

## 4. Dental microwear and Paleoanthropology: Cautions and possibilities

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### Abstract

Fifty years ago, investigators realized they could gain insights into jaw movement and tooth-use through light-microscope analyses of wear patterns on teeth. Since then, numerous analyses of modern and fossil material have yielded insights into the evolution of tooth use and diet in a wide variety of animals. However, analyses of fossils and archeological material are ultimately dependent on data from three sources, museum samples of modern animals, living animals (in the wild or in the lab), and *in vitro* studies of microwear formation. These analyses are not without their problems. Thus, we are only *beginning* to get a clearer picture of the dental microwear of the early hominins. Initial work suggested qualitative differences in dental microwear between early hominids, but it wasn't until Grine's analyses of the South African australopithecines that we began to see quantitative, statistical evidence of such differences. Recent analyses have (1) reaffirmed earlier suggestions that *Australopithecus afarensis* shows microwear patterns indistinguishable from those of the modern gorilla, and (2) shown that the earliest members of our genus may also be distinguishable from each other on the basis of their molar microwear patterns. While this work hints at the possibilities of moving beyond standard evolutionary-morphological inferences, into inferences of actual differences in tooth use, we still know far too little about the causes of specific microwear patterns, and we know surprisingly little about variations in dental microwear patterns (e.g., between sexes, populations, and species). In the face of such challenges, SEM-analyses may be reaching the limits of their usefulness. Thus, two methods are beginning to catch attention as possible "next steps" in the evolution of dental microwear analyses. One technique involves a return to lower magnification analyses, using qualitative assessments of microwear patterns viewed under a light microscope. The advantages of these analyses are that they are cheap and fast, and may easily distinguish animals with extremely different diets. The disadvantages are that they are still subjective and may not be able to detect subtle dietary differences or artifacts on tooth surfaces. Another technique involves the use of scale-sensitive fractal analyses of data from a confocal microscope. Advantages include the ability to quickly and objectively characterize wear surfaces in 3D over entire wear facets. The main disadvantage lies in the newness of the technique and challenges imposed by developing such cutting edge technology. With the development of new approaches, we may be able to take dental microwear analyses to a new level of inference.

## Introduction

Paleoanthropologists are, in many ways, like forensic scientists who travel through time. They must use any available clues to help decipher what went on, eons ago; and only by considering the total range of evidence can they begin to appreciate the limits of what can be said about past behaviors. Unfortunately, much of the evidence available to paleoanthropologists is not *direct* evidence, in the sense of something visible on a bone or tooth, caused directly by something that happened during the individual's lifetime. For instance, the relative size of certain bones may or may not be indicative of what an animal actually did, as the animal may have, for example, relatively long hindlimbs simply because its ancestors had relatively long hindlimbs. So, when looking through the evidence, paleoanthropologists are constantly forced to evaluate their data, to see what they can, and cannot, say about the hypotheses being tested.

The most common elements in the human fossil record are teeth – largely because they are the most resilient structures in the body. For the most part, they are made of inorganic materials, and they tend to remain intact well after death. Thus, it is perhaps no surprise they have provided many clues about the paleobiology of our ancestors. For instance, analyses of tooth shape have shown that species adapted to eat tough, elastic foods generally have longer molar shearing crests than do species adapted to eat hard and brittle foods (Kay, 1975; Kay and Hylander, 1978; Lucas, 1979, 2004). However, most of these studies have focused on analyses of unworn teeth (see Ungar, 2004, 2007 for a revolutionary new perspective on this topic). Yet, like death and taxes, tooth wear is one of life's inevitabilities. As soon as a tooth reaches occlusion, it begins to wear down. In some cases, such as in guinea pigs, wear even begins *in utero* (Ainamo, 1971; Teaford and Walker, 1983). Its first steps are imperceptible to the

naked eye – microscopic scratches and pits nicking the surface. But those microscopic effects add up, leading to the formation of wear facets on the teeth, and eventually dentin exposure, as the overlying enamel is worn away. So, while the shape of unworn teeth can tell us a great deal about what a tooth is *capable* of processing, tooth *wear* can give us insights into how a tooth was actually used. This paper will focus on the evidence provided by microscopic wear patterns on the chewing surfaces of teeth – what is often referred to as dental microwear analyses. This is different from most other analyses of fossils, because it is *direct* evidence of past behavior – ultimately based on microscopic wear caused by food or abrasives on food during an animal's lifetime. As a result, this technique has the potential to yield information about prehistoric diet and tooth use at a unique level of resolution.

### *Postmortem Wear*

One of the first questions that springs to mind in contemplating dental microwear analyses of fossils is: if a tooth has been lying in the ground for thousands or millions of years, how do we know that the wear on it was really caused during the animal's lifetime? Actually, it is surprisingly easy (Teaford, 1988b), because the wear patterns caused during chewing are laid down in regular patterns at specific locations on teeth (see Figure 1a). By contrast, when a tooth is buried in the ground it is subjected to wear at innumerable, unusual locations and angles (see Figure 1b) (Puech et al., 1985; Teaford, 1988b; King et al., 1999b). This so-called postmortem wear is certainly a problem when analyzing fossils – but generally not because we cannot recognize it. Instead, it is a problem because we *can* recognize it, and have to eliminate many specimens from our analyses.

Obviously, the degree of postmortem wear can be a function of many factors, such as the length of time a specimen has been exposed

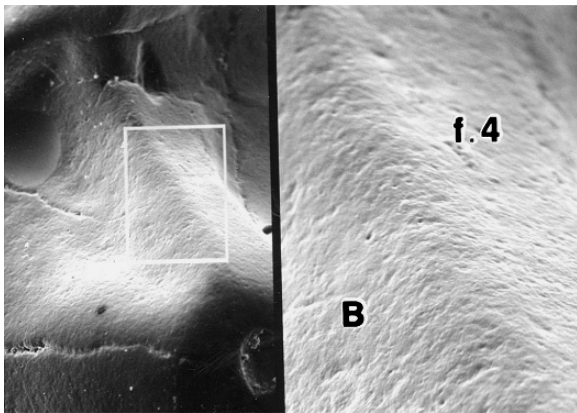
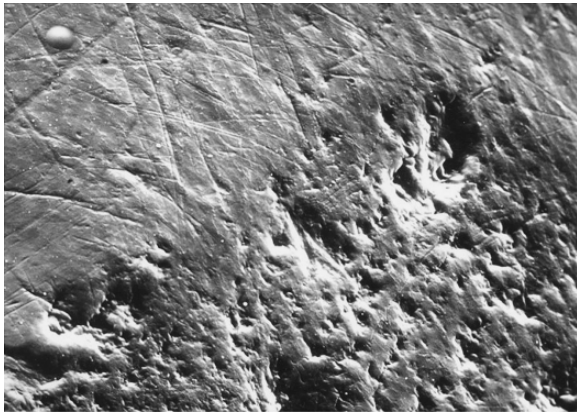


Figure 1. a. SEM micrograph of occlusal and nonocclusal surfaces of a molar of *Cebus apella* (from Teaford, 1988b). The boundary between surfaces curves diagonally across the image so that the lightly scratched nonocclusal surface is in the top third of the micrograph. b. Postmortem abrasive wear on 50 million year old *Cantius* molar (from Teaford, 1988b). B = buccal side of metacone, and f.4 = facet 4 on mesial occlusal aspect of metacone. Thus the boundary between occlusal and nonocclusal surfaces passes diagonally from the top left to the bottom right of the higher magnification image on the right. Identical pitting on both surfaces indicates that both have been subjected to postmortem wear.

to the elements; the presence of destructive acids in the postdepositional environment; whether or not the tooth was excavated or collected on the surface; how it was prepared in cleaning; the types of preservative applied to its surface, etc. As a result, the proportion of

fossil specimens useful for dental microwear analyses may vary dramatically from site-to-site – e.g., less than 25% at Koobi Fora, or more than 60% at Olduvai (personal observations).

### Brief History of Dental Microwear Analyses

Assuming we can recognize the effects of postmortem wear, how has dental microwear traditionally been analyzed? Initial analyses were qualitative in nature and based on light microscope assessments of tooth surfaces. For instance, Butler and Mills (Butler, 1952; Mills, 1955, 1963) noticed characteristic orientations of scratches on the teeth of different mammals, providing the initial evidence for two “phases” of jaw movement in primates. Similarly, Dahlberg and Kinzey (1962) noted the possibility of documenting differences in diet based on (among other things) differences in the amount of microscopic scratching on teeth. Subsequent work by a number of people rekindled interest in the topic (Walker, 1976; Puech, 1977; Rensberger, 1978; Walker et al., 1978; Puech and Prone, 1979; Ryan, 1979; Puech et al., 1980; Walker, 1980, 1981; Grine, 1981; Puech et al., 1981; Ryan, 1981; Rensberger 1982), as workers generally shifted to using the scanning electron microscope, due to its superior depth of focus and resolution of detail. Of course, finer microscopic resolution raised the possibility of finer dietary distinctions – as long as that information could be put to efficient use. This led numerous workers to begin quantifying dental microwear, by counting the incidence of scratches and pits, measuring their length and width, and attempting to measure their orientation, using various forms of computer-controlled digitizers or calipers in conjunction with SEM micrographs or enlarged prints of them (e.g., Fine and Craig, 1981; Gordon, 1982, 1984b, c; Teaford and Walker, 1984;

Teaford, 1985; Grine, 1986; Kelley, 1986; Solounias et al., 1988; Young and Robson, 1987). However, as the number of studies began to grow, it quickly became apparent that many people were using very different methods to measure dental microwear. This presented researchers with an array of methodological difficulties (Covert and Kay, 1981; Gordon, 1982; Gordon and Walker, 1983; Kay and Covert, 1983; Gordon, 1984b, 1988; Teaford, 1988a), some of which are still haunting us (see “cautions” below). In an attempt to standardize techniques, Ungar developed a “semi-automated” procedure for measuring dental microwear (Ungar et al., 1991; Ungar, 1995), a method that is still used by many researchers today. To use it, images need to be stored in a specific digital format so they can be opened by a freeware package known as “Microware” (<http://comp.uark.edu/~pungar/>). Given the complexity of SEM micrographs, each microwear feature within each micrograph still needs to be identified and “measured” by the researcher, using a mouse and cursor on a computer screen. So, while the technique provides a standardized series of measurements for analysis and stores them in a format readily accessible to most statistical packages, the work is still very time-consuming. The availability of this standardized technique, however, prompted work on an even wider range of taxa. Unfortunately, initial attempts to take analyses one step further, using a combination of image processing and image analysis (Kay, 1987; Grine and Kay, 1988), were limited by the capabilities of the software at the time.

### Review of Studies of Modern Material

Given the number of potential avenues of investigation, it is best to review the different approaches before returning to some of the methodological challenges facing dental microwear analyses.

### *Analyses of Museum Material*

Analyses of mammalian teeth from museum collections have always served as a major source of information, by demonstrating correlations between certain diets, or patterns of tooth use, and certain microwear patterns. These correlations depend on which teeth are analyzed, because anterior teeth are used differently than posterior teeth, with the incisors and canines being used to *ingest* food, and the premolars and molars being used to *chew* food once it has been ingested.

Analyses of incisor microwear have yielded two basic conclusions. First, animals that use their incisors very heavily in the ingestion of food show higher densities of incisal microwear features (Ryan, 1981; Kelley, 1986, 1990; Ungar, 1990, 1994). Second, the orientation of striations on the incisors reflects the direction of preferred movement of food (or other items) across the incisors (Walker, 1976; Rose et al., 1981; Ryan, 1981; Ungar, 1994). Thus, for example, the orang-utan, which generally uses its incisors a great deal in preparing food, shows more scratches on its incisors than does the gibbon, and those scratches often run in a more mesiodistal direction, reflecting a tendency to pull branches mesiodistally between the front teeth (Ungar, 1994). Analyses of incisor microwear have also yielded an interesting insight that may be more generally applicable – i.e., that the size of abrasives may be reflected in the size of microscopic scratches on the teeth, and that this, in turn, may be indicative of feeding height in the canopy, as phytoliths in leaves are generally larger than the abrasive particles in clay-based soils. (Ungar, 1990, 1994).

Further back in the mouth, analyses of molar microwear have demonstrated a few more points. Following in the footsteps of the earliest dental microwear analyses, correlations between orientations of jaw movement and scratches on mammalian molars continue

to yield insights into chewing in a variety of mammalian species (Gordon, 1984c; Rensberger, 1986; Young and Robson, 1987; Hojo, 1996). More recent work has demonstrated that grazers tend to show more microscopic scratches on their molars as compared to browsers (Solounias and Moelleken, 1992a, b; Solounias and Hayek, 1993; Solounias and Moelleken, 1994; MacFadden et al., 1999), and animals that eat hard objects usually show large pits on their molars, while leaf-eaters tend to have relatively more scratches than pits on their molar enamel (Teaford and Walker, 1984; Teaford, 1988a) (Figure 2). Those “hard objects” can evidently include hard nuts, but also smaller items like insect exoskeletons (Strait, 1993; Silcox and Teaford, 2002). Microwear is also found on the buccal or lingual (“nonocclusal”) surfaces of molars, which may give additional indications of the abrasiveness of the diet, the size of food items, or even the degree of terrestriality

(Puech, 1977; Lalueza Fox, 1992; Lalueza Fox and Pérez-Pérez, 1993; Ungar and Teaford, 1996). Even more interestingly, museum analyses of molar microwear have yielded glimpses of subtler differences associated with dietary variation. Differences have ranged from those between closely-related genera (Solounias and Hayek, 1993; Teaford, 1993; Daegling and Grine, 1999; Oliveira, 2001), to those between subspecies (e.g., *Gorilla gorilla berengei* vs. *G.g. gorilla*) (King et al., 1999a), to those between populations within the same species (e.g., *Cebus nigrivittatus*) (Teaford and Robinson, 1989). Obviously, such analyses are only as good as the dates and locations of collection for the museum samples, and the published dietary information for those species. For instance, there are very few collections that provide the exact date and precise location of collection for each specimen, with some having little more than “British East Africa” for the location and

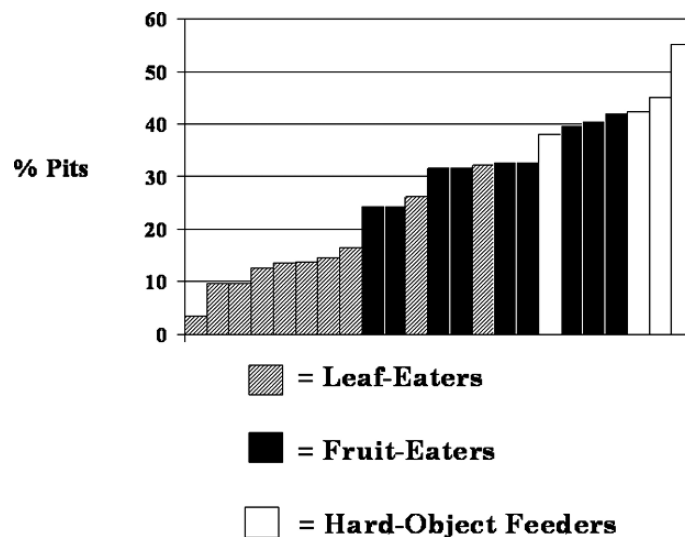


Figure 2. Histogram of the incidence of pitting on molars in primates with different diets (data from Rafferty et al., 2002, Teaford, 1988a, 1993, and Teaford and Runestad, 1992). Leaf-eaters = (left to right in figure) *Gorilla gorilla berengei*, *Theropithecus gelada*, *Colobus guereza*, *Procolobus badius*, *Nasalis larvatus*, *Allouatta palliata*, *Semnopithecus entellus*, *Alouatta seniculus*, *Procolobus verus*, and *Presbytis aygula*. Fruit-eaters = (left to right in figure) *Pan troglodytes*, *Papio cyncocephalus*, *Ateles belzebuth*, *Saimiri sciureus*, *Aotus trivirgatus*, *Macaca fascicularis*, *Pithecia pithecia*, *Mandrillus sphinx*, and *Cercopithecus nictitans*. Hard-object feeders = (left to right in figure) *Chiropotes satanus*, *Pongo pygmaeus*, *Cebus apella*, and *Lophocebus albigena*.

the name of the expedition for the date. As a result, finer-resolution studies of diet and dental microwear based on museum samples are relatively rare.

### *Analyses of Live Primates*

Unfortunately, double-checking correlations between dental microwear and diet in live animals, in the lab or in the wild, is not easy either. In fact, keeping animals in a laboratory setting is extremely difficult and expensive. Moreover, since the animals have to be anesthetized to make copies of their teeth, the exact timing and type of anesthesia is often a matter of discussion and debate, as most veterinarians prefer to stick with “tried-&-true” methods (e.g., the use of ketamine administered after 8–12 hours of fasting) which leave the animals rigidly hard to work with, salivating excessively, and with thick organic films built-up on their teeth. As a result, it is perhaps not surprising that the only successful study using laboratory animals to-date is one from the 1980s. Teaford and Oyen (1989a, b) raised a group of vervet monkeys on hard and soft diets to check for the effects of food properties on craniofacial growth. As the hard diet consisted of monkey chow and apples, and the soft diet water-softened monkey chow and pureed applesauce, you might expect the effects on the teeth to be relatively similar as both diets had the same basic ingredients and were very abrasive. However, there were two surprising differences. First, the incisors of the soft-food animals were more heavily worn than those of the hard-food animals, because the former were routinely rubbing handfuls of food across their incisors, whereas the latter were hardly using their incisors at all. Second, in the molar region, animals on the soft diet showed smaller pits on the occlusal surfaces, perhaps due to adhesive wear caused by repeated tooth-tooth contacts in chewing. The laboratory study also reaffirmed what

had been noted in museum studies: that molar facets used for shearing or crushing showed different microwear patterns. Finally, the laboratory study also showed that the turnover in dental microwear could be quite rapid in animals with an abrasive diet, as all of the microwear features in an area sampled by an SEM micrograph would change in 1–2 weeks, depending on whether the animal was raised on the hard or soft diet (Figure 3).

A more feasible option, for studies of live primates, might involve the use of human volunteers fed specific food items. However, regulations concerning the use of human subjects make such work difficult, if external funding is to be sought, and despite the amount of *other* research done on dental patients, surprisingly little work has involved the use of dental microwear (e.g., Morel et al., 1991). A pilot study by Noble and Teaford (1995) using American foods normally thought to be hard or abrasive did reaffirm that few foods in our diet (e.g., popcorn kernels) scratch enamel. From a different perspective, rates of microscopic wear (Teaford and Tylanda, 1991) have also been used to gain insights into dental clinical problems, for instance, monitoring the incidence of tooth-grinding in patients with various symptoms of temporomandibular joint disease (Raphael et al., 2003). Otherwise, remaining work has focused primarily on the wear of dental materials, where the presence/absence of specific materials has, for instance, been shown to change rates of wear of certain dental restorative materials (e.g., Turssi et al., 2005; Wu et al., 2005), where the use of certain dental clinical procedures has been shown to cause certain types of microscopic wear (e.g., Plagmann et al., 1989; Östman-Andersson et al., 1993) and various forms of “microabrasion” have been shown to aid in the whitening of teeth (Allen et al., 2004; Chafaie, 2004; Bezerra et al., 2005).

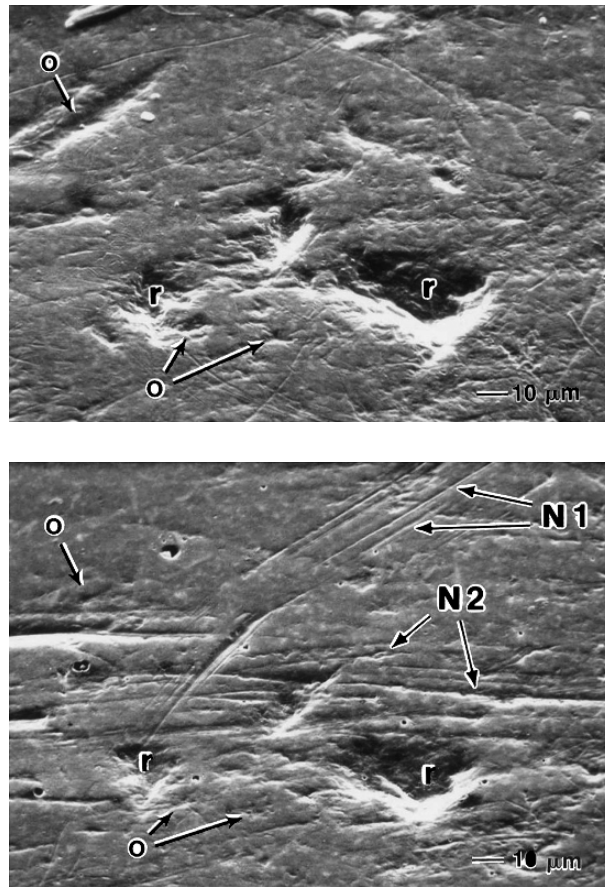


Figure 3. Changes in dental microwear over a 3-day period in a laboratory vervet monkey fed monkey chow and apples. Top = baseline micrograph. Bottom = follow-up micrograph of same surface, after three days. (“R” = reference features in both micrographs, “O” = features nearly obliterated between baseline and follow-up, and “N” = new features appearing on follow-up micrograph) (from Teaford and Oyen, 1989b).

Of course, laboratory studies of living animals are limited in how they can change diets, and most laboratory diets are not nearly as diverse as diets in the wild, where seasonal, geographic, and annual differences in diet have the potential to have a huge impact of dental microwear patterns. Thus, work with animals in the wild is a potential goldmine of information, as demonstrated by the pioneering study of Walker et al. (1978) on hyraxes, where skulls were collected directly from the same area in which behavioral observations were recorded. Unfortunately, while studies of living primates in the wild have been attempted a number of times, they have

usually met with little success. Primates often live in forested habitats where they are hard to see, and even harder to catch. Even in open habitats (e.g., baboons in the East African savanna), the work is difficult.

Thus far, only two studies have consistently yielded high-quality copies of primate teeth in the wild. The first is the on-going study at La Pacifica in the Guanacaste region of Costa Rica (Teaford and Glander, 1991; Ungar et al., 1995; Teaford and Glander, 1996; Dennis et al., 2004). There, howling monkeys (*Alouatta palliata*) are regularly observed, captured, and released in a dry tropical forest setting. That work has certainly verified some

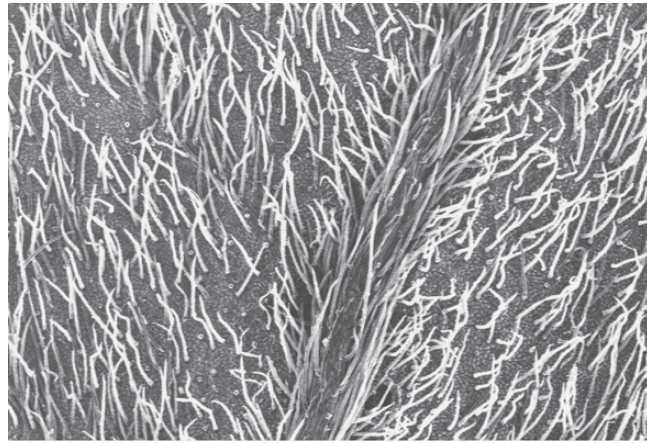
of the standard correlations from museum analyses (e.g., leaf-eating and scratches on teeth). It has also given us glimpses of other complicating factors. For instance, the amount of molar microwear may vary from season to season, and between riverine and nonriverine microhabitats (Teaford and Glander, 1996). The studies at La Pacifica have also shown that tooth wear generally proceeds at a rapid pace in the wild – at about 8–10 times the pace of that in U.S. dental patients (Teaford and Glander, 1991). This has led to the idea of the “Last Supper” phenomenon (Grine, 1986) – i.e., that, in some situations, dental microwear may only record the effects of the most-recently eaten foods on the teeth, although some investigators feel that microwear on the sides of the teeth may show far slower turnover (Pérez-Pérez et al., 1994).

Recently, a second long-term study has begun to yield high resolution casts of primate teeth in the wild (Nystrom et al., 2004). The study populations, from the anubis-hamadryas hybrid zone of Awash National Park, Ethiopia, have been the focus of multidisciplinary work for over thirty years (e.g., Nagel, 1973; Phillips-Conroy, 1978; Sugawara, 1979; Phillips-Conroy and Jolly, 1986; Phillips-Conroy et al., 1991; Szmulewicz et al., 1999; Phillips-Conroy et al., 2000; Dirks et al., 2002) and have yielded fascinating insights into the behavioral, ecological, and anatomical ramifications of species hybridization in the wild. The precise timing of dental microwear analyses in this case (before the heavy onset of new leaves and grasses in this seasonal environment), allowed Nystrom et al. (2004) to implicate “small-caliber environmental grit” as the main cause of the observed microwear patterns, which included no significant differences between the sexes, age groups, or different troops.

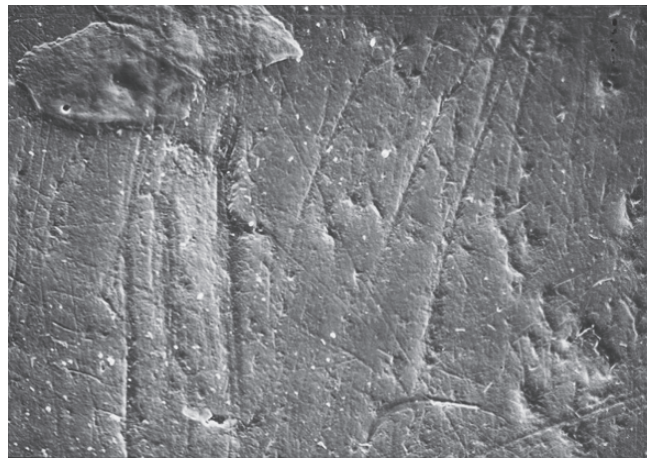
Studies such as these make us look very carefully at the specific causes of dental microwear, and what can and cannot be

documented in changes in dental microwear patterns. In fact, many foods are not hard enough to scratch teeth (Lucas, 1991), and, in modern human diets, exceptionally few foods could be expected to scratch teeth, because the foods are so clean, cooked and processed. Still, without such processing, some foods (e.g., certain leaves), include abrasives which can cause striations on teeth (Lucas and Teaford, 1995; Danielson and Reinhard, 1998; Reinhard et al., 1999; Gügel et al., 2001; Teaford et al., 2006) (Figure 4a). Others include acids, which can etch the teeth (Figure 4b) (Puech, 1984b; Puech et al., 1986; Teaford, 1988a, 1994; Ungar, 1994; King et al., 1999b). In addition, as suggested by many authors (e.g., Puech, 1986a; Teaford, 1988a; Pastor 1992, 1993; Teaford, 1994; Ungar, 1994; Ungar et al., 1995; Nystrom et al., 2004), many microwear patterns might be caused by what might be termed the *indirect* effects of food on dental microwear. For instance, certain cooking procedures or methods of food preparation (e.g., cooking food directly within the ashes of a campfire) may introduce abrasives into foods, causing a high incidence of microscopic scratches on teeth – scratches not caused by the foods themselves, but by the methods with which they were prepared (Pastor, 1992, 1993; Teaford and Lytle, 1996). Similarly, animals may also eat soft foods, and still show many scratches on their teeth – if the food is coated with abrasives (e.g., earthworms coated with dirt) (Silcox and Teaford, 2002). Finally, if an animal has a soft but tough diet, tooth-on-tooth wear can yield characteristic microwear patterns as enamel edges penetrate the food and grind past each other yielding a high incidence of small pits on their teeth – pits probably caused by the adhesive wear of enamel on enamel (Puech et al., 1981; Walker, 1984; Puech, 1984a, 1986a; Puech et al., 1986; Radlanski and Jäger, 1989; Teaford and Runestad, 1992; Rafferty et al., 2002).

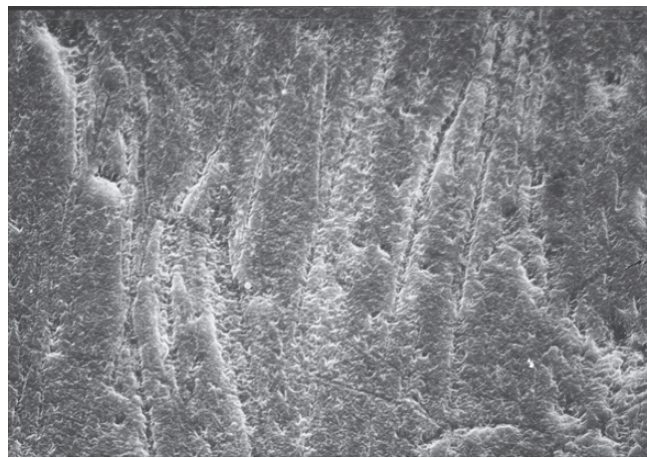




a



b



b

Figure 4. a. SEM micrograph of long silica “trichomes” on leaf routinely eaten by *Alouatta palliata* in Costa Rica (from Teaford et al., 2006). b. Chemical wear of a molar of *Alouatta palliata*. Top = baseline micrograph. Bottom = follow-up micrograph after 2–3 second exposure to a 30 % solution of phosphoric acid (note the removal of smaller microwear features) (from Teaford, 1994).

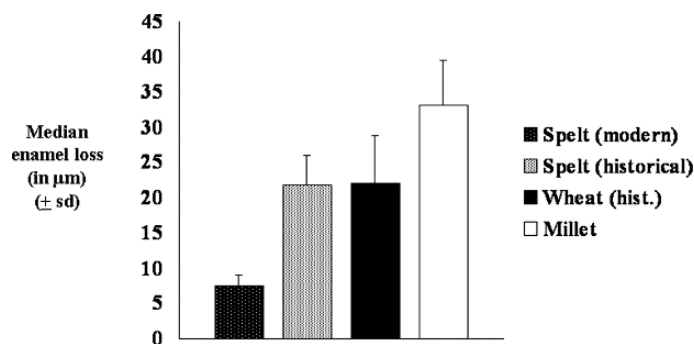


Figure 5. Differences in the amount of enamel lost through in vitro abrasion of enamel by different cereal grains (data from Gügel et al., 2001).

### *In Vitro Laboratory Studies*

So, if studies of living primates are so difficult, why not do experimental studies of dental enamel abraded by different foods? Early studies showed that substances like acids could have a profound effect on enamel surfaces (Mannerberg, 1960; Boyde, 1964). Still, experimental work has proceeded in fits and spurts. Some studies have demonstrated that the orientation of scratches on a tooth's surface can indeed reflect the orientation of tooth-food-tooth movements (e.g., Ryan, 1979; Teaford and Walker, 1983; Gordon, 1984c; Walker, 1984; Teaford and Byrd, 1989; Morel et al., 1991). Other studies have shown that certain agents, such as wind-blown sand, or various acids, can leave characteristic microwear patterns on teeth (Puech and Prone, 1979; Puech et al., 1980, 1981; Gordon, 1984a; Puech et al., 1985; Puech, 1986a; Rensberger and Krentz, 1988; King et al., 1999b). However, there have been surprisingly few controlled studies of the wear patterns caused by different types of foods.

Peters (1982) used standard physical property-testing equipment while examining the effects of a range of African foods on dental microwear, ultimately showing that few foods could actually scratch enamel, with extraneous abrasives being one of the prime culprits instead (see also Puech et al., 1986). Only with more detailed analyses did

subsequent work (e.g., Gügel et al., 2001) begin to demonstrate the effects of specific foods on microwear patterns (e.g., “cereal-specific” microwear related to phytolith content in certain grains) (Figure 5).

### **Analyses of Paleontological Samples**

When dental microwear analyses are aimed at the past, they often raise more questions than they answer, largely because they give new and different glimpses of the intricacies of previous behavior. Of course, interpretations of results are dependent on our knowledge of present-day correlations between diet and dental microwear. Thus, while we often have significant differences in dental microwear between teeth from different sites or time periods, the exact meaning of those differences may be subject to discussion and debate until better data are available for modern species.

Paleontological analyses have included a wide variety of animals, ranging from rodents (Rensberger, 1978, 1982), horses (MacFadden et al., 1999), and ungulates (Solounias and Hayek, 1993; Solounias and Moelleken, 1992a, b, 1994; Solounias and Semperebon, 2002), to carnivores (Van Valkenburgh et al., 1990), tyrannosaurids (Schubert and Ungar, 2005), and conodonts (Purnell, 1995). But within the primates, dental microwear analyses have also led to some major insights.

Analyses of Miocene hominoid material have helped document an impressive array of dietary adaptations in the early apes (Teaford and Walker, 1984; Ungar, 1996; King et al., 1999a). By contrast, analyses of Plio-Pleistocene cercopithecoid material have documented a surprisingly limited array of dietary adaptations in East Africa (Lucas and Teaford, 1994; Leakey et al., 2003), but a larger array in South Africa (El-Zaatari et al., 2005), while also yielding insights into the degree of terrestriality in some species (Ungar and Teaford, 1996). Molar microwear analyses have also helped to document the effects of phylogenetic constraints in fossil apes by documenting similar functions in taxa which have undergone shifts in molar morphology through time (Ungar et al., 2004).

As might be expected, analyses of human ancestors have focused on whichever fossils are available. For the anterior teeth, qualitative studies have suggested similarities between early hominin incisor wear and that observed on modern primates that routinely employ a great deal of incisal preparation (Puech and Albertini, 1984). Quantitative analyses of *Australopithecus afarensis* suggested incisal microwear similarities with those documented for lowland gorillas or perhaps savanna baboons (Ryan and Johanson, 1989). More detailed analyses of *Paranthropus robustus* and *Australopithecus africanus* (Ungar and Grine, 1991) showed great variability within each species in most standard microwear measurements. However, the greater density of features on the incisors of *A. africanus* helped to show that this species placed a higher emphasis on incisal preparation than in *P. robustus*.

In the molar region, qualitative analyses have raised many possibilities that have been often repeated in the literature. For instance, the robust australopithecines (e.g., *Paranthropus*) have been characterized as indistinguishable from modern chimpanzees or orang-utans (Walker, 1981), perhaps with

more abrasive molar wear than in the gracile australopithecines (e.g., *Australopithecus*) (Puech et al., 1985; Puech, 1986b; Puech et al., 1986). By contrast, *Homo habilis* has been characterized as using high occlusal pressures, but on foods that can chemically etch the enamel (Puech et al., 1983; Puech, 1986b).

Quantitative analyses have begun to refine these interpretations, from many different perspectives. Studies of non-occlusal microwear have focused primarily on more recent, European taxa, such as the Neanderthals, together with specimens now attributed to *Homo heidelbergensis*. Initial analyses portrayed the Neanderthals as more carnivorous than their immediate predecessors, or subsequent *Homo sapiens* (Lalueza Fox and Pérez-Pérez, 1993; Lalueza et al., 1996). However, subsequent work has raised the possibility of sexual differences in diet in *Homo heidelbergensis* (Pérez-Pérez et al., 1999), and a more heterogeneous diet for the Neanderthals, with a shift in food processing in the Upper Paleolithic (Pérez-Pérez et al., 2003).

Quantitative analyses of fossil hominin occlusal microwear began with Grine's pioneering work on the South African australopithecines, where *Paranthropus robustus* was shown to exhibit more microwear and more pitting on its molars than did *Australopithecus africanus* (Grine, 1981, 1986, 1987; Grine and Kay, 1988; Kay and Grine, 1989). This lent a lot of support to Robinson's ideas of dietary differences among the australopithecines, with the so-called robust forms consuming harder foods that required more variable grinding movements in chewing. Recent work has taken analyses a step further by incorporating samples of australopithecines and early *Homo* from East and South Africa (Ungar et al., 2001; Teaford et al., 2002b). The work is still being completed, but initial results gave further credence to Ryan and Johanson's (1989) idea of similarities between

*Australopithecus afarensis* and lowland gorillas, this time for the molars (Teaford et al., 2002b; Grine et al., 2006). In conjunction with other morphological data for the australopithecine grade of human evolution (Teaford and Ungar, 2000; Teaford et al., 2002a), they also helped to make the distinction between dental *capabilities* and dental *use*, as the capability to process certain foods may well have been of critical importance in certain situations. Meanwhile, analyses of early *Homo* have begun to help sort through the variable assemblage that now encompasses early *Homo*, with *Homo erectus/ergaster* showing a higher incidence of pitting on its molars than that found in *Homo habilis* (Ungar et al., 2006), suggesting the consumption of tougher or harder food items by the former group, again, as a possible critical fallback food (Figure 6).

As for more recent human populations, the transition from hunting-gathering to agriculture has left a complex signal in the microwear record, depending on which populations are examined, in which habitats, etc. (Bullington, 1991; Pastor, 1992; Pastor and Johnston, 1992; Schmidt, 2001; Teaford, 1991, 2002; Teaford et al., 2001). Once the change to agriculture was made, human diets did not simply stay stagnant. Some became more homogeneous, as evidenced

by fairly uniform microwear patterns, while others became more variable (Molleson and Jones, 1991). Some cereal diets left characteristic microwear patterns remarkably similar to those documented in laboratory studies (Gügel et al., 2001). Some changes in food processing, most notably the boiling of foods, led to a marked decrease in the amount of microwear at some sites (Molleson et al., 1993). The net effect, however, is that, with the advent of food preparation (in particular, cooking), the effects of food on human teeth changed dramatically, leaving modern nonhuman primates as perhaps the best modern analogues for analyses of the earliest hominins.

### Cautions

While at first glance, it might seem that we know a great deal about dental microwear and diet, in reality, all we have are tiny windows into a complex world. Studies of living primates have really only been carried out on two species (*Alouatta palliata* and *Papio hamadryas*), in two habitats (the dry tropical forest of Costa Rica and the thornbush and savanna grassland of Ethiopia). Those settings certainly have their inherent complexities (e.g., dramatic seasonal changes in rainfall

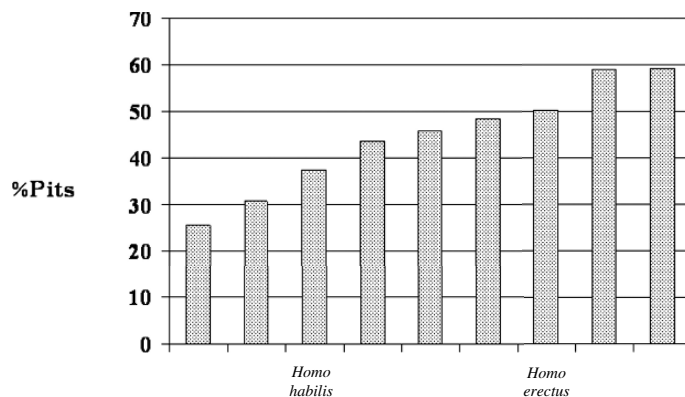


Figure 6. Histogram of the incidence of pitting on molars of *Homo habilis* and *Homo erectus* and extant primates (data from Ungar et al., 2006). From left to right, comparative samples include *Gorilla gorilla*, *Homo sapiens* (Arikara), *Homo habilis*, *Pan troglodytes*, *Homo sapiens* (Aleut), *Papio cynocephalus*, *Homo erectus*, *Cebus apella*, *Lophocebus albigena*.

and resource availability), but how representative are they of all the other ecological zones in the world? Would dental microwear patterns differ for primates in other habitats? Undoubtedly. How might other species share a habitat with either of these species, and how would that be reflected in differences in dental microwear? What is the magnitude of seasonal, annual, geographic, and inter-specific differences in dental microwear for other species elsewhere in the world? How does the incidence of dental microwear relate to specific abrasives and foods in the wild? Clearly, a massive amount of work has yet to be done on live primates in the wild if we are to use that information to help interpret results from fossil samples. Unfortunately, that work may need to be done quickly, as major sources of information for dental microwear analysis may be vanishing before our eyes, as huge tracts of the earth's environment disappear or are damaged beyond repair. In the process, habitats and organisms of crucial importance for future microwear interpretations may be lost, effectively leaving certain questions unanswerable.

Meanwhile, laboratory studies have barely begun to sort through the intricacies of dental microwear formation. As noted earlier, the effects of specific food items have yet to be documented in any systematic fashion, and the effects of foods naturally consumed in the wild have yet to be examined in any detail, with the work from Costa Rica and Ethiopia giving us just a teasing glimpse of possibilities. As primate diets are normally quite variable, and as dental microwear features can change quite quickly (Teaford and Oyen, 1989b; Teaford and Glander, 1991), what are the effects of different food items on overall microwear patterns within a specific diet? Will items that are abrasive, hard, or acidic effectively swamp other microwear patterns? Will the so-called "Last Supper" phenomenon vary between species or populations? Again, much more work needs to be done.

Analyses of museum material have probably been pushed closer to their limits than studies of living animals, but only because there are relatively few museums where the associated collection data is of sufficient detail to aid the documentation of geographic or seasonal differences in diet and dental microwear. Moreover, there are virtually no collections of primate material for which dietary information has been collected before the animals were collected. Thus, virtually all studies of museum samples are limited in their resolution by the lack of associated dietary information for the animals in question. Similarly, analyses of archeological and paleontological material are limited by the size and extent of collections (and sometimes, in the case of fossils, access to them), and by the associated information for those collections (e.g., geological information, paleoecological interpretations, presence of associated cultural remains, etc.).

Still, when fossils are found, our current methods may lead to answers, or questions, requiring a different resolution of details than what we had anticipated. Thus, for instance, they force us to consider questions about subtle intraspecific differences in diet – questions that most analyses of museum material cannot begin to answer. Similarly, "what you see is what you get" in fossils, in terms of dental samples. So preservation may be poor, postmortem wear may be rampant, and, for some collections, we may even have an overabundance of certain tooth types for which we have no analyses of modern material (noting that most analyses to-date have focused on incisors or molars). In the face of such problems and possibilities, innumerable questions still need to be answered. For instance, what is the relationship between the biomechanical demands of processing certain foods and the generation of microwear patterns? Can the structural capabilities of bone, or variations in enamel properties (e.g., Cuy et al.,

2002), be correlated with variations in microwear pattern within and between jaws? For that matter, what *is* the relationship between microwear patterns between upper and lower jaws? We know their patterns are roughly similar (Teaford and Walker, 1984), but can analyses of upper-lower microwear integration shed new light on jaw movements and food processing in mammals? What about the microwear of other dental materials like dentin? Until now, investigators have shied away from it, mainly because it is hard to clean without introducing artificial microwear patterns. However, since it is softer than enamel, might it be an indicator of even subtler diet distinctions?

Despite all these questions, when all is said and done, the biggest challenge facing dental microwear analyses is a methodological one. Standard scanning electron microscope analyses are difficult, costly, time-consuming, and (most notably) subjective, in that the “measurement” of certain microwear features depends on the recognition of “landmarks” that may be defined differently by different researchers. Even with the use of semi-automated, computerized, digitizing routines (Ungar et al., 1991; Ungar, 1995), inter-observer error rates are often unacceptably high, ranging from 3 to 13% depending on which measurements, of which types of features, are being measured (Grine et al., 2002). Thus, measurements computed by different researchers should probably not be compared directly, leaving researchers few alternatives but to either have one person do all the measuring (e.g., Organ et al., 2005), or average the measurements, computed for the same specimens, by a number of individuals (e.g., Ungar et al., 2006). When this is all coupled with the fact that most analyses to-date have used relatively small samples (even for species with variable diets), the net effect is that dental microwear analyses have barely begun to live up to their potential.

Recently, workers have begun to address this issue through the use of two new approaches – lower magnification work by light microscopy (Solounias and Semprebon, 2002; Semprebon et al., 2004), and a higher magnification combination of confocal microscopy and scale sensitive fractal analysis (Ungar et al., 2003; Scott et al., 2005). In the former, epoxy casts are viewed at a magnification of 35X while a fiber optic light source is used to direct light obliquely across the cast. Features are then quickly counted as “pits” and “scratches,” and also grouped into various size categories (e.g., “fine” versus “hypercoarse” scratches). Its potential advantages include the fact that it is much quicker than standard SEM analyses, making possible the use of larger sample sizes. Also, because the analysis is done at lower magnifications, larger surface areas are covered, giving more representative coverage of the tooth. Third, published tests of inter-observer error hint at better replicability than standard SEM-based analyses (Semprebon et al., 2004), although published measures of error rates are not presented in a form that is comparable between studies. However, the technique is not without its drawbacks either. First, it requires significant training to master – i.e., it is not the sort of thing where you can merely pick up a dissecting microscope and go measure teeth! Second, inter-observer error rates have yet to be reported for the categorization of features into different sizes. As many of the diet differences reported to-date (e.g., Godfrey et al., 2004) depend upon the accurate identification of features of different sizes, how readily can those measures be generated by different observers? Moreover, because the technique works at low magnifications, it may only yield information on gross dietary categorizations. The fact that data have been combined for shearing and crushing facets (Semprebon et al., 2004), with no evident differences between those facets, suggests this may be the

case. Until further work is done, claims such as those by Godfrey et al. (2004) that there were no dietary differences between species of *Megaladapis* should be viewed extremely cautiously, as they may be nothing more than a reflection of the limitations of the technique. Finally, the low magnification technique may only be able to detect the most obvious effects of postmortem wear. Thus, since we already know that at some fossil sites (e.g., Koobi Fora) over 75% of specimens are not usable due to postmortem wear, can this technique successfully recognize postmortem wear? Only further work will tell.

As for the confocal technique, once again, an epoxy cast is examined, but this time at a series of higher magnifications using a white light confocal microscope. Resultant x, y, and z coordinates can be used to create “photo-simulations” of the surface, or 3D models of the surface (Figure 7). Of course, even though the resolution of the system in the z-dimension is outstanding (in fractions of microns), the resultant maps of tooth surfaces are nothing more than pretty pictures without some form of analysis. What makes this system uniquely useful is that scale-sensitive fractal analyses have been used to characterize the wear surfaces. These analyses are based on the assumption that the apparent area of a rough surface (and the apparent length of a profile from a rough surface) will change with the scale of measurement. Thus, for a relatively smooth surface, a limited number of large patches may accurately characterize the surface area, whereas for a rough surface, a much larger number of small patches may be needed to accurately characterize surface area. So, if you systematically vary the scale of measurement, and thus the size of the patches, and plot them against changes in relative area, you can use the slope of that plot as a measure of the complexity of that surface. Similarly, if the orientation of profiles across the surface is changed systematically, a measure of the degree of difference (or

“anisotropy”) of the orientation of surface features can be calculated. The net effect is that the entire wear surface can be analyzed or characterized rather than treating each pit or scratch as a “feature” to be measured. As those analyses are completed at a series of different scales, they will provide a more objective picture of which magnifications are most useful for making dietary distinctions. Thus, it would seem to be the closest thing available to putting a specimen in and getting useful numbers out. Its advantages include speed, as large numbers of specimens can be processed quickly. But it is also objective and thus repeatable, in that the only subjective component is in the choice of which specimens to use. Also, unlike all previous types of analyses, it includes measures of height or depth, thus opening new possibilities for analysis. Finally, due to the scale-sensitive nature of its analyses, it effectively covers a wide range of magnifications to objectively determine at which resolution relevant dietary/functional distinctions can be made. However, with all that said, it is still a work in progress, and as a result, there are still some disadvantages. First, by anthropological standards, white light confocal microscopes are rare and expensive. Second, new analytical software is still being developed, so most workers still do not have access to the software, and those who do are still determining which fractal analyses will be most useful. Third, a database for future interpretations is still being gathered and comparisons with data generated by previous techniques are still being completed. Fourth, some postmortem wear seems to be detectable by an absence of detail in the objective measurements or characterizations, but it still may be dependent on visual inspection (or, ironically, SEM examination) to determine which surfaces of fossil teeth are suitable for use. Initial results are promising (Scott et al., 2005), yielding insights into diet variability in the South African australop-

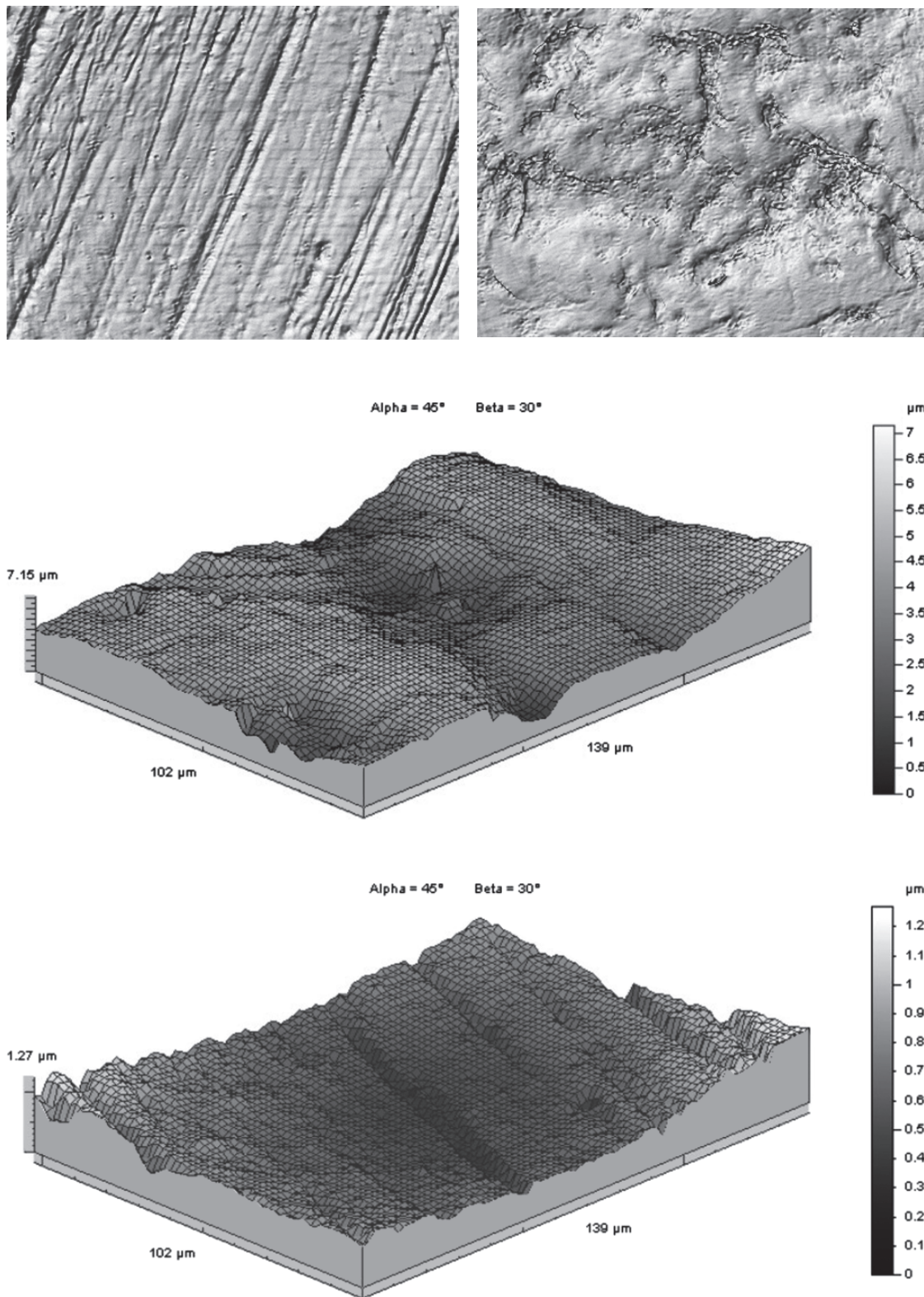


Figure 7. 3D models and “photosimulations” of the teeth of *Cebus apella* (top right image and middle image) and *Alouatta palliata* (top left and bottom image) derived from 3D coordinate data from a confocal microscope. (Note the dramatic difference in the scales of the 3D maps for each specimen).



ithecines, including the possible importance of critical fallback foods in their diets. With the added capability of providing data in three dimensions, it also raises the possibility of answering innumerable new questions concerning topics like the volume of tooth loss in different wear regimes, and the depth of enamel removed by certain abrasives or bite forces, thus giving hope for even better correlations between tooth use and wear patterns.

### Conclusions

Dental microwear analyses have come a long way in the past 25 years. While some pieces of information may remain invisible, we always need to be open to new opportunities, as the effects of some foods, or the means of documenting them, may be hard to anticipate. Each method of data collection, and each piece of evidence, has its strengths and weaknesses. Dental microwear analysis is certainly no exception, as it definitely has its limitations. But it also has the potential to give us direct glimpses of the past. As such, it can tell us about how teeth were actually used rather than what they were evolutionarily capable of doing. So we need to better understand its strengths and weaknesses. New methods raise new hopes of doing so. Of course, in the long run, the picture we are trying to decipher is incredibly complicated. So we also need to consider every piece of evidence, be it dental microwear, or otherwise. With a little luck and foresight, we will have the good fortune to contribute to a better understanding of the origin and evolution of human diet, among many other things!

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