Looking at teeth in a new light

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Teeth are the most common elements in the mammalian fossil record. Thus it is not surprising that they have yielded many insights into the lives of extinct creatures. When researchers in the 1970s noted that subtle differences in molar tooth shape could be correlated with significant dietary differences (1–7), it opened the door for a vast array of "functional analyses" of teeth in which various measurements of tooth shape were statistically compared between modern and prehistoric species (8–11). Yet there was one underlying limitation to all of that work: it was ultimately based on landmark-based, point-to-point measurements of unworn teeth. Because teeth begin to wear down as soon as they are used, most fossil teeth were unavailable for functional analyses. In essence, as wear progressed, the reference points for the measurements in question changed dramatically, making accurate measurements difficult, if not impossible (Fig. 1). This issue of PNAS contains a report by Ungar and M'Kirera (12) that changes that in dramatic fashion, bringing tooth measurements into the 21st century.

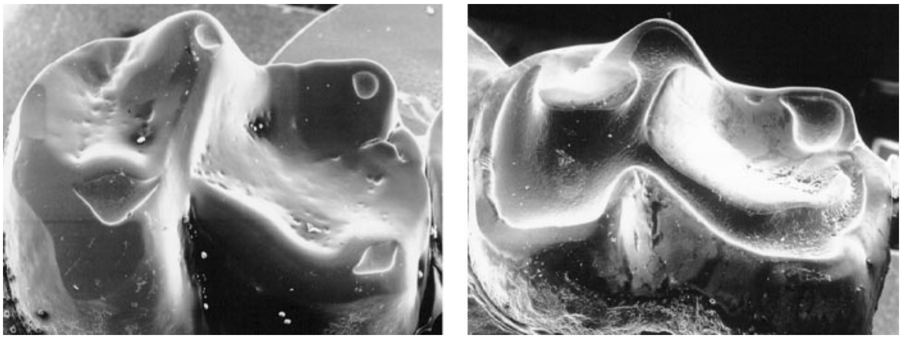

Fig. 1. Nine years of wear on a mandibular molar from a Costa Rican howling monkey (*Alouatta palliata*). (*Left*) Baseline, July 1989. (*Right*) Follow-up, July 1998.

Researchers have long been able to create 3D coordinate models of teeth (13–15). But, as in all such enterprises, the main problem has been what to do with the resultant 3D information. It makes pretty pictures, but how does it contribute to statistical comparisons of data samples? Ungar and M'Kirera (12) take a major step forward by using geographic information systems technology to analyze high-resolution coordinate data generated by a laser scanner. In the process, they have changed tooth analyses forever.

Until now, analyses of tooth shape have relied on simple length measurements (2, 3), occasionally combined into rather crude angular measurements (16) or measures of areas (17, 18). Ungar and M'Kirera (12) make a change of course by advocating the use of summary measurements for entire tooth surfaces, measurements such as the average slope and angularity of the surface. Rather than using 3D coordinates to merely compute more and more complicated versions of the same measurements, they use a new approach, emphasizing summary characterizations of surfaces, not point-to-point linear measurements. These measures are appropriate for worn tooth surfaces, because they do not require the identification of homologous points. All they require is a tooth surface.

This is not to imply that functional studies of tooth wear have never been attempted. For >100 years, investigators have been aware of differences in tooth wear between taxa (19–21). However, until now, most investigators have relied either on qualitative assessments or rather crude measures of wear to compare rates and patterns of tooth wear between species. The qualitative assessments have yielded some classic insights into the evolution of chewing and diet in many species. For instance, the molars of many herbivores have been shown to develop alternating enamel and dentin bands as tooth wear progresses, which are quite useful in the cutting and slicing of tough foods (22–24). The differential wear of enamel and dentin has even allowed insights into the direction of chewing movements, including prenatal chewing movements in guinea pigs (25, 26). In other animals, such as primates, the presence of different types of molar wear facets on less-worn teeth has also been used to monitor the evolution of chewing (27–29). Still, these qualitative assessments have their limitations in that they are only able to document the most obvious differences, not the more subtle ones that might be discernible through statistical analyses.

Most attempts at quantification have focused on the rates of tooth wear, either in controlled laboratory settings (30–32) or analyses of museum samples of many individuals of different ages (33–35). The former have had the advantage of strict control over the diets of animals of known ages. However, the broader implications of such studies for analyses of fossils are limited by (*i*) the artificial nature of the diets in question and (*ii*) the fact that longitudinal data samples are simply unattainable for fossils. Analyses of museum samples, by contrast, face many of the same problems found in analyses of fossils. But interpretations are complicated by the lack of control over crucial variables like diet. In essence, investigators must assume that individuals within the "populations" represented by museum samples had roughly similar diets, although there is usually no way to know for sure.

The net effect of previous work has been to leave us with glimpses of the diets and chewing movements of prehistoric creatures, but not much else. In fact, investigators have generally steered clear of a crucial question about the evolution of teeth and diet: if tooth shape is indeed important for the processing of foods, then as tooth wear progresses, does tooth shape reach a point of diminishing usefulness or is dental function somehow maintained despite wear? Work on herbivores suggests that dental function might be maintained, at least to certain ages (36, 37). However, studies that have attempted to answer this question are few and far between, largely because of the aforementioned difficulties in measuring worn teeth. Ungar and M'Kirera (12) have now circumvented that problem by changing how teeth are analyzed. In the process, they have shown that tooth wear does not

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change the functional differences between the teeth of our closest living relatives, chimpanzees and gorillas. This finding has profound implications for studies of dental morphology and paleobiology, because it implies that dental function is somehow maintained despite tooth wear. Moreover, the geographic information systems analyses will allow researchers to tap into tremendous reserves of modern and fossil specimens already collected and catalogued in museums. The number of new research questions raised by that article will be immense!

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