Ungar, Peter and Williamson, Malcolm 2000. Exploring the Effects of Toothwear on Functional Morphology:
A Preliminary Study Using Dental Topographic Analysis. *Palaeontologia Electronica,* vol. 3, issue 1, art. 1: 18pp., 752KB.
http://palaeo-electronica.org/2000_1/ gorilla/issue1_00.htm

Submission: 19 November 1999, Acceptance: 7 February 2000

EXPLORING THE EFFECTS OF TOOTH WEAR ON FUNCTIONAL MORPHOLOGY: A PRELIMINARY STUDY USING DENTAL TOPOGRAPHIC ANALYSIS

Peter Ungar and Malcolm Williamson

ABSTRACT

Mammalian tooth form reflects the material properties of foods. Much research has focused on relationships between aspects of dental morphology and diet. Understanding these relationships allows us to infer feeding adaptations from the teeth of fossil forms. Most such studies have focused on unworn (rather than worn) teeth because these are easier to characterize and compare among species. Nevertheless, tooth shape changes with wear, and most fossil teeth are worn. How does wear affect functional efficiency? Can dental morphology of worn teeth be used to infer diets of fossil species? The study described here presents a new way to examine the shapes of worn teeth so that we may begin to answer these important questions.

Geographic information systems (GIS) were used to model teeth as topographic landscapes. A laser scanner generated a digital elevation model of the occlusal surface, and slope, angularity, surface area, relief, and modal aspect of each cusp, and other variables were quantified. Data on worn gorilla molars are given as an example. Although some aspects of morphology (e.g., surface area, occlusal relief) change with wear, others evidently do not. For example, cusp angularity showed no consistent change through the wear sequence, suggesting maintenance of some aspects of chewing efficiency. We conclude that this approach can be used to characterize and compare occlusal morphology in variably worn teeth. This will allow us to evaluate changes in chewing efficiency as teeth wear, a prerequisite to the inclusion of worn teeth in studies of mammalian dental functional anatomy.

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KEY WORDS: GIS, gorillas, morphometrics, teeth, functional anatomy

PLAIN LANGUAGE SUMMARY:

Tooth shape reflects diet in mammals because foods with different material properties require differently shaped teeth to break them down. For example, sharp blade-like teeth would better slice raw meat than would blunt, hammer-like teeth suited to crushing hard, brittle foods. Paleontologists have used relationships between tooth shape and diet in living mammals to infer feeding adaptations from the shapes of fossil mammal teeth. Most such studies have relied on unworn (rather than worn) teeth because it is easier measure functional aspects of their shape and to compare measurements among species. Still, tooth shape changes with wear, and most fossil teeth found are, in fact, worn. For an example of the investigation of tooth wear by more conventional means, and its use as a basis for inferring the diet of some Paleocene ungulates, see E.W. Dewar, 1997, Journal of Vertebrate Paleontology, vol.17A.

The study described here offers a new way to characterize and compare dental anatomy among variably worn teeth. This approach uses geographic information systems (GIS) to examine teeth as topographic landscapes, modeling their cusps and grooves as mountains and valleys. Slope, aspect, surface area, volume, and other measures can be measured and compared among specimens. This is demonstrated with a series of variably worn teeth from one species, the gorilla. Results show that some attributes, such as surface area and slope, decrease with more and more wear. Other attributes, such as angularity of the surface do not seem to change with tooth wear, suggesting the maintenance of some aspects of chewing efficiency. We conclude that dental topographic analysis will allow us to measure the ways that teeth change shape as they wear, permitting the evaluation of changes in chewing efficiency, and perhaps even the reconstruction the diets of fossil mammals using worn teeth.

Glossary:

Dental topographic analysis: a method for modeling the shapes of the biting surfaces of teeth as topographic surfaces for analysis using Geographic information systems technology.

Digitial elevation model: a set x,y,z data where x and y values represent points on a two-dimensional surface and z values indicate elevation.

Functional morphology: the study or relationships between the shape of a biological structure and how it functions.

Geographic information system (GIS) - a system for assembling, storing, manipulating, analyzing, and displaying geographically referenced information

INTRODUCTION

The fundamental fact that teeth wear has been the bane of dental functional anatomists for decades. Researchers have known for a very long time that tooth form reflects function in living mammals, and they have conducted very elegant studies to demonstrate relationships between aspects of occlusal morphology and diet within various mammalian orders. Most such studies have been limited to unworn and slightly worn teeth. The problem with this is that teeth change shape as they wear, and natural selection does not stop when this happens. So how can we infer function from worn teeth? Geographic information systems (GIS) provide one tool to address this issue. In this study, we demonstrate how GIS can be used to assess functional changes in tooth form among variably worn molars of one mammalian species, *Gorilla gorilla* (Savage and Wyman) 1847.

Tooth Shape and Diet

Most paleontologists who reconstruct fossil mammal diets use the comparative method (Anthony and Kay 1993). They look at relationships between diet and tooth size, shape, or wear in living species to infer diet from the dental remains of fossil forms. There has been a great deal of effort spent on uncovering these relationships. For example, Kay and Hiiemae (1974) associated specific dental morphologies in primates with shearing, crushing, and grinding. Food is sheared between the leading edges of crown crests. Shearing blades generally are reciprocally concave to minimize contact area. In contrast, food is crushed between planar surfaces on the teeth. Grinding involves both shearing and crushing components, where two smooth surfaces are occluded and moved across one another in the manner of a mortar and pestle. Different foods require different actions to break them down for further processing in the stomach.

Kay (1978, 1984) devised a method for measuring the shear potential of a tooth and found that the resultant value, the shearing quotient (SQ), accurately tracks diet in all extant higher-order primate taxa. First, the lengths of mesiodistally running crests connecting the main cusps of lower second molars are summed and regressed over tooth length (in $\log_{10}$ space) for a group of closely related frugivorous species. Frugivorous species alone are used to control for allometric changes in animals that have similar adaptations. The SQs are computed as deviations from the regression line. Thus, positive values indicate longer shearing crests and more occlusal relief than expected of a frugivore and negative values indicate shorter crests and less occlusal relief than expected. For all higher-order primate taxa, folivores and insectivores have higher SQ values than frugivores. Further, among fruit-eaters, those that specialize on hard foods have even lower SQs and blunter teeth than those that more often eat soft fruits (Anthony and Kay 1993; Kay and Covert 1984; Meldrum and Kay 1997). Such studies have served as baselines for paleobiological reconstruction and have provided important clues concerning the diets of fossil primates (e.g., Fleagle et al. 1996; Kay and Simons 1980; Strait 1991; Ungar and Kay 1996; Williams and Covert 1994).

GIS and Tooth Shape

SQ studies have not focused on worn teeth because of difficulties in comparing and measuring crests lengths for variably worn specimens. As a tooth wears, one would expect changing occlusal relief to affect shearing crest length. So how can we best characterize occlusal morphology in worn specimens? This raises one of the most important issues in dental functional anatomy today - how does tooth wear affect function? Because dental morphology affects the magnitude, direction, and rate of change of stress on food particles, tooth shape should reflect the mechanical properties of those foods eaten (Spears and Crompton 1996). How do changes in tooth shape that result from wear affect chewing efficiency? The first step in answering this important question is to develop a technique that can characterize various aspects of occlusal morphology in worn specimens.

Dental topographic analysis is one such technique (Zuccotti et al. 1998). This approach models occlusal surfaces as three-dimensional landscapes using GIS. GIS is an approach used to compare layers of different types of data connected by locations in geographic space. It is a system for assembling, storing, manipulating, analyzing, and displaying geographically referenced information. Many GIS tools have been created to examine and model the physical surface of the Earth. If teeth can be modeled as landscape surfaces, these tools can be applied to provide data on cusp surface area, volume, slope, aspect, and three-dimensional relief. Other functionally relevant aspects of morphology, such as the amount of fluid that could accumulate in a tooth's basin and the directions and intensity of drainage over the occlusal surface, can also be examined with GIS. Such measures may provide insights into food moisture content and other food properties. Walker (1968), for example, noted that pteropodid bats extract juice with low-cusped teeth surrounding a depressed central basin. Studies of occlusal topography are thus likely to be very helpful for reconstructing diets based on biomechanical models of tooth function.

Few researchers have thus far used a GIS approach to the study of tooth shape. Reed (1997) published an abstract describing one technique. He obtained three-dimensional coordinates of small primate teeth with a reflex microscope and interpolated smooth surfaces using Imagine (ERDAS, Inc.). Features were identified with the help of contour lines in ArcInfo (ESRI, Inc.) and relative proportions of area dedicated to cusps, crests, and basins were calculated. Reed suggested that differences in these proportions might reflect diet differences among primates.

Zuccotti et al. (1998) applied GIS techniques to the study of occlusal morphology in great apes. These authors used an electromagnetic digitizer to collect three-dimensional data from each occlusal surface. Resulting data were imported into GRASS (U.S. Army Construction Engineering Laboratory), and tooth surfaces were interpolated using a thin-plate splining model. Cusps were isolated using the lowest elevation contour lines that fully surrounded those cusps, and slope and volume were calculated for each. Drainage patterns and overflow area were also calculated for each tooth (see Materials and Methods section).

Jernvall and Selänne (1999) suggested an alternative approach for smaller teeth (<10 mm in diameter) using a laser confocal microscope. These authors acquired a series of cross-section pictures of the occlusal surfaces of teeth and stacked them together to provide a three-dimensional model of the tooth's surface. Digital elevation models were constructed from the image stacks using the 3D-view version of NIH-Image (U.S. National Institutes of Health), and imported into GIS software (MapFactory, Thinkspace Inc.). Jernvall and Selänne (1999) then demonstrated that various new measurements can be taken. For example, they used the areas of longitudinal and transverse slopes to determine cusp elongation to identify subtle differences in selenodonty in hedgehogs.

As with shearing quotient studies, GIS approaches have thus far focused attention on unworn teeth. The study described here evaluates the potential of dental topographic analysis to document and analyze functionally relevant aspects of occlusal morphology in variably worn teeth of *G. gorilla.* This study presents a first step toward assessing the functional effects of tooth wear and perhaps even allowing the inclusion of worn teeth in functional analyses that consider occlusal relief in three dimensions. We reconstructed a wear sequence for lower second molars of gorillas using variably worn teeth by scaling and aligning these teeth in an identical manner. We then quantified functionally relevant aspects of morphology for comparison. Results demonstrate the potential of this approach for providing a model of changes in tooth shape with wear. Wear sequence models may be compared among taxa and analyzed for their relevance to tooth function.

MATERIALS AND METHODS

This study examined molar teeth of gorillas, *G. gorilla,* housed at the Field Museum of Natural History in Chicago, Illinois, USA. This taxon was chosen because of the large body of work focused on primate dental functional anatomy and because gorilla teeth evince substantial visible morphological change with wear. Kay (1981) has speculated that high cusps and thin tooth enamel in primate folivores, such as the gorilla, would lead to sharp edges at the sites of dentine exposure, which would improve shredding and slicing abilities of the tooth with wear. Methods described here were designed to examine such aspects of the morphology of worn teeth.

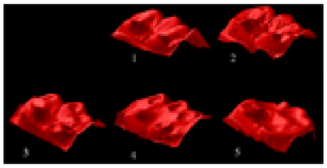

Figure 1.

Five variably worn lower second molars were selected to include a range of wear from unworn to extremely worn (Figure 1). High-resolution replicas were prepared as follows. First, dental impressions were taken using a polyvinylsiloxane putty (President's Jet, Coltene, Inc.). Molds were allowed to harden, and casts were prepared using Epotek 301 resin and hardener (Epoxy Technologies, Inc.). This procedure has been demonstrated to produce casts with resolutions to less than one micron (Beynon 1987; Ungar 1996), more than sufficient for detailed analyses of the occlusal surfaces. Tooth replicas were then coated with a thin layer of Magniflux Spotcheck SD-S2 Developer (Illinois Toolworks, Inc.) to mitigate cast translucency.

Data Collection and Preparation

Data collection and preparation for analysis involved several steps. First, three-dimensional point data representing the occlusal surface of each tooth were collected. Data points for individual teeth were then aligned and scaled and imported into the GRASS 4.1 (U.S. Army Construction Engineering Laboratory) GIS package as a digital elevation model (DEM). Each DEM was then regridded and cropped for analysis.

We collected point data using a modified Surveyor 500 laser scanner with an RPS 450 laser (Laser Design, Inc.) (Figure 2). The scanner has a maximum resolution of 0.0254 mm in x, y, and z dimensions and a maximum work envelope of 152.4 mm × 152.4 mm × 304.8 mm. The laser can scan the occlusal table of a gorilla molar and record hundreds of thousands of data points representing that surface in just a few minutes. In this study, we created a DEM from points sampled at an interval of 0.0508 mm. This resolution preserves subtle aspects of occlusal morphology, yet limits data files to an easily manageable size.

Figure 2.

This approach to data collection differs from those described by other authors. Reed (1997) suggested using a reflex microscope (Reflex Measurement Ltd.) to collect coordinate data for teeth. The reflex microscope is, however, an impractical tool for dental topographic analysis. It requires the researcher to identify each individual point on a tooth's surface, an extremely tedious and time-consuming endeavor when hundreds if not hundreds of thousands of points are needed to adequately characterize a tooth's surface. In another study, Zuccotti et al. (1998) suggested that a 3Draw Pro (Polhemus Corp.) electromagnetic digitizer might be used to collect such data. In that case, a stylus is passed over the occlusal surface, and points are collected at a rate of 70 per minute. This procedure is impractical for smaller mammalian teeth (including most primates) because the resolution of this digitizer is only 0.13 mm. The MicroScribe-3D (Immersion Corp.) would have a similar limitation, with a published accuracy of 0.38 mm (0.23 mm for the 3DX model). Finally, Jernvall and Selänne (1999) suggested the use of a confocal microscope. These authors used a Zeiss Axiovert 135M microscope with the BioRad MRC-1024 confocal system and an American Laser Corporation 60WL argon/krypton laser . This approach is very effective for digitizing small teeth, but is currently of limited use in dental topographic analyses because the maximal working envelope for the system described by Jernvall and Selänne restricts tooth sizes to less than 10 mm in diameter, somewhat smaller than many mammal teeth. The laser scanner presents a good compromise between work envelope and resolution because it is capable of collecting data for all but the smallest mammal teeth. (We have resolved occlusal morphology on bat teeth less than 1 mm in diameter.) Laser scanning can quickly generate a large dataset of points representing the occlusal surfaces of most mammalian molar teeth.

Figure 3.

Once data were collected, individual DEMs had to be aligned and scaled so that measurements would be consistent among specimens. This was accomplished using three points: the lowest points on the anterior and posterior foveae and the junction between crests connecting the metaconid and entoconid (Figure 3). These landmarks were chosen because they are the lowest points consistently identifiable on the occlusal surface, thereby allowing inclusion of the most worn teeth in this study. Data Sculpt software (Laser Design, Inc.) was used to align these three points to the x-y plane, with the x-axis passing through the two foveae. Each tooth was then scaled to the mean distance separating pairs of landmarks on that tooth. The aligned and scaled DEMs were exported in ASCII data files as x, y, z data points to the GRASS 4.1 (U.S. Army Construction Engineering Laboratory) GIS software package.

Because rotational alignment of data results in an irregular matrix, inverse-distance weighting was used to re-grid the coordinates to a regularly spaced surface model. In order to further assure the comparability of specimens, each DEM was cropped to the horizontal plane intersecting the lowest point on the occlusal surface. This also eliminated the problem of surface overhang (more than one z-value for an x-y pair), such as often occurs down the buccal and lingual sides of the tooth as the enamel cap approaches the cervix. Individual cusps were delineated on the basis of contour lines (isometric lines connecting points of identical elevation). The areas defined by individual cusps were used as masks to filter out data from other parts of the tooth. This allowed separate consideration of data for each cusp.

Once the DEM was aligned, scaled, and cropped, we used standard GIS algorithms to compute descriptive statistics for each cusp. These included average slope, average delta slope (the second derivative of elevation), topographic aspect or surface orientation (in thirty-degree increments), surface area, and a relief index. The relief index is a ratio of three-dimensional surface area to two-dimensional (x, y) surface area. We also calculated the volume of fluid required to "fill" the central basin of each tooth to the point that it would overflow. This is a useful and repeatable measure of basin volume that reflects the morphology of the tooth.

RESULTS

Results of this study are presented in Figures 4, 5, 6, 7, and 8 and Tables 1, 2, 3, 4, 5, and 6. These illustrate changes in some aspects of occlusal morphology with wear and identify other attributes that may not change in a consistent manner as a tooth wears. These results use teeth of different specimens to create a model of an occlusal wear sequence for the taxon. Although the scaling, alignment, and cropping procedures described above minimize differences between specimens, we must remember that individual variation can still complicate wear sequence patterns (see Discussion). Each attribute can be considered individually.

Slope

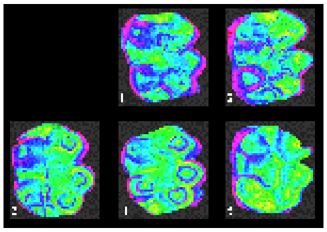

Figure 4.

Slope is one measure of topographic relief of the occlusal surface. Although one might expect to observe a consistent decrease in mean slope as cusps become more worn, this pattern is obscured by dentin exposure, and resulting steeply walled pits (Figure 4; Table 1). There is a general decrease in slopes for all cusps between the first and the fifth wear stages. Further, four of five cusps show decreasing slope values between stages 1 and 2 and between stages 4 and 5. On the other hand, only three cusps show decreasing values between stages 2 and 3, and two show decreasing values between wear stages 3 and 4.

Delta Slope

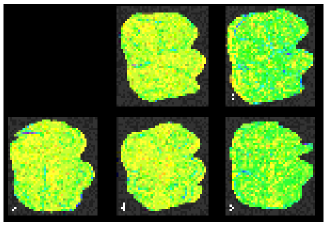

Figure 5.

The rate of change of slope is an indicator of the angularity of a surface, with high numbers representing sharper edges. There is no pattern of increasing or decreasing change in slope between adjacent wear stages (Figure 5; Table 2). There is also no pattern evident between the least and the most worn specimens. Therefore, there is no consistent change in the angularity of the surface for each cusp. This may be related to enamel penetrance and steeply angled dentin island walls for each of the cusps, although more work needs to be done to confirm this relationship.

Surface Area

Surface area of the cusps is calculated using the two-dimensional x-y area and slope data. We would predict a general decrease in surface area as slope decreases and tooth surface is worn away. Results indicated that patterns for the buccal cusps (the protoconid, hypoconid and hypoconulid) and lingual cusps (the metaconid and entoconid) differ (Figure 6; Table 3). As expected, the surface areas of the buccal cusps show a general decrease through the wear sequence, with the lowest values seen at wear stage 5. On the other hand, there is no such pattern for the lingual cusps. This may reflect the fact that, in these primates, buccal cusps of lower molars wear much more rapidly than do lingual cusps. In fact, lingual shearing crests on gorilla lower molars can preserve much of their length well after the buccal cusp morphology has begun to wear away.

Relief Index

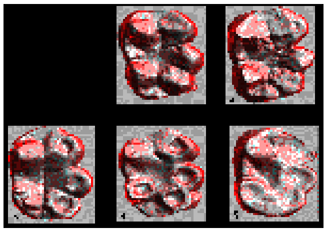

Figure 6.

We developed a relief index to provide a more direct measure of occlusal relief than could be obtained by examining surface area alone. This is a ratio of the three-dimensional surface area to the two-dimensional x-y area. The greater the occlusal relief, the higher the relief index. As expected, all five cusps show a trend toward decreasing relief from stage 1 through stage 5 (Figure 6; Table 4), although there is some variability. Also as expected, the decrease in relief is greatest on the buccal side of the crown.

Topographic Aspect

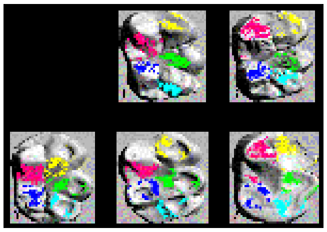

Figure 7.

The measurement of aspect offers intriguing possibilities for observing functional changes of cusps though the wear sequence. It may be possible to assess changes in occlusal relationships between upper and lower teeth by observing variation in modal aspect (Table 5). The colors in Figure 7 relate to modal aspect increment for each cusp, not to particular aspect direction. Perhaps the most obvious change in these data is on the buccal cusps between the fourth and fifth stages, where the prevailing aspect switches by 180 degrees! This may indicate a decreased effectiveness of the tooth as a guide for chewing motions (Kay and Hiiemae 1974). Still, a combined study of maxillary and mandibular dentitions will be necessary to evaluate the potential of this approach.

Basin Volume

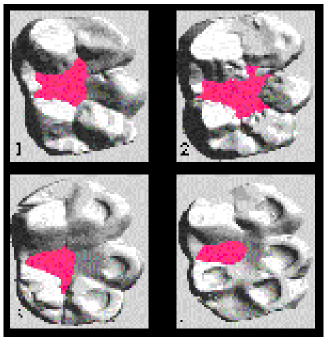

Figure 8.

The last variable to consider is central basin volume. We expected that as a tooth wears, the basin volume would increase gradually because the worn cusps should allow more fluid to accumulate before flowing off the molar. Instead, we saw an increase in volume between stage 1 and stage 2, followed a sharp decrease through stages three and four (Figure 8; Table 6). Due to the extreme wear seen in stage 5, the basin actually flowed right over the buccal cusps, preventing useful measurement.

DISCUSSION

This study demonstrates that dental topographic analysis can be used to document morphological differences between variably worn teeth. We expect that natural selection continues to act on individuals as their teeth wear and therefore should select for a morphology that will maintain chewing efficiency throughout the life of the tooth. Characteristics such as cusp slope, aspect, surface area, relief, and basin volume can be quantified using GIS algorithms. These may be of interest in assessing functional changes in chewing efficiency as teeth wear. Still, this list is certainly not exhaustive, and techniques described here may allow measurement of many other relevant attributes, such as the area of a polygon connecting the tips of the cusps, or the difference between the actual volume of the tooth and the “cylindrical” volume (measured as the product of tooth area in the x-y plane and height of the tallest cusp).

The delta slope results, although preliminary, are particularly intriguing. There is no apparent change in angularity of gorilla tooth surface from less to more worn specimens. This evidently reflects the steep walls of the occlusal pits that form as enamel gives way to softer dentin as the tooth wears. Such a phenomenon may be comparable to that seen in herbivorous ungulates that have complex infoldings and lophs designed to form sharp edges with dentin exposure for shearing and grinding tough foods. If so, it might provide evidence that thin tooth enamel in primate folivores, such as the gorilla, would lead to sharp edges at the sites of dentin exposure to improve shredding and slicing abilities of the tooth with wear (Kay 1981). Clearly, however, a comprehensive study of large numbers of individuals representing various folivorous taxa is needed to adequately test this hypothesis. Studies of food particle size in gut and fecal samples of younger and older individuals will provide an independent test of changes in chewing efficiency (e.g., Perez-Barberia and Gordon 1998).

This paper set out to demonstrate the potential of GIS to examine morphological changes in variably worn mammal teeth. The next phase of this research will involved a series of repeatability tests, followed by a temporal study of individual tooth wear. A temporal study will give us an idea of variation within species in tooth wear sequences, a necessary step if we are to use variably worn teeth of different individuals to construct a species-specific wear sequence. On the other hand, we are limited to variably worn teeth of different individuals in the fossil record, so such studies of extant groups will be needed to form an adequate baseline for comparison with extinct taxa.

ACKNOWLEDGMENTS

We thank Lucy Flynn Zuccotti for collecting molds of the gorilla teeth and Dr. William Stanley for permission to study collections at the Field Museum of Natural History in Chicago. This paper was much improved with the help of comments by three anonymous reviewers. Computer systems were provided by Intergraph Corporation and SUN Microsystems, and the Surveyor 500 laser scanner was purchased with funds granted by the University of Arkansas. This project was supported in part by U.S. National Science Foundation grant SBR 9804882.

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Figure 1. Specimens used in this analysis. Digital elevation models as they appear in Datasculpt (LaserDesign Inc) before export to a GIS package. Specimens show increasing wear from stages 1 though 5.

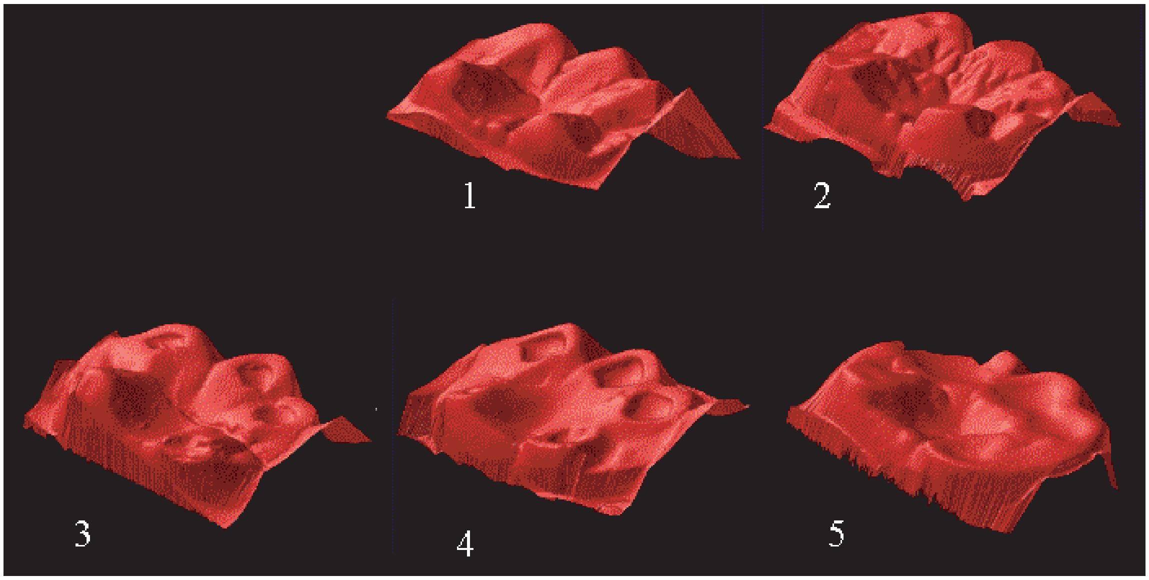
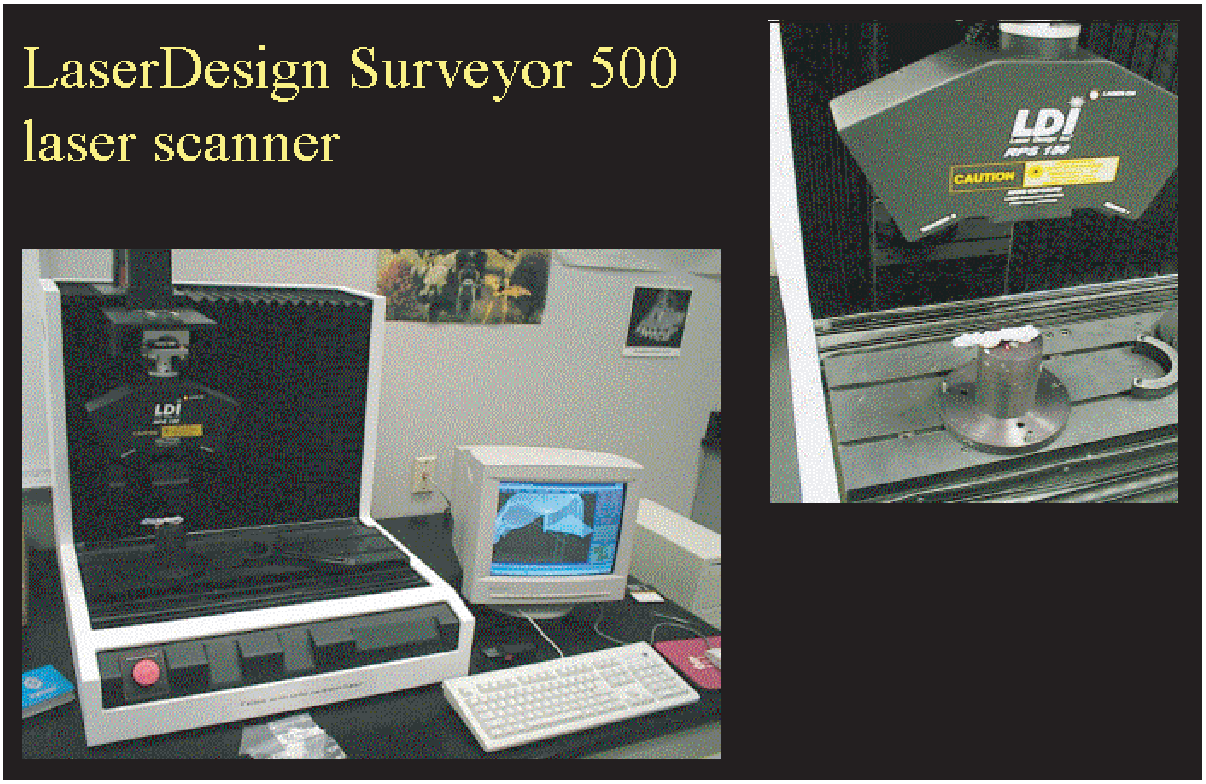


Figure 2. Laser scanner used in this study.



LaserDesign Surveyor 500
laser scanner

Figure 3. Data points used to scale and orient specimens. A = anterior fovea; B = posterior fovea; C = intersection of crests adjacent to the metaconid and entoconid. Individual cusps are labeled.

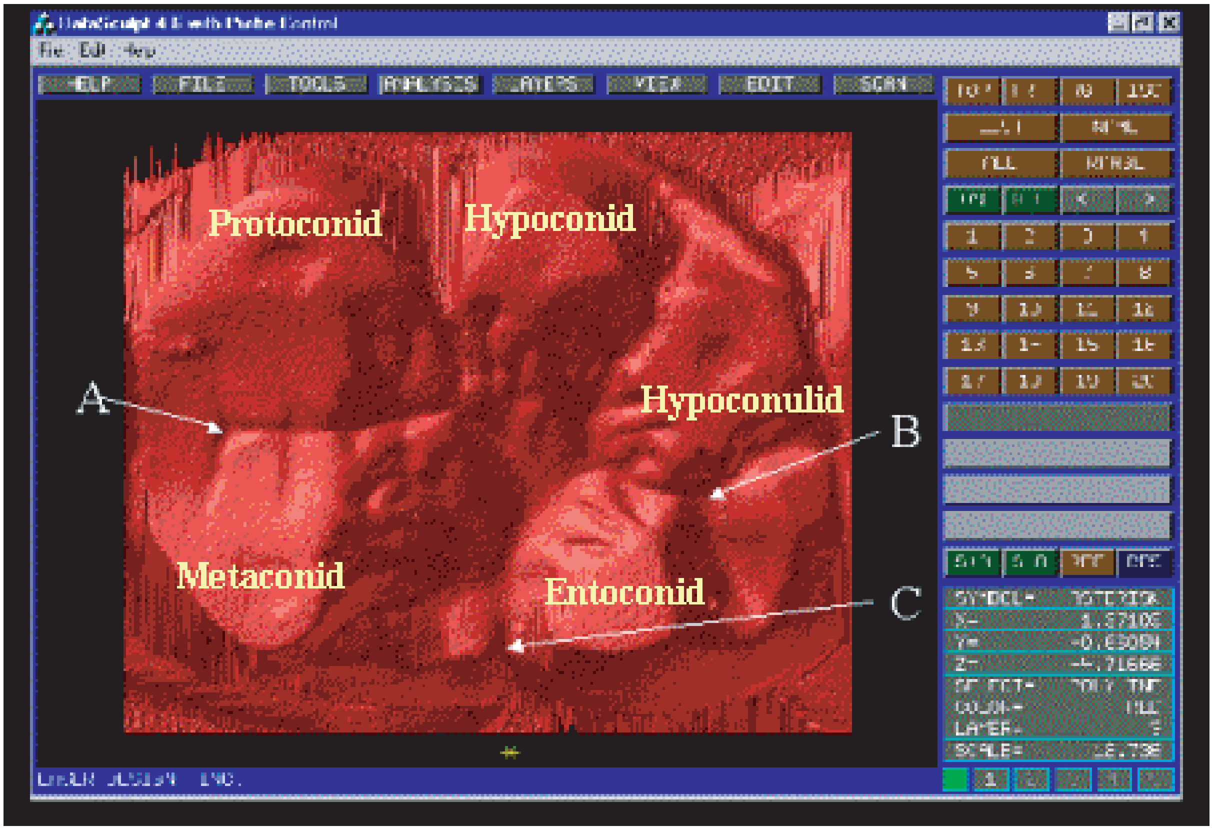


Figure 4. Slope data for specimens representing each wear stage. Higher frequency colors represent steeper slopes. Higher frequency colors (i.e., violet, blue) represent higher values than do lower frequency colors (i.e., yellow, green).

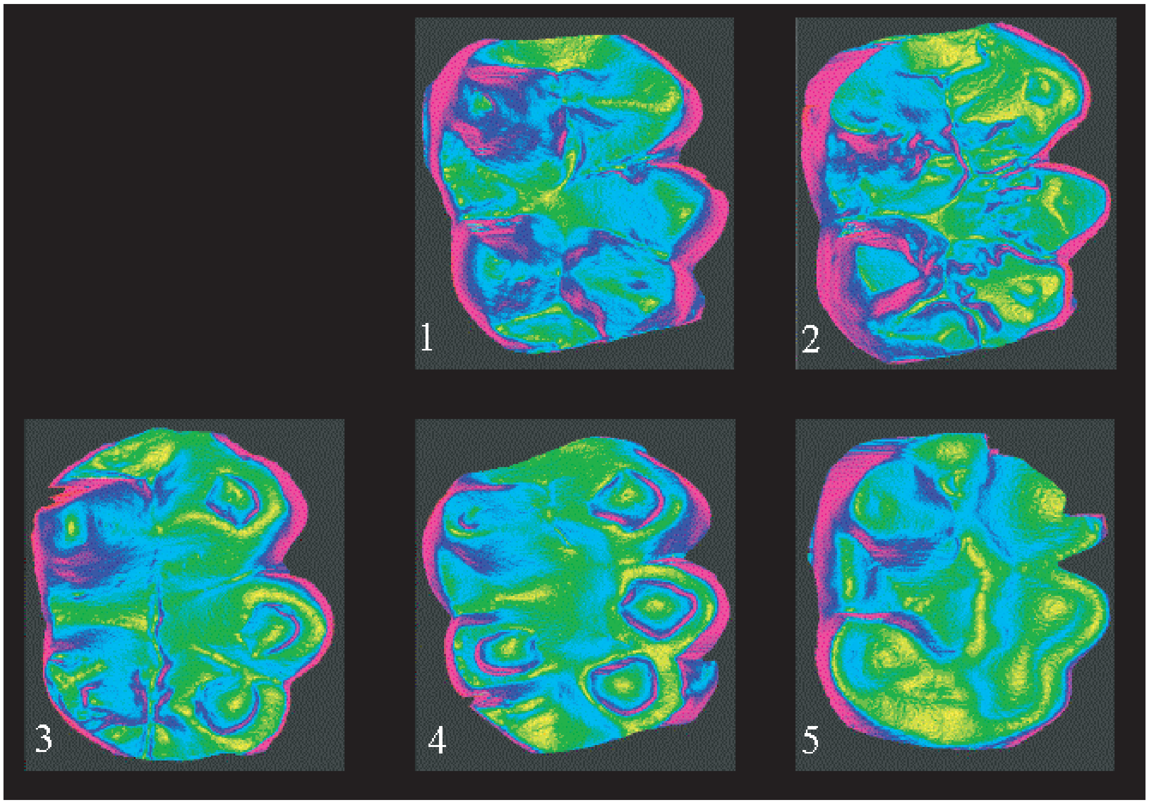


Figure 5. Delta slope data for specimens representing each wear stage. Higher frequency colors represent steeper slopes. The lack of great contrast reflects minimal differences in values. Higher frequency colors (i.e., violet, blue) represent higher values than do lower frequency colors (i.e., yellow, green).

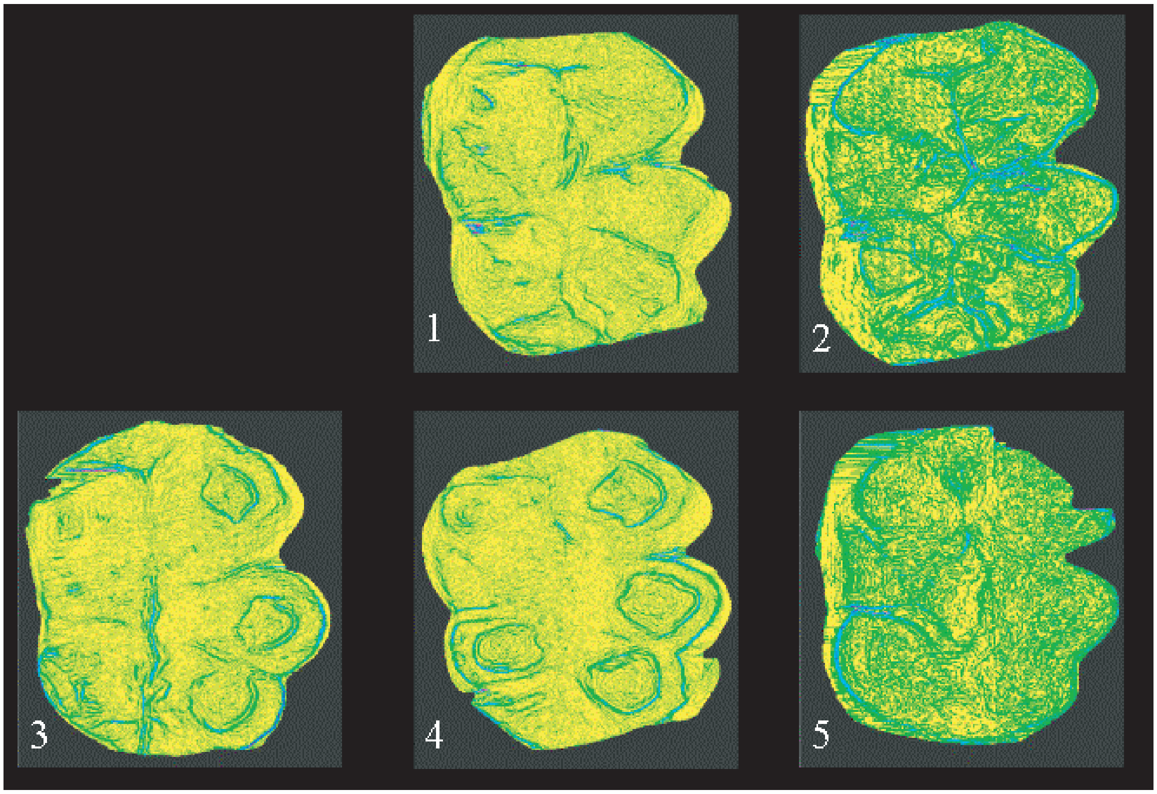


Figure 6. Shaded relief images with contour lines (in red) representing each wear stage.

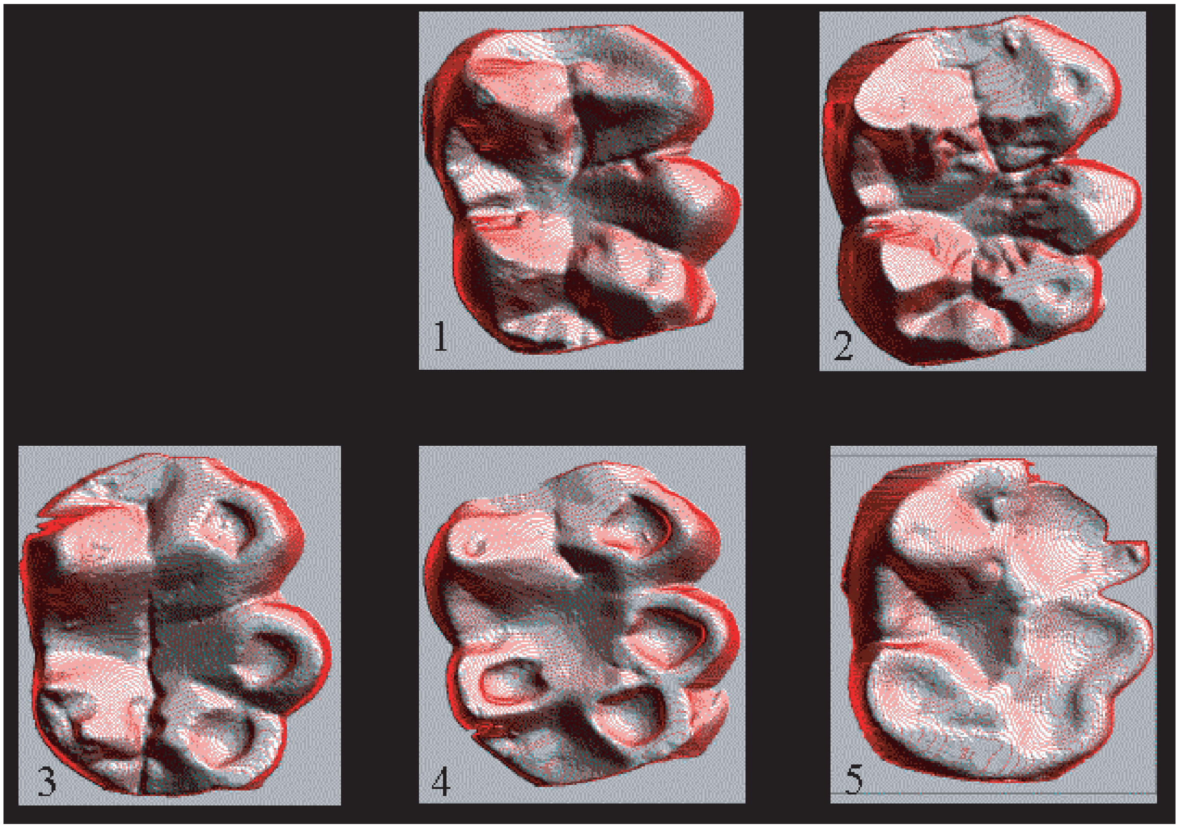


Figure 7. Aspect data for specimens representing each wear stage. The various colors show locations of modal aspect for each cusp. Note that different colors are used to represent modal aspect values for different cusps.

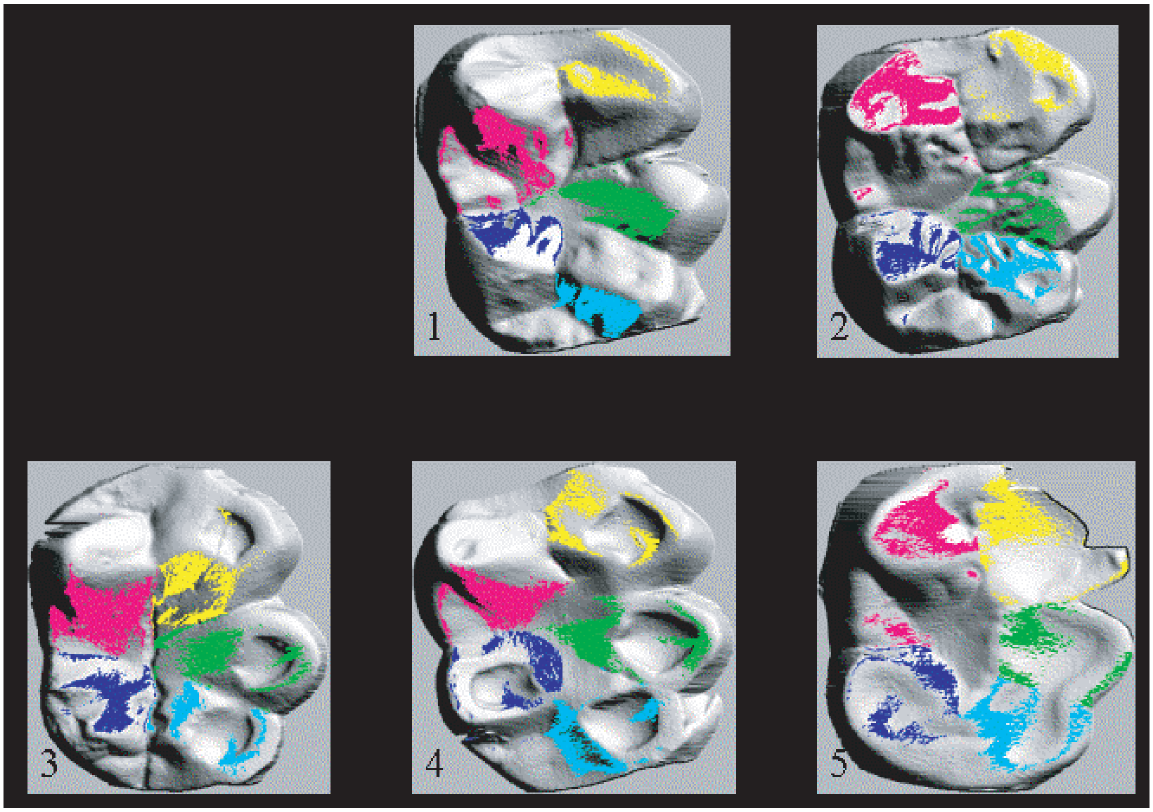


Figure 8. Central basin volume. The areas denoted in red represents the maximum volume of fluid that would be retained in each basin.

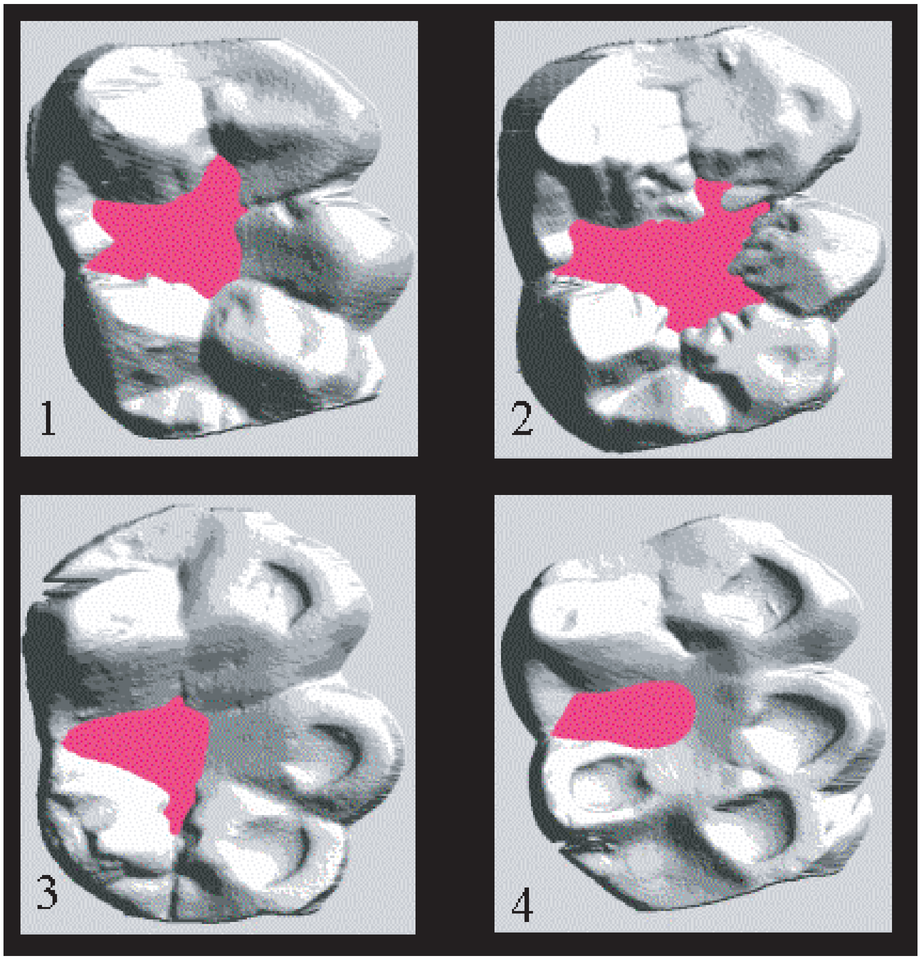


Table 1. Average slope of each cusp.

Wear	Protoconid	Hypoconid	Hypoconulid	Entoconid	Metaconid
1	36.06	40.86	44.36	48.84	45.86
2	27.04	32.82	33.41	51.01	43.99
3	32.88	30.86	29.82	39.35	44.61
4	33.71	33.30	33.15	36.85	38.59
5	28.41	22.72	24.31	32.76	43.13

Table 2. Delta slope for each cusp.

Wear	Protoconid	Hypoconid	Hypoconulid	Entoconid	Metaconid
1	1.85	1.69	1.79	1.80	1.80
2	1.95	1.95	2.02	1.75	1.79
3	1.76	1.92	2.02	2.00	1.76
4	1.78	1.85	1.83	2.02	1.64
5	1.71	1.70	1.69	1.86	1.72

Table 3. Surface area (scaled units) for each cusp.

Wear	Protoconid	Hypoconid	Hypoconulid	Entoconid	Metaconid
1	23.86	23.33	21.86	22.60	39.89
2	24.71	21.00	18.54	29.64	47.25
3	28.03	21.97	16.55	18.65	35.43
4	29.32	26.95	23.84	23.34	30.28
5	18.70	16.69	14.34	22.68	39.90

Table 4. Relief index for each cusp.

Wear	Protoconid	Hypoconid	Hypoconulid	Entoconid	Metaconid
1	1.53	1.66	1.61	1.81	1.73
2	1.33	1.45	1.48	1.81	1.64
3	1.40	1.48	1.34	1.57	1.92
4	1.40	1.47	1.33	1.57	1.47
5	1.21	1.11	1.17	1.55	1.58

Table 5. Modal aspect (30 degree cells) for each cusp.

Wear	Protoconid	Hypoconulid	Hypoconid	Entoconid	Metaconid
1	181-210	271-300	301-330	151-180	1-30
2	151-180	271-300	181-210	121-150	121-150
3	331-360	271-300	181-210	121-150	1-30
4	211-240	241-270	271-300	181-210	1-30
5	61-90	61-90	91-120	121-150	91-120

Table 6. Basin volume.

Wear	Raw volume	Scaled volume
1	573.81	166.76
2	836.71	206.55
3	306.66	90.72
4	287.52	71.48
5	(basin undefined)	