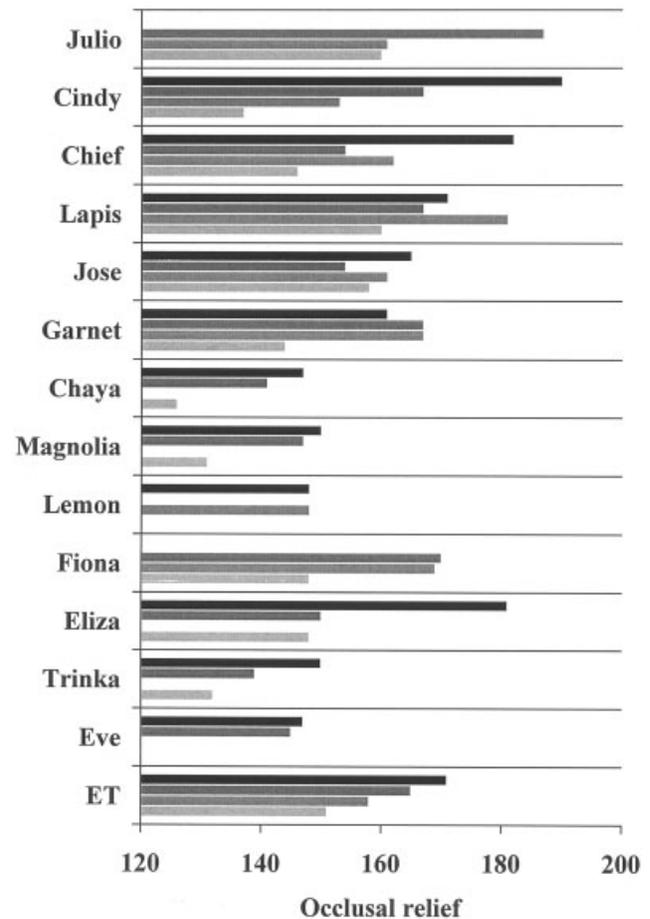


Fig. 3. Relief changes over time for individuals for initial capture (black), year 2 (dark gray), year 4 (lighter gray), and year 7 (lightest gray).

statistically significant between the initial capture and years 2 and 7, but not between the initial capture and year 4. Again, this might in part be due to the fact that only six of the individuals studied could be captured 4 years after initial darting.

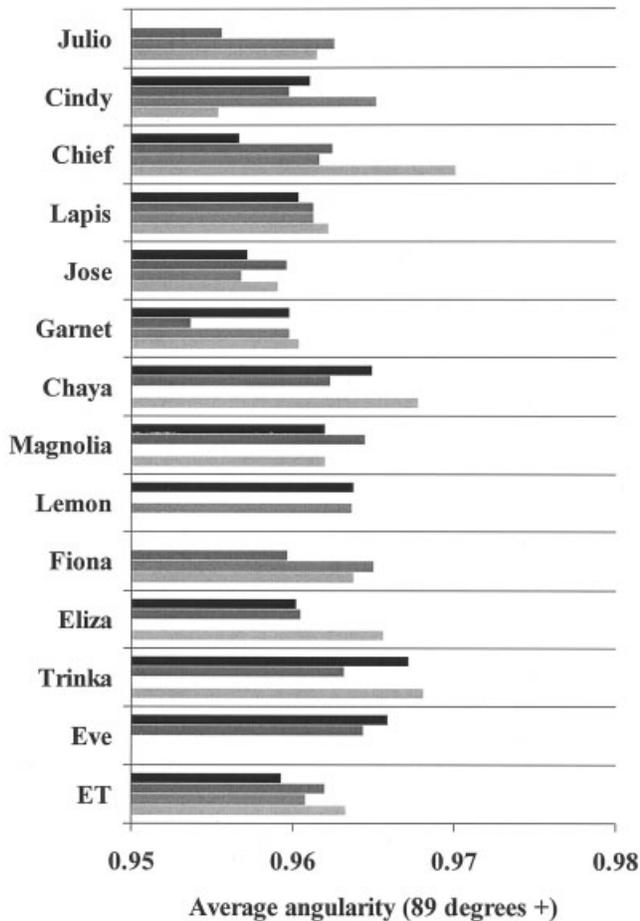
Unlike slope or relief, occlusal surface angularity showed no significant change between the initial sample and years 2 or 4. Angularity did show a significant drop between the initial capture period and year 7.

**Habitat comparisons**

Results for habitat comparisons are presented in Table 2. There were no significant differences in slope, relief, or angularity changes over time between river and nonriver habitat samples. While this suggests a lack of differences in patterns of gross tooth wear between the habitats, we must point out that small sample sizes make this result tentative.

**DISCUSSION**

Results presented here indicate that La Pacifica howling monkeys show some consistent changes in their molar morphologies over time. Specifically, as



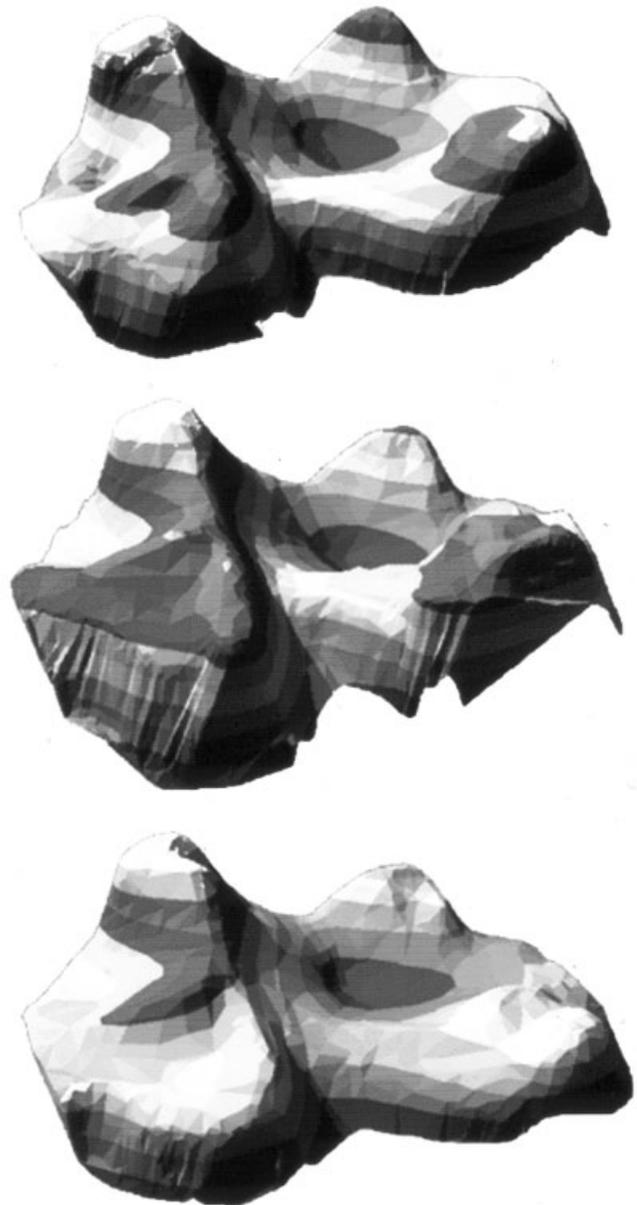
**Fig. 4.** Angularity changes over time for individuals for initial capture (black), year 2 (dark gray), year 4 (lighter gray), and year 7 (lightest gray).

**TABLE 2.** Wilcoxon two-sample test comparisons between habitats

Interval	N	Slope		Relief		Angularity	
		$t_s$	P	$t_s$	P	$t_s$	P
2 years	6.5	22.0	0.1775	24.0	0.3290	32.0	0.7922
4 years	3.3	14.0	0.2000	15.0	0.1000	6.0	0.1000
7 years	4.4	13.0	0.2000	12.0	0.1143	23.0	0.2000

one might expect, occlusal surface slope and relief decline through time (Fig. 5). In other words, as an individual's teeth wear down, they become flatter. The lack of a significant change in occlusal relief between initial capture and year 4 is probably due to small sample sizes and a lack of statistical power in that case.

The general trend toward decreasing slopes and occlusal relief in howlers is neither surprising, nor unexpected. Similar results were reported for gorillas and chimpanzees (Ungar and Kirera, 2003; Kirera and Ungar, 2003). These ape studies used wear sequences generated from museum collections, assuming that individuals of a given taxon wear their teeth in similar manners. This assumption is essential if different specimens are to be used to recon-



**Fig. 5.** Digital elevation model of Fiona M<sub>2</sub>, captured in 1992 (top), 1994 (middle), and 1999 (bottom), showing changes in morphology over time.

struct wear-related changes in tooth shape in fossil taxa.

Given that primates evince species-specific dietary adaptations (Sussman, 1978, 1987), dental morphology should reflect material properties of foods of crucial importance for survival and reproduction (Lucas, 1979), whether those foods are consumed frequently or infrequently (Kay, 1973, 1975, 1978; Rosenberger and Kinzey, 1976; Kinzey, 1978). However, we must remember that primates often have variable diets, and this can pose problems for interpretations. In fact, primate diets may vary in many ways. For instance, *Cebus apella* has a variable diet that includes foods of a wide range of hardness, whereas *Alouatta palliata* has a variable diet

that includes foods of varying toughness. Each of these diets puts different demands on the teeth. Thus, just because two species have variable diets doesn't necessarily mean their teeth will be similar in shape.

Taking this a step further, it follows that, even if teeth of a given taxon should wear in a specific manner to keep them mechanically efficient for fracturing the foods in its diet, if two taxa have different yet variable diets, their wear patterns may or may not be similar. Given these potential complexities, it is not surprising that no one has demonstrated that individuals within a species actually do wear their teeth down in similar manners. The longitudinal study described here is the first to offer evidence of this using morphological "traits" accurately discernible in worn specimens.

The lack of evident changes in cusp angularity between initial capture and years 2 and 4 is also interesting, and again, consistent with findings for chimpanzees and gorillas (Ungar and Williamson, 2000; Ungar and Kirera, 2003). This suggests that, despite wear, occlusal surface angularity remains fairly constant for much of the life of a howling monkey molar tooth. Thus, as suggested by Teaford and Glander (1996) based on changes in molar shearing crests with wear, at least one functional aspect of occlusal morphology appears to remain fairly consistent as howler teeth wear.

The *lack* of change in angularity for younger individuals may be related to the development or maintenance of complicated changes in slope at the margins of dentin exposures formed as enamel gives way to softer dentin during tooth wear. The maintenance of sharp edges between enamel and dentin for much of the life of a howler tooth would be comparable to the pattern seen in herbivorous ungulates that have complex infoldings and lophs designed to form sharp edges with dentin exposure for shearing and grinding tough foods (Rensberger, 1973; Fortelius, 1985). Kay (1985) reasoned that folivorous primates with thin tooth enamel should have sharp edges at the sites of dentin exposure to improve the shredding and slicing abilities of a tooth with wear. Ungar and Kirera (2003) noted that increased angularity or jaggedness of a surface resulting from dentin exposure would dramatically change the direction of forces acting on a food item, increasing potential damage to that item. Lucas and Teaford (1994) suggested, in addition, that such edges might aid in the retention of foods between cross-lophs used in processing tough, pliant foods.

Once the tooth is reduced to an enamel rim with a single dentin island, surface jaggedness should drop. This evidently explains the change in angularity in the present study between initial capture and year 7. Again, as suggested by shearing crest lengths (Teaford and Glander, 1996), the change in angularity once the enamel is completely gone would suggest that tooth functional efficiency does ultimately decrease with extreme wear. Still, surface angular-

ity is a complex variable, and more work is needed to fully assess its functional significance.

It is also notable that patterns of morphological change (and stasis) with wear hold for both river and nonriver howler groups. While one might expect to see subtle differences in gross wear to correspond to reported microwear differences (Teaford and Glander, 1996), no significant differences between habitats were found in this study. It may be that species-specific wear sequences are independent of subtle dietary differences that characterize conspecifics living in different habitats. Indeed, intraspecific microwear differences related to habitat are generally not of sufficient magnitude to swamp interspecific differences (Teaford and Robinson, 1989). Alternatively, it may be that the sample sizes available for this study are not sufficient to show subtle differences in slope, relief, or angularity change over time. Larger samples will hopefully ultimately resolve this.

What do the results from this study tell us about future analyses of dental function? The pioneering work of Kay, Kinzey, Lucas, and others opened peoples' eyes to the importance of subtle differences in tooth shape to dental function. The present study gives us a glimpse of the potential of analyses of tooth wear in interpretations of dental function. For example, Lanyon and Sanson (1986) examined the relationship of tooth wear to chewing efficiency in koalas. They reasoned that the length and configuration of cutting edges on molar teeth were maintained through the initial stages of tooth wear. However, with heavy wear, tooth morphology changed enough to interfere with the efficient processing of food as, in older individuals, food particle size began to increase, indicating that chewing efficiency ultimately decreased with age. This may be consistent with results of the current study, wherein the teeth of *A. palliata* maintained occlusal angularity throughout much of the wear sequence, though this value evidently declined with extreme wear. Dental topographic analysis provides an approach whereby we can document and compare differences between taxa in how occlusal morphology changes with wear.

A next step in studying this intriguing dental functional complex will be to analyze how each individual breaks down food items. Different individuals will chew their food in ways that differ subtly. This subtle difference in individual chewing processes can have a tremendous effect on the wear of a tooth and ultimately on how efficient the tooth is during mastication. Such studies will lead to better inferences about the relationships between tooth wear, morphology, and functional efficiency, and they may ultimately shed new light on the evolution of tooth form, as functional efficiency is either maintained, or diminished, throughout the lifetime of individuals in different habitats or different species.

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## APPENDIX. Raw for each individual by age and group

Name/year	Age	Plainometric	Surface	Relief	Slope	Angularity
Group 1 (Nonriver)						
Et 1992	4	0.064000	0.110000	171.875000	42.525500	89.959387
Et 1994	6	0.055000	0.091000	165.454545	37.943277	89.962048
Et 1996	8	0.055000	0.087000	158.181818	37.616635	89.960817
Et 1999	11	0.060000	0.091000	151.666667	36.798923	89.963394
Eve 1992	8	0.067000	0.099000	147.761194	33.387700	89.965989
Eve 1994	10	0.068000	0.099000	145.588235	32.372134	89.964467
Trinka 1992	11	0.065000	0.098000	150.769231	33.731140	89.967229
Trinka 1994	13	0.069000	0.096000	139.130435	31.597880	89.963249
Trinka 1999	18	0.067000	0.089000	132.835821	26.407668	89.968143
Group 7 (river)						
Eliza 1992	8	0.060000	0.109000	181.666667	36.548882	89.960243
Eliza 1994	10	0.066000	0.099000	150.000000	33.359408	89.960562
Eliza 1998	14	0.060000	0.089000	148.333333	28.432512	89.965673
Fiona 1994	8	0.064000	0.109000	170.312500	39.013814	89.959707
Fiona 1996	10	0.066000	0.112000	169.696970	37.528186	89.965020
Fiona 1999	13	0.064000	0.095000	148.437500	32.312895	89.963806
Lemmon 1989	14	0.075000	0.111000	148.000000	31.736576	89.963843
Lemmon 1994	19	0.076000	0.113000	148.684211	29.537016	89.963764
Magnol 1989	10	0.069000	0.104000	150.724638	34.718801	89.962056
Magnol 1992	13	0.070000	0.103000	147.142857	35.023053	89.964540
Magnol 1999	20	0.073000	0.096000	131.506849	26.572130	89.962093
Group 19 (river)						
Chaya 1992	20	0.059000	0.087000	147.457627	32.678409	89.964902
Chaya 1993	21	0.062000	0.088000	141.935484	31.463341	89.962357
Chaya 1999	27	0.060000	0.076000	126.666667	24.754024	89.967837
Garnet 1992	6	0.070000	0.113000	161.428571	37.174121	89.959883
Garnet 1994	8	0.080000	0.134000	167.500000	40.172621	89.953738
Garnet 1996	10	0.082000	0.137000	167.073171	37.925851	89.959863
Garnet 1999	13	0.074000	0.107000	144.594595	33.211987	89.960498
Jose 1992	3	0.080000	0.132000	165.000000	41.081646	89.957251
Jose 1994	5	0.064000	0.099000	154.687500	38.282415	89.959646
Jose 1996	7	0.084000	0.136000	161.904762	38.300970	89.956845
Jose 1999	10	0.082000	0.130000	158.536585	36.091152	89.959157
Lapis 1992	8	0.070000	0.120000	171.428571	39.307312	89.960457
Lapis 1994	10	0.076000	0.127000	167.105263	39.916074	89.961342
Lapis 1996	12	0.080000	0.145000	181.250000	37.223376	89.961322
Lapis 1999	15	0.073000	0.117000	160.273973	35.138306	89.962270
Group 33 (Nonriver)						
Chief 1992	18	0.079000	0.144000	182.278481	34.660395	89.956799
Chief 1994	20	0.079000	0.122000	154.430380	29.945449	89.962547
Chief 1996	22	0.089000	0.145000	162.921348	32.005770	89.961720
Chief 1999	25	0.078000	0.114000	146.153846	28.399442	89.970171
Cindy 1992	7	0.066000	0.126000	190.909091	41.129159	89.961198
Cindy 1994	9	0.073000	0.122000	167.123288	38.089365	89.959881
Cindy 1996	11	0.075000	0.115000	153.333333	36.903670	89.965273
Cindy 1999	14	0.069000	0.095000	137.681159	31.208154	89.965416
Julio 1994	2	0.077000	0.144000	187.012987	41.169519	89.955664
Julio 1996	4	0.071000	0.115000	161.971831	38.171204	89.962631
Julio 1999	7	0.071000	0.114000	160.563380	33.246535	89.961554

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