DENTAL EVIDENCE FOR DIET IN PRIMATES

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Abstract: *Paleoanthropologists have long been concerned with the reconstruction of fossil primate and especially early hominid dietary adaptations. This paper summarizes the literature relating studies of primate tooth allometry, morphology and especially wear to diet and feeding adaptations. Such studies indicate that the sizes and shapes of teeth and the patterns of microscopic wear on their surfaces do indeed reflect diet and feeding adaptations. Current approaches allow the assessment of both general dietary adaptations and some more specific information such as the hardness of food items habitually consumed. In addition, the degree of incisor use in food preparation and other behaviors (e.g., cultural practices) can also be assessed using dental remains.*
Key words: *Diet reconstruction; Tooth morphology; Microwear; Primates.*

Introduction

Diet and ecological niche are inextricably linked with the concepts of competition, natural selection and evolution in general. As such, paleoanthropologists have long recognized the importance of diet to aspects of the biology and ecology of living and past primates. While paleontologists have taken numerous approaches to the inference of trophic adaptations, studies of dental allometry, morphology and wear have proven to be particularly useful to this end. This paper provides an historical perspective on and review of techniques currently used to associate primate teeth with aspects of diet and feeding adaptations.

This review is not meant to be an exhaustive, comprehensive examination of all research conducted on primate teeth but, rather, it emphasizes some of the more common approaches taken by dental researchers to deduce aspects of diet and feeding behaviors of extinct primates. Particular attention is given to developments in the promising field of dental microwear analysis.

Dental Allometry

Researchers have used relative sizes of teeth as an indicator of their importance in food processing and, thereby, to infer dietary differences among primates. Two types of dental allometry study are most commonly found in the literature: (1) the relation of a tooth's size to the sizes of other teeth in the mouth, and (2) the relation of tooth size to body size (or some presumed reasonable correlate thereof).

Cheek tooth allometry

Much of the research conducted on primate dental allometry has centered on debates concerning interpretations of tooth size differences among early hominids. According to Robinson (1954, 1963), for example, 'robust' australopithecines had large cheek teeth suited to triturating tough, herbivorous food items, whereas 'gracile' australopithecines possessed a smaller postcanine dentition suggestive of a more omnivorous diet.

Pilbeam and Gould (1974, 1975) challenged this scenario. They proposed that among mammals, cheek tooth size varies allometrically with basal metabolic rate and, therefore,

that the relative size differences between 'robust' and 'gracile' australopithecine postcanine teeth do not reflect dietary differences but, rather, indicate metabolic equivalence at different body sizes. This 'metabolic equivalence' model has been supported by other authors (e.g., Martin 1979, Walker 1979, 1981, Wolpoff 1982, Demes & Creel 1988), who argue that those australopithecines with larger cheek teeth also had larger muscles of mastication to maintain a constant force per unit tooth area. It was therefore argued that the more 'megadont' australopithecines would have processed greater quantities of the same foods consumed by the smaller toothed early hominids.

Kay (1975a, 1978) countered this argument by demonstrating that within dietary categories, extant primate cheek tooth surface area varies isometrically with body size and, therefore, that differences in relative molar size do indeed suggest dietary differences. A number of other authors have followed suit, and suggested that relative cheek tooth size probably relates to the nutritional quality of foods eaten such that lower energy fare would need to be consumed in greater quantities, and therefore require relatively larger cheek teeth to expand occlusal area for processing (Goldstein et al. 1978, Corruccini & Henderson 1978, Wood 1979, Wood & Stack 1980, Gingerich et al. 1982, McHenry 1982, 1984, 1988).

Incisor size and cheek tooth size

Robinson (1954, 1963) also viewed front tooth size (relative to cheek tooth size) as an indicator of diet and ingestive behaviors. He suggested that the relatively large incisors of 'gracile' australopithecines are well designed for processing meat and a variety of other food items, while the diminutive incisors of the 'robust' forms are consistent with an herbivorous diet requiring extensive mastication but little incisor use.

Groves and Napier (1968) attempted to test Robinson's proposition by considering the ratio of the length of the incisor row to that of the molar row in extant hominoids. This ratio was found to be highest for *Pan troglodytes,* lowest for *Gorilla gorilla,* and intermediate for *Pongo pygmaeus.* They suggested that these results are consistent with diet such that (1) predominantly frugivorous chimpanzees require larger incisors for husking fruits, (2) gorillas show molar predominance because of the need to triturate coarse vegetable matter, and (3) orangutans have intermediate dental proportions because of marked seasonality in their diets.

Such results led Jolly (1970a) to speculate that incisor size reduction in 'robust' australopithecines reflects a *Theropithecus*-like seed eating adaptation that required little anterior tooth use. Incisor reduction was attributed to both the 'somatic budget effect' (wherein selection favored the smallest size consistent with function) and the "Oppenheimer effect" (in which a lack of stress limits alveolus development and room for anterior teeth). While Jolly's scenario is now considered unlikely (Dunbar 1976), his efforts are laudable for stimulating further research on relative incisor size in a wide variety of primates, including strepsirrhines (Jolly 1970b, Kay & Hylander 1978, Eaglen 1986), platyrrhines (Kinzey 1974, Eaglen 1984), cercopithecoids (Hylander 1975, Goldstein et al. 1978) and hominoids (Groves 1970, Simons and Ettel 1970, Conroy 1972, Simons & Pilbeam 1972).

Cheek tooth row gradients

A number of researchers have also considered cheek tooth size gradients among early hominids. For example, Wood (1981) and Wood and Abbott (1983) noted that 'robust' australopithecine premolars and M3s are relatively larger than those of early *Homo.*

Lucas, Corlett and Luke (1985) suggest that tooth size gradients are related to bolus formation, such that bolus forming hominids would be expected to have buccolingually expanded teeth in the middle of the tooth row, whereas hominids that do not form bolus' would need the whole row buccolingually elongated to provide more sites of action to spread small abrasives throughout the mouth.

Incisor size and body size

As the research described above indicates, molar size may, in and of itself, reflect dietary adaptations. Therefore, it can be argued that in order to infer anterior tooth use from relative size, incisors should be considered independent of molars, lest size differences in the former merely reflect differences in the latter.

Hylander (1975) conducted the first such study by plotting incisor row widths against body weights for several anthropoid species. He proposed that the directions and magnitudes of residuals from the least squares line reflect dietary differences among the primates such that anthropoids feeding on large fruits require larger incisors for extensive manipulation prior to mastication, while those that feed on smaller food objects (i.e., berries, leaves, etc.) require less incisal preparation, and therefore smaller incisors. Enlarged incisors of frugivores were also seen as an adaptive response to increase wear potential given increased use.

These results were corroborated in complementary studies by Goldstein et al. (1978) and Eaglen (1984). Goldstein et al. (1978) verified that cercopithecine "omnivores" and frugivores have significantly wider incisors than do folivores. These authors even suggested that incisor width is more highly correlated with diet than is postcanine tooth area. Eaglen (1984) examined the allometric relationships between incisor row length and body weight in several platyrrhines, and found that those monkeys with relatively larger incisors tend to consume foods that require relatively greater incisal preparation. A similar relationship between incisor size and diet does not exist for strepsirrhines (Kay and Hylander 1978, Eaglen 1986), presumably because selection of the tooth comb for grooming behaviors confounds any dietary signals.

Dental Morphology and Diet

The study of dental morphology has proven to be particularly useful for the inference of diet from dental remains. The overwhelming majority of such studies have involved analyses of cheek teeth.

Cheek teeth

Gregory (1922) speculated that the evolution of primate tooth shape involved improvement of mechanical efficiency for chewing. Subsequent researchers (e.g., Simpson 1933, Crompton & Sita-Lumsden 1970, Hiieme & Kay 1972) have built on this idea, and viewed cheek teeth as guides for jaw movement. Kay and Hiieme (1974) argued that insectivorous primate molars show reciprocally concave blades designed for shearing foods between the leading edges of the crown crests. In contrast, frugivore molars possess cusp tips oriented more parallel to the occlusal plane for crushing and grinding food items. This has been confirmed for various primate taxa (e.g., Seligsohn and Szalay 1978, Rosenberger and Kinzey 1976, Kinzey 1978). Lucas (1980) further

emphasized the differences between insectivore/folivore blade and frugivore mortar-and-pestle type dentitions in a biomechanical analysis of dental morphology.

In addition, Kay (1978, 1984) has devised a reliable odontometric method to determine the shearing potential of a tooth. His approach involves a comparison of total shearing crest length (relative to tooth length) among several taxa. Kay demonstrated that insectivorous and folivorous primates tend to possess molars with greater shear potential than do frugivorous species. This and similar procedures have been used to infer trophic adaptations in a wide variety of fossil primates including Eocene prosimians (Strait 1991), Oligocene anthropoids (Kay & Simons 1980), and Miocene hominoids (Kay 1977a,b).

Incisor morphology

Considerably less attention has been given to the dietary implications of anterior tooth form, perhaps in part because of a perceived consistency in morphology within euprimate suborders. Still, differences in morphology between prosimian and anthropoid incisors have been considered in some detail. The characteristic strepsirrhine tooth comb is widely accepted to be a specialization for grooming (Kay and Hylander 1978, Eaglen 1986, Rosenberger and Strasser 1985), whereas the broad, spatulate incisors of anthropoids are generally related to a shift towards anterior tooth use in ingestion, or incisal biting. Kay and Hiieme (1974) note, for example, that while *Saimiri* and *Ateles* often employ their incisors in extensive food item manipulation, neither *Tupaia* nor *Galago* bite foods with their incisors.

Dental researchers also have recognized morphological differences among the incisors of modern humans and fossil hominid taxa, particularly regarding the incidence of shovelling [the enclosure of a central fossa on the lingual surface by prominent mesial and distal ridges (Hrdlicka 1920)]. This characteristic has been noted in extinct hominids (Weidenreich 1937, Robinson 1956, Carbonell 1963, Brace 1967, 1975, Smith 1976), and has been used to assess genetic affinities of various modern human groups (Hrdlicka 1920, Leigh 1925, Pederson 1949, Dahlberg 1963, Carbonell 1963, Bailit et al. 1968, Hanthara 1977, Goose 1977). Shovelling is usually viewed as an adaptation to strengthen or support incisors against bending moments caused by pulling and prying (Brace 1967, 1975, Cadien 1972, Smith 1976).

Dental wear studies

Studies of tooth wear provide the most direct evidence available for the re-construction of diet and tooth use behaviors. Dental wear is caused either by contact of opposing teeth during mastication (attrition), or by contact between teeth and food (abrasion). The patterns of wear on cheek teeth have been used to provide evidence for both jaw movements, and the material properties of those food items that cause characteristic scratches or pitting on occlusal surfaces. Investigations of incisor wear have been employed for deducing ingestive behaviors involving anterior tooth use, although these analyses are fewer in number than molar studies. Studies of dental wear differ from analyses of dental morphology or size because dietary reconstructions from wear evidence are independent of adaptive explanations and their inherent assumptions (see Gould & Lewontin 1978, Lewontin 1978).

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Jaw movements and attritional facets

Butler and Mills employed patterns of dental wear to infer jaw movement in several mammals (Butler 1952, Butler & Mills 1959, Mills 1955, 1963, 1967, 1973). They suggested that upper and lower teeth meet at a number of facets corresponding to buccal and lingual phases of mandibular movement. Kay and Hiiemae (1974) combined occlusal wear facet and dental morphology analyses with cinefluorographic studies on chewing cycles to confirm that wear facets indicate patterns of jaw movement and occlusion.

Differences in facet type and inclination have led to the inference of differences in masticatory behaviors, and thus, have allowed paleontologists to deduce consistency or sizes of food particles eaten by various fossil primates (e.g., Gingerich 1972, Mills 1973, Kay 1977, Kay & Hiiemae 1974, Crompton & Kielan-Jaworowska 1978, Grine 1981).

Incisor bevelling and labial edge rounding

No comparable studies have been conducted on the anterior dentitions (these teeth do not generally function in mastication), but some researchers have speculated that gross anterior tooth wear may form facet inclinations consistent with certain ingestive behaviors. For example, Every (1970) noted that C/P_3 honing in baboons maintains canine sharpness (see also Walker, 1984). He speculated that other primates (particularly hominids) might possess canines specialized into horizontally sharpened shearing devices, capable of effective segmentive biting. Szalay (1975) and Peters (1981) extended this scenario to the incisors, and argued that a sharpened edge between the incisal and labial surfaces (especially among 'robust' australopithecines) might indicate slicing and cutting behaviors.

Wallace (1975, 1977) suggested that differences in the angle formed between the incisal wear facet and the labial surfaces of early hominid incisors were consistent with ingestive behavior differences. He argued that while 'gracile' australopithecine incisors showed a marked upward and inward bevel, 'robust' forms began their wear sequences with relatively flatter incisal wear planes. Wallace viewed this difference as an adaptation to improved crushing in the 'robust' australopithecines. Subsequently, Ungar (1988) and Ungar and Grine (1991) demonstrated that angle of bevelling is unrelated to feeding behavior in many extant primate taxa, and that the patterns seen in the australopithecines are likely a consequence of ontogenetic changes in incisor procumbency in the face of edge-to-edge wear.

Microwear and diet: molar studies

Researchers have also examined the microscopic traces of wear that abrasive items leave on teeth for evidence of the types of foods eaten. In 1959, Baker et al. examined microscopic wear on New Zealand sheep teeth. They noted heavy cratering on molars, and suggested that because opal phytoliths and quartz in the soil are harder than enamel, these minerals might produce wear features during food processing. This was corroborated by the presence of fractured phytoliths and angular quartz fragments in the feces of sheep studied.

Dental microwear analyses entered the anthropological literature in 1963, when Dahlberg and Kinzey examined a number of anatomically modern human teeth with the aid of a simple light microscope. These authors proposed that food properties might be determined by the nature of microscopic scratches on the enamel of hominid teeth.

Subsequent researchers have, for the most part, turned to the scanning electron microscope (SEM) to examine microwear because of image clarity, depth of field, and the resolution of detail possible with this instrument.

Rensberger (1978), for example, employed an SEM to examine rodent molars, and related differences in incidences of different microwear types to food properties, tooth shape, enamel microstructure, occlusal pressure and chewing rates. In addition, Walker et al. (1978) demonstrated molar microwear correlates to seasonal changes in the diet of *Procavia johnstoni*. When these hyraxes browsed, they showed pits as the dominant microwear features. Grazing, on the other hand, appeared to produce a preponderance of parallel scratches. *Heterohyrax brucei* microwear confirmed the associations of browsing and grazing with microwear features, and fecal analyses suggested opal phytoliths as the abrasive agent responsible for scratches in grazers.

These pioneering studies have suggested the utility of dental microwear to yield details about the foods and oral behaviors that abrade teeth. Much of the research that has followed has focused on assessing the limitations and potentials of this approach.

Covert and Kay (1981), for example, conducted experimental research in an attempt to provide some control over diet. Opossums were fed cat food supplemented either by plant fiber or by insect chitin, while a third group was fed only cat food. Covert and Kay (1981) reported a lack of obvious microwear differences among these groups, and suggested that microwear could not distinguish herbivory from insectivory. Subsequently, Peters (1982) experimentally produced microwear on a human tooth using a number of abrasive agents, and noted that chert fragments (grit) caused microscratches similar to those of opal phytoliths.

Gordon (1982, 1984) responded that microwear technique refinements, such as quantification and subsequent statistical analyses would likely reveal microwear patterning not obvious in studies such as those of Covert and Kay or Peters. Furthermore, SEM analyses of chimpanzee molars suggested to Gordon that tooth position, facet type, and the individuals sex and age contributed to variation in feature density and dimensions, and therefore should be controlled for in microwear investigations.

Gordon and Walker (1983) suggested that Covert and Kay's study was invalid because of a lack of control over these parameters, as well as an inappropriate choice of dietary medium and additives, insufficient duration of the experiment, and a lack of quantification of results. Kay and Covert (1983l, 1984) rebutted by reiterating the notion that grit and plant opals leave similar microwear, and by questioning studies (i.e., Gordon 1982) on museum collections because of a lack of dietary control.

Still, Gordon's investigations set the precedent for quantitative analyses in molar microwear studies, and subsequent research has demonstrated empirically that microwear can be used to discriminate primates with differing diets. Teaford and Walker (1984) for example, examined the molars of several anthropoid species and confirmed that microwear can be used to distinguish among primates with different diets such that frugivores show a higher percentage of pits than do folivores and, among frugivores, harder object feeders can be differentiated by even higher relative frequencies of pits. This seems to be the case even among congeners with similar dental morphologies and more subtle dietary differences (Teaford 1985, 1986).

In addition, Teaford and Oyen (1989a) have conducted long-term experimental studies on vervet monkeys to confirm that pit frequencies can be related to food object

hardness. Their observations demonstrate significant differences in microwear between those monkeys fed dry, hard monkey chow and those fed wet, soft chow; the former show more microwear on crushing facets than do the latter.

Investigations by Teaford and Oyen (1989a,b,c) also have been useful for determining the life expectancy of microwear features. These studies have indicated that although turnover rate varies dramatically depending upon the material properties of foods eaten, in some cases, microwear features can be formed and obliterated within 24 hours. These results suggest that large samples are important in interspecific comparisons of dental microwear involving species with variable diets, and further, that dental microwear has the potential to reveal changes in feeding behavior over relatively short periods of time.

Subsequent research has continued to refine and expand microwear approaches. For example, studies have begun to consider microwear in wild primate populations with well documented diets (Teaford & Robinson 1989, Teaford & Glander 1991). Results are preliminary, but it is clear that seasonal and ecological zone differences are reflected in molar microwear patterns, and that microwear may have the potential to discriminate diets and feeding behaviors to a greater extent than was indicated in early experimental work, or analyses of museum collections (see Teaford & Runestad 1992).

Fossil primates

The ability of molar microwear studies to reveal aspects of the diets of extinct primates is manifested by the existence of characteristic patterns of such wear on fossil mammal cheek teeth. Researchers have indicated distinctive molar microwear patterns for a great variety of fossil taxa, including aplodontids (Rensberger 1982), multituberculates (Krause 1982), carpolestids (Biknevicius 1986), Miocene hominoids (Teaford & Walker 1984, Daegling & Grine 1987), ruminants (solounias et al. 1988), Pleistocence felids (van Valkenburgh et al. 1990), Eocene prosimians (Strait 1991, Broadfield 1992), subfossil lemurs (Rafferty & Teaford 1992) and Pleistocene cercopithecines (Teaford & Leakey 1992).

Still, most microwear research on fossil mammals has focused on the cheek teeth of early hominids (Grine 1977, 1981, 1984, 1986, 1987a,b, Grine & Kay 1988, Puech 1979, 1982,1986a,b,c,Puech & Albertini 1983, 1984, Puech et al. 1980, 1983, 1985, 1986a,b,c, 1990a,b,c Walker 1981). Puech, for example, speculated that high feature incidences on *Australopithecus afarensis* and East African 'robust' australopithecine teeth might indicate the consumption of grit laden vegetable matter in the presence of flourides precipitated during volcanic activity. He further conjectured that microwear patterns on various archaic *Homo sapiens* and Neandertal cheek teeth might indicate either a hunter-gatherer or a baboon-like subsistence strategy.

In another study, Walker (1981) took a comparative approach, and equated molar microwear patterns in East African Plio-Pleistocene hominids with those of mandrills, chimpanzees and orangutans, suggesting more frugivorous adaptations for these early hominids. Grine's (1981, 1986) research further suggests the consumption of soft fruits and perhaps leaves by *Australopithecus africanus*. In contrast, however, high pitting incidences and other features indicated to Grine that South African 'robust' australopithecines more habitually consumed harder food items. Such investigations indicate the potential of molar studies to reveal differences in microwear that may be related to the diets of extinct primates in general, and fossil hominids in particular.

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Researchers have also begun to examine microwear on incisor teeth of a wide variety of mammals, including such disparate groups as Canadian moose (Young & Marty 1986) and Australian kangaroo (Young et al. 1987). Microwear analyses have been conducted on the incisors of numerous extant primates, both prosimian (Jacobs 1981, Rose et al. 1981) and anthropoid (Ryan 1980, 1981a, Teaford 1983, Kelley 1986, 1990, Ungar 1990a, 1990b, 1992, in prep).

Prosimian anterior dental microwear studies have associated fine vertical grooves with hairs contacting the mesial and distal sides of the lower incisors during grooming (Rose et al. 1981). Such evidence of grooming has been found also on Miocene lorisoid (i.e., *Nyctoceboides simpsoni*) and Eocene Omomyiform (*Necrolemur, Microchoerus*) incisors (Jacobs 1981, Schmid 1983), and may be of direct relevance to arguments concerning the origin of the tooth comb in prosimians (Martin 1972, Szalay & Seligsohn 1977).

Walker (1976) was the first researcher to examine microwear on extant anthropoid incisors. He examined several *Colobus polykomos, Macaca fascicularis, Papio anubis,* and *Presbytis phayrei* incisors using a light microscope, and concluded that terrestrial monkeys possess more striated dentine surfaces than arboreal forms because of feeding substrate, siliceous material in the food and the mechanical demands of food breakdown. Striation orientation differences between colobines and cercopithecines also led to speculation that colobines preferentially strip leaves laterally across the incisors.

Subsequently, Ryan (1980, 1981) employed an SEM to examine incisor microwear in a series of humans, gorillas, chimpanzees and baboons. He attributed differences in microwear patterns to feeding behaviors and the use of teeth as tools as reported in the ethnographic and ethological literatures. Surface "polish" was attributed to stripping of fine abrasives across the tooth's surface, large pits were associated with crushing gritty foods between incisors and large gauges were associated with cultural activities such as hide processing.

Following Ryan's initial work, Teaford (1983) examined the anterior dentitions of *Presbytis rubicunda* and *P. cristata* to assess the effects of seed pod manipulation and marked underbite in the latter on incisor microwear patterns. His examinations revealed that *P. rubicunda* possesses a higher proportion of labio-lingually oriented enamel microwear striations than does *P. cristata*. He concluded that microwear differences between the two colobines might reflect incisor function differences.

Kelley (1986, 1990) has also examined anterior dental wear in various anthropoid taxa. Though he did not quantify microwear feature attributes, Kelley associated labial face striation density with broad dietary category, and suggested that folivorous species generally exhibit less microwear than do frugivores, presumably because frugivory involves more incisal processing of food items than folivory and fruits are more likely to score enamel than are other plant parts. Deviations from this model were explained as the result of minor dietary components, the physical properties of specific food items, and food procurement behaviors (Kelley 1990).

Finally, Ungar (1990, 1992, in prep) has related incisor microwear to observations of use in the wild for *Alouatta seniculus, Cebus olivaceus, Macaca fascicularis, Presbytis thomasi, Hylobates lar* and *Pongo pygmaeus*. Results of this study confirm the relationship between density of microwear striations (along with presence of dental

calculus) and the habitual use in incisors to process food items. In addition, striation breadth is related to the types of abrasives causing the wear (i.e., larger phytoliths presumably cause thicker scratches that smaller clay soil particles), and striation orientation is related to the direction that food items are scraped across the incisors.

Fossil hominoids

Researchers have also begun to look to microwear on fossil incisors to infer diet nd anterior tooth use behaviors in extinct hominoid species. Ryan (1980, 1981b), Brace et al. (1981), and Ryan and Johanson (1989), for example, have employed results from Ryan's study of extant primates to deduce incisor use in *Australopithecus afarensis* and Neandertals. He noted polish, fine wear striae, pit clusters *A. afarensis,* suggesting that the Hadar hominids engaged their incisors primarily in incisor stripping of gritty plants and roots. In contrast, Ryan attributed large gouges seen on Neandertal incisors to cultural practices.

Kelley (1986) compared the resuts of his study on extant primates with microwear patterns on the incisors of various Miocene hominoids. He observed that *Proconsul africanus, Proconsul major, Rangwapithecus gordoni* and *Sivapithecus* from the Siwaliks and Pasalar all show dense labial face incisor microwear, and speculated that these primates may have been primarily frugivorous. In contrast, *Proconsul nyanzae, Ouranopithecus macedoniensis* and *Dryopithecus laietanus* were said to show sparse wear, suggesting limited incisor use in food preparation and, by implication, a more folivorous trophic adaptation. *Rudapithecus hungaricus* was said to fall intermediate in wear density, and be characterized by a mixed diet.

Other researchers have also examined microwear on the incisors of early hominids. Puech and Albertini (1984), for example, suggested that labiolingually oriented crenulations and striations on *Australopithecus afarensis* incisors are consistent with frequent stripping of food items between clenched upper and lower anterior dentitions. Further, Puech (1984, 1986b) claimed that similar furrows and fine wear striae are found in conjunction with evidence of acid etching on *Homo habilis* incisors. This was said to be consistent with the scraping or stripping of acidic food items across the teeth.

Finally, Ungar and Grine (1991) examined anterior dental microwear in *Australopithecus africanus* and 'robust' australopithecines from South Africa. Results indicate that the 'gracile' australopithecines show significantly higher densities of microwear on their incisor surfaces than do 'robust' forms. In contrast, the 'robust' australopithecines were said to more often display etched enamel prism sheaths. These results are consistent with the more common use of the incisors by the 'gracile' australopithecines in abrasive food item manipulation, but perhaps the more frequent consumption of moderately acidic food items by the 'robust' forms.

Discussion

Results from the studies described above indicate that the sizes and shapes of teeth and the patterns of microscopic wear on their surfaces do indeed reflect diet and feeding adaptations. New technologies are allowing dental researchers to make use of more sophistocated equipment (e.g., McLarnon 1987, Kay 1987, Grine & Kay 1988, Unger et al. 1991) to improve the resolution with which we see the past. Present techniques allow us to assess general dietary adaptations such as preferences for fruits, leaves or insects

(*sensu* Clutton-Brock & Harvey 1977), and some more specific information such as the mechanical properties (e.g., hardness) of food items consumed. In addition, the degree of incisor use in food preparation and other behaviors (i.e., cultural practices) can also be assessed using dental remains.

In sum, a variety of approaches are currently taken to deduce diet and feeding behaviors from fossil primate teeth. The studies of dental allometry and morphology reflect general dietary adaptations, while studies of wear provide details about specific behaviors and food items eaten. Such studies are complementary and, when used with other sources of information (craniomandibular biomechanics, postcranial remains, isotope analyses, contextual studies, etc.) can help provide a more complete picture of fossil primate trophic adaptations.

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