Dental Allometry, Morphology, and Wear As Evidence for Diet in Fossil Primates

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Feeding adaptations are of great interest to primatologists whether they study living or fossil species. Diet underlies many of the behavioral and ecological differences that separate extant taxa; it is also important in defining ecological niche, with all its implications for the ecology and evolution of extinct forms. While we can directly observe most living primates to see what they eat, deductions about the diets of fossil forms must be based on indirect evidence. Most attempts have focused on teeth, which tend to dominate fossil assemblages and, as durable parts of the digestive system, offer a fairly direct glimpse at what past primates ate. Most recent work in this domain has employed the comparative method, in which researchers attempt to relate dental evidence to diet in living primates to form a baseline for the inference of feeding behaviors from teeth in fossil forms (Fig. 1). The idea is simple enough: we observe the manifestation of an anatomical feature in a fossil and look for a corresponding condition in living primates. If, every time we observe that trait in living primates, it functions in a given

way, we assume that it functioned the same way for the fossil form.

Three main categories of dental evidence have come to dominate the literature: 1) tooth size, or dental allometry; 2) tooth shape, or dental morphology; and 3) tooth wear, especially dental microwear. Researchers have set out to discover relationships among diet and patterns of tooth size, morphology, and wear in a wide range of living primates. Consistent associations have allowed workers to infer or, perhaps more precisely, to predict diet from teeth in fossil forms.[1] In this paper I review these common approaches to relating teeth to diet in primates. Such approaches have contributed much to our understanding of fossil primate feeding behaviors and, when taken together, can provide important perspectives on dietary adaptations and diversity throughout the history of our order.

DENTAL ALLOMETRY

Since the early 1970s, paleobiologists have considered the functional implications of relative tooth sizes in adult primates. Debates stem from Robinson's[2] observation that *Paranthropus* had smaller incisors and larger molars than did *Australopithecus.* He reasoned that these differences reflected functional specializations. Robinson related large molars in the "robust" australopithecines to an herbivorous diet that required grinding large quantities of tough vegetable foods. In contrast, he related the relatively larger front teeth of "gracile" australopithecines to a more omnivorous diet requiring extensive incisal preparation of meat and other foods during ingestion. Groves and Napier[3] provided evidence for this by comput-

ing incisor to molar row-length ratios for living apes, finding that chimpanzees have the largest incisor-to-molar-size index and gorillas the lowest. They suggested that chimpanzees need stronger incisors for husking fruits, whereas gorillas eat coarse vegetable foods that require considerable mastication but little incisal preparation.

Unfortunately, we cannot tell whether differences in incisor-to-molar size ratios reflect selection on incisors, molars, or both. Therefore, most subsequent workers have chosen to focus on either incisors or molars, and to consider tooth size with respect to body size.

Cheek Tooth Allometry

Most discussion of this subject has revolved around debates about whether molar size varies isometrically with body size or is positively allometric and proportional to basal metabolic rate. Pilbeam and Gould[4] reasoned that cheek tooth size should be proportional to energy requirements because a larger occlusal surface might process more of a given type of food in a given amount of time. As evidence, they noted that among a broad range of mammals, including primates, rodents, suids, and cervids, molar surface areas scale at about 0.75 power of body mass, the same rate that metabolism increases with body mass. They argued, based on weight estimates of the day, that early hominid molars were likewise "metabolically scaled" and, therefore, that "positive allometry of tooth area in australopithecines affords no evidence for differences in diets or behavior."[4]

Kay[5] countered by noting that relationships between body size and occlusal area should be assessed by

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Figure 1. *Alouatta seniculus* at Hato Masaguaral, Venezuela. Studies of living primates in the wild can provide important insights into relationships between feeding behaviors and dental allometry, morphology, and wear.

comparing animals with similar diets. Because different foods need to be chewed to different degrees, a sample representing a mix of diets would confound attempts to determine the relationship between tooth area and the rate at which food can be processed. Kay examined molar size in a number of primate taxa identified as frugivores, folivores, and insectivores, and found that within each of these categories primate postcanine tooth surface area varied isometrically, not with positive allometry. Therefore, if australopithecine molar area was positively allometric, larger and smaller forms probably would have eaten different foods.

These results were corroborated in independent tests.[6,7] Although molar size varies isometrically within diet categories, it is positively allometric across them. Why might this be so? Perhaps larger mammals eat abundant low-energy foods, whereas smaller taxa tend to eat foods with a higher energy and protein content.[8]

Larger primates would therefore require more tooth surface area for processing greater quantities of lower energy foods.

Subsequent workers[9,10] have presented data that have been considered to be consistent with metabolic or functional equivalence models for the early hominids. These authors have argued that because "robust" australopithecines had both relatively larger molars and attachment sites for the muscles of mastication, their bite force per unit of tooth area might have remained constant. If so, the more megadont hominids could have processed greater quantities of the same food items—a case of functional equivalence. Others, however,[11,12] have maintained that functional equivalence models are unlikely. Jungers[13] and McHenry,[14] who have independently reconstructed australopithecine body weights using estimates based on various aspects of skeletal size, have both found that "gracile" and "robust" australopithecines from

South Africa were essentially of equivalent body weight. Therefore, the notion that positive dental allometry in the australopithecines reflects a metabolic equivalence model is no longer tenable.

While theory dictates that larger primates should have relatively large teeth to process greater quantities low-quality foods, specific associations between tooth size and broad diet category have not held for primates. This idea might explain why folivorous noncercopithecoid primates have relatively larger molars than do frugivores, but it does not explain why insectivorous noncercopithecoids have relatively larger molars than do frugivores.[15] Further, it certainly does not explain why frugivorous Old World monkeys have larger molars than do folivorous cercopithecoids.[16] As such, inferences of broad diet category from molar size in higher primates are prob-

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lematic. Kay and Cartmill[17] noted that in order for a morphological trait to be useful for predicting a behavior, it must be associated with that behavior in all animals that possess the trait. Therefore, molar size, at least in the absence of good phylogenetic control, cannot be considered useful for predicting diet in fossil primates.

Incisor Allometry

Following Robinson's[2] work, many researchers have considered relative incisor size to be indicative of diet. Jolly[18] speculated that small incisors relative to molars in australopithecines could be associated with terrestrial seed-eating, as seen today in *Theropithecus.* While this idea has been the subject of some controversy,[19] Jolly's efforts have stimulated considerable research on relative incisor size in
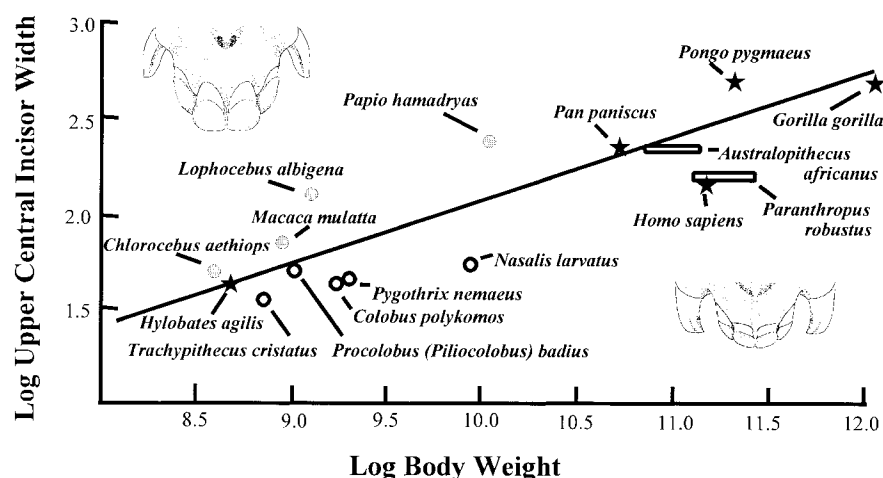
Figure 2. Regressions of maxillary central incisor mesiodistal widths (mm) versus body weights (gm) for selected male extant catarrhine taxa, *A. africanus* and *P. robustus.* Closed circles = colobines, open circles = cercopithecines, stars = hominoids. Rectangles for fossil taxa designate presumptive male body size ranges (based on data from Fleagle[21] and Swindler[84]). The regression line is based on extant species representing several catarrhine genera.[69]

a wide variety of living and fossil primates.

Most incisor allometry work from the mid-1970s onward considered incisor size relative to body size rather than relative to cheek tooth size. Hylander[20] examined maxillary incisor row lengths in 57 anthropoid species and found that those with relatively larger incisors tend to consume larger, tougher fruits, whereas those with smaller incisors tend to feed on smaller foods or ones such as leaves or berries that require less extensive incisal preparation. He reasoned that broader incisor rows provide more working area for the preparation of larger foods (e.g., fruits) and a greater surface area for wear of incisors as the result of frequent use.

Others have since extended this line of reasoning to suggest direct associations between large incisors and fruits and between small incisors and leaves (see Fig. 2).[1,7,21] For example, Goldstein and coauthors verified not only that cercopithecine frugivores and "omnivores" have wider incisors than do colobine folivores, but that incisor size is actually a better predictor of diet than is molar area. Eaglen,[22] in a similar study on platyrrhines, found that New World monkeys with relatively larger incisors tend to consume foods that require greater incisal preparation than do the foods eaten by monkeys having smaller front teeth

(but see Rosenberger[23] for further discussion).

Eaglen warned, however, that platyrrhines as a group tend to have smaller incisors than do catarrhines, so that incisor size comparisons should be made bearing in mind phylogenetic effects. The same holds for comparisons with strepsirrhines which, as a group, have even smaller incisors. In fact, Eaglen[24] found that anterior tooth size does not relate at all well to broad dietary differences in strepsirrhines. On the other hand, some aspects of front tooth size do reflect phyletic differences among strepsirrhines. So, again, phylogeny can be important in determining relative incisor size independent of tooth function.

Relationships between diet and anterior tooth size do not necessarily hold when comparing specific catarrhine taxa either. For example, incisor size differences in sympatric Sumatran monkeys and apes cannot be explained by differences in broad food-type preferences (frugivory versus folivory), the size of food items, or degree of habitual incisor use alone. While gibbons have absolutely and relatively much smaller incisors than do sympatric orangutans, the latter spend more than four times as much of their feeding time eating leaves.[25] Although there may be compelling evidence for a tendency among closely related anthropoids for those species with larger

incisors to use these teeth more often in food processing, inferences of diet or ingestive behaviors from incisor size alone should be approached with caution, particularly when comparing distantly related taxa or those with uncertain phyletic affinities.

As a case in point, Groves and Napier[3] argued that *Aegyptopithecus* and *Dryopithecus,* as defined at the time, had relatively small incisors compared with their molars, suggesting a gorilla-like folivorous adaptation. Similarly, Harrison[26] has argued on the basis of incisor size that most of the Early Miocene catarrhine taxa he studied (*Dendropithecus, Proconsul,* and *Rangwapithecus*) are folivorous. Indeed,

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early catarrhines as a group have relatively smaller incisors than do extant hominoids.[27] Perhaps, then, the relatively smaller incisors in these forms reflect phylogenetic history rather than diet per se. Again, platyrrhines as a group have smaller incisors than do extant cercopithecoids, but do not tend to be more folivorous. Therefore, incisor size alone may not be all that useful for inferring the diets of fossil primates, especially when comparing distantly related forms or those with uncertain phyletic affinities.

In sum, while diet and ingestive behaviors probably influence tooth size, phylogenetic history plays an important role that can make it ex-

tremely difficult to tease function from phylogeny. This is especially true where relationships between tooth size and diet are opposite in different groups (e.g., molar sizes in hominoids versus cercopithecoids). Fortunately, studies of dental morphology have been rather more effective in distinguishing diets among extant primates.

DENTAL MORPHOLOGY

Most prosimians have elongated, mesiodistally narrowed lower front teeth that form a tooth comb. Their upper front teeth tend to be diminutive, with a diastema between the central incisors. In contrast, most anthropoids have broader, more spatulate incisors. These differences have been related to specializations for grooming in the former group and a shift toward incisal biting during ingestion in the latter.[28] There are also differences in incisor shape within each of these higher-level taxa that undoubtedly relate to differences in tooth use. For example, gorillas, as compared with other hominoids, have short, stubby incisors with very thick cingula. Baboons, on the other hand, have long, curved, labio-lingually narrow incisors that are virtually devoid of cingula. To this point, however, there have been few studies of the functional implications of such differences.

In contrast, many workers have considered the functional implications of primate molar form. Kay and Hiiemae,[28] for example, associated specific dental morphologies with shearing, crushing, and grinding (though Lucas and Teaford[29] have recently suggested alternative terms). 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 teeth. Grinding involves both shear and crush components. In this case, two smooth surfaces are occluded and moved across one another in the manner of a mortar and pestle. Kay and Hiiemae[28] applied this model to the fossil record, arguing for a progressive transformation from shearing to crushing and grinding from the middle Paleocene paromomyid *Palenochtha* to the Eocene adapid *Pelycodus* (=*Can-tius*) to the Oligocene catarrhine *Aegyptopithecus.* These authors suggested that this transformation marks a shift from insectivory to frugivory.

Other workers have associated specific crown morphologies with shearing, crushing, and grinding. For example, Rosenberger and Kinzey[30] noted features associated with shearing in the more insectivorous *Callithrix* and the more folivorous *Alouatta,* but rounded or flattened cusps associated with crushing in more frugivorous *Cebus* and *Pithecia.* Further,

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Seligsohn and Szalay[31] suggested that the occlusal morphologies of *Lepilemur* and *Hapalemur* are consistent with an emphasis on cutting edges for leaf-eating by the former and puncturing or point penetration for the preparation of bamboo stems by the latter.

In sum, reciprocally concave, highly crested teeth have been associated with insectivorous and folivorous diets, whereas rounded or flatter cusped teeth have been associated with a more frugivorous diet. Kinzey[32] warned, however, that these general food categories are simplications, pointing out that dental morphology might not only reflect primary specializations, but also critical, though less often eaten, food resources.

Similarities between the molars of leaf- and insect-eaters reflect the fact that plant fiber and insect chitin form resistant, almost two-dimensional sheets and rods that are more efficiently broken by shearing than by crushing. Moreover, chitin and leaf cellulose are both structurally complex and present similar challenges to the digestive tract. In contrast, frugivores consume more crushable three-dimensional fruits and nuts, which often contain proteins and easily digested simple sugars. Because shearing crest length correlates inversely with chewed particle size, and because more finely ground particles are digested more completely, it makes sense that a diet of leaves or insects should select for longer-crested teeth.[33] This is consistent with findings that colobines have finer ground foods in their stomachs than do cercopithecines.[86]

So how can we distinguish folivores from insectivores? Kay[34] demonstrated that the weight of insectivorous primates tends to range below about 350 gm, whereas that of folivorous primates tends to exceed 700 gm. Frugivores overlap these ranges. Therefore, in combination, shearing crest lengths and body weights can usually distinguish frugivores, folivores, and insectivores.

Molar Shearing Quotient Studies

Kay[34] devised a "shearing quotient" (SQ), a measure of the relative shear potential of a tooth. First, the lengths of mesiodistally running crests connecting the main cusps of lower second molars are summed. A least-squares regression line is fit to frugivorous extant species in logarithmic space with mesiodistal occlusal surface length as the independent variable and summed crest length as the dependent variable (Fig. 3). Frugivorous species alone are used to control for allometric changes in animals with similar adaptations. SQs are computed as deviations from the frugivore regression; that is, as measures of differences between observed and "ex-
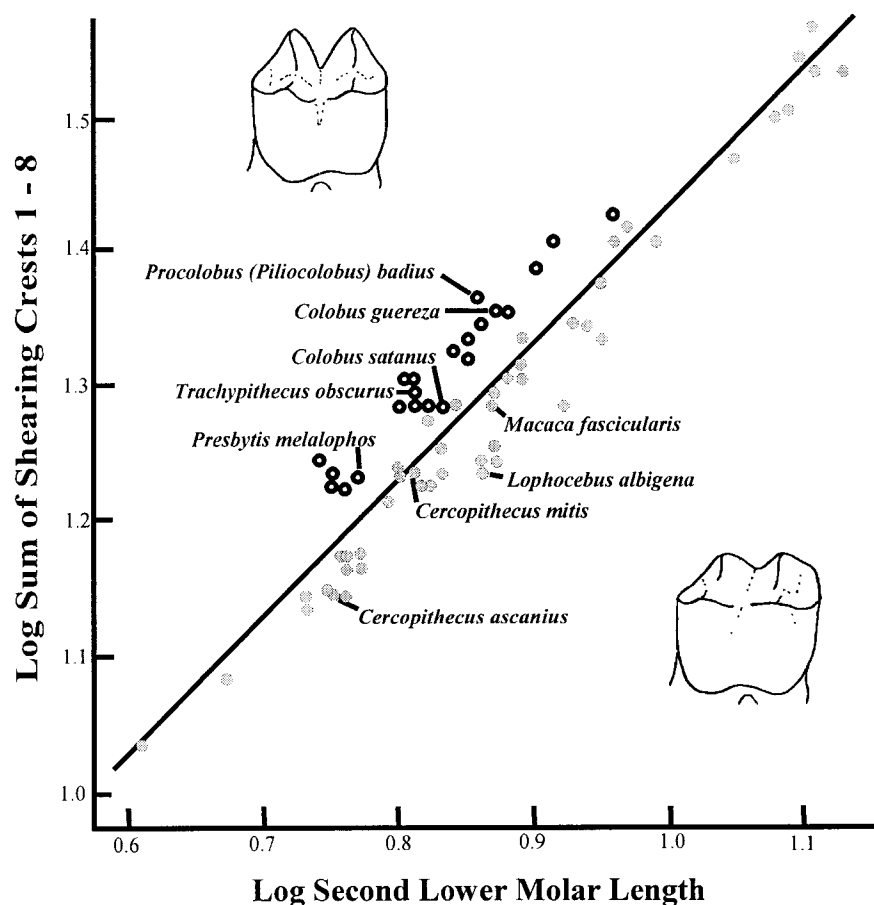
Figure 3. Regression of summed shearing crest length (mm) versus second lower molar length (mm) for cercopithecoids (data courtesy of Richard Kay). Closed circles = colobines, open circles = cercopithecines. Cercopithecine data were used to generate the graph.

but one of these taxa, SQs fell within the frugivorous extant hominoid range. The exception, *Simonsius grangeri,* had longer crests, suggesting folivory. Kay[36] also suggested that the SQs of most early Miocene African catarrhines, including *Proconsul, Dendropithecus,* and *Limnopithecus,* had shearing crests consistent with frugivory, though *Rangwapithecus* had longer crests suggesting folivory.

Ungar and Kay[37] also applied this technique to European Miocene catarrhines and again identified considerable variation, with SQs suggesting a range of diets from folivory to soft-fruit frugivory to hard-object feeding (see Fig. 4, Box 1). Further, Kay and colleagues have quantified SQs for fossil platyrrhines, comparing values with those for extant frugivorous platyrrhines. These results again suggest a range of diets, including insects, leaves, soft fruits, and hard fruit seeds.[1,80] Using two different approaches, Williams and Covert[38] and Strait[39] compared crest lengths for a variety of Eocene omomyids. While their results differed for individual taxa, most taxa had shearing crests of moderate length; none had the extremely long, specialized crests of the "soft-object" faunivore.

SQ studies have not been conducted on early hominids because their cusps are generally low and bulbous. Kay[40]

pected" shearing crest lengths for a given tooth length. The higher the SQ, the relatively longer the crests. Kay's results demonstrate that folivores and insectivores do indeed have higher SQs than do frugivores. Further, among frugivores, hard-object specialists have even lower SQs than do soft-fruit eaters, indicating that the former have extremely blunt teeth designed for crushing.[1,80] This relationship between SQ and diet holds for all major extant primate groups: strepsirrhines, platyrrhines, cercopithecoids, and hominoids.

SQ studies have been applied to the fossil record by superimposing extinct primate values on an extant primate regression plot. In this way, results for fossils can be compared with those for a baseline series of living primates. For example, Kay and Simons[35] examined shearing crest lengths for several Oligocene anthropoids from the Fayum Depression in Egypt. For all
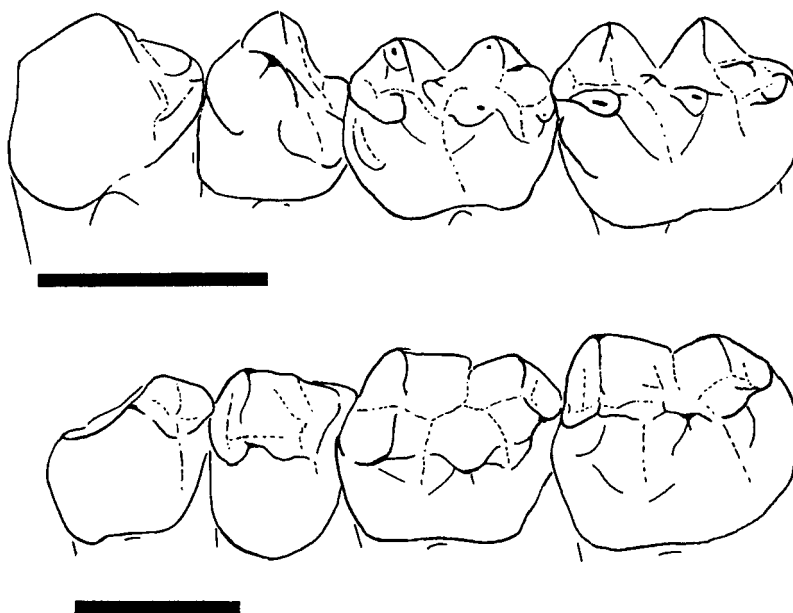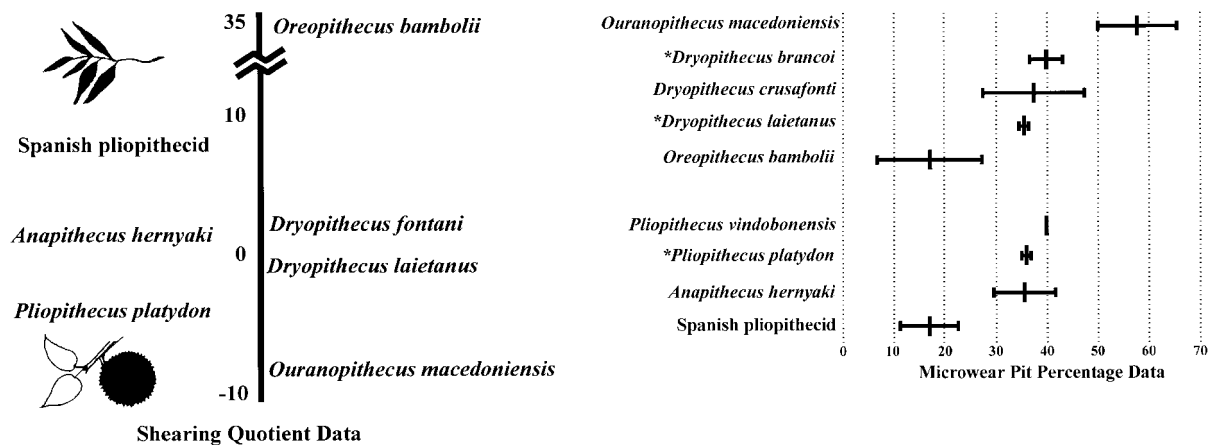

Figure 4. Occlusolateral views of the right lower third premolar through second molar of *Oreopithecus bambolii* (top) and *Ouranopithecus macedoniensis* (bottom). Note differences in cusp height and shearing crest lengths. Scale bars = 2 cm.

Box 1. Reconstructing the Diets of European Miocene Apes

Shearing quotient data (left) and microwear pit percentages (right) for European Miocene apes. For the bottom graph, vertical lines indicate mean values and horizontal lines indicate standard deviations (except if indicated by an asterisk, in which case they represent ranges—n = 2). Data from Ungar[74] and Kay and Ungar.[37]

Most paleoanthropologists agree that the split among living great apes and that between humans and African apes occurred during the latter part of the Miocene epoch. We know little about the circumstances surrounding these divergences because there are so few fossil hominoids from the late Miocene of Africa. Still, we can look to the comparatively abundant European fossil record for clues concerning the diversity of ape adaptations at the time. There were basically two groups of ape-like primates in Europe during the middle to late Miocene: a relict group of primitive catarrhines, the pliopithecids (e.g., *Anapithecus* and *Pliopithecus*) and a group of great apes (*Dryopithecus, Oreopithecus,* and *Ouranopithecus*). Aspects of the diets of these taxa have been reconstructed using both dental microwear and molar shearing crest analyses.[37,74]

The shearing crest and occlusal surface lengths of available unworn or nearly unworn lower second molars were measured for individuals representing seven species of European Miocene apes. Actual shearing crest lengths for each taxon were compared to those expected for living frugivorous apes given occlusal surface length by computing SQs. Positive SQs indicate longer crests than expected of a soft-fruit eater, whereas negative SQs suggest shorter crests. Further, second molars of nine European Miocene fossil primate species were examined by scanning electron micros-

copy at 500× magnification. Photomicrographs were taken of those crushing surfaces that preserved antemortem microwear. The ratios of pits to scratches on those surfaces were calculated following usual procedures (see text).

Results from both the shearing crest and microwear studies lead to remarkably similar dietary reconstructions. First, the shearing crest study indicates extremely long shearing crests for *Oreopithecus bambolii* and the pliopithecids from Castell de Barbera, Spain, suggesting a diet dominated by leaves. In contrast, *Ouranopithecus macedoniensis* had very blunt crests, more like those of extant monkeys that feed on hard objects. *Anapithecus hernyaki, Pliopithecus platydon, Dryopithecus fontani,* and *Dryopithecus laietanus* were intermediate, with SQs hernyaki, Pliopithecus platydon, Dryo pithecus fontani, and *Dryopithecus la-iclustered within the range of those extant hominoids that eat soft fruits.*

The microwear results also suggest three groupings of taxa, with *Ouranopithecus macedoniensis* showing the greatest incidence of pitting, *Oreopithecus bamboli* and the pliopithecid from Castell de Barbera having the greatest incidence of scratches, and a cluster of taxa, including *Dryopithecus brancoi, D. crusafonti, D. laietanus, Pliopithecus vindobonensis, P. platydon,* and *Anapithecus hernyaki* having intermediate pit percentage values.

The degree of difference between *Ouranopithecus* and the *Anapithecus-Dryopithecus-Pliopithecus* group is comparable to that found between extant hard-object feeders such as *Lophocebus* and *Cebus apella* on one hand and soft-fruit eaters, including *Pan troglodytes* and *Cebus capucinus* on the other. Further, the difference hernyaki, Pliopithecus platydon, Dryopithecus fontani, and *Dryopithecus lai hernyaki, Pliopithecus platydon, Dryopithecus fontani,* and *Dryopithecus lai-between the Anapithecus-Dryopithecus-Pliopithecus group and the Oreopithecus-Castell de Barbera pliopithecid group is comparable, on one hand, to that between soft-fruit eaters such as Pan troglodytes and Cebus capucinus and, on the other,* to folivores such as *Colobus guereza and Alouatta palliata.*

In sum, both the microwear and shearing crest data indicate substantial dietary diversity for both pliopithecids and hominoids during the middle to late Miocene in Europe. In both cases, *Ouranopithecus* comes out looking like a hard-object feeder. *Oreopithecus* and the pliopithecid from Castell de Barbera appear to have been folivores, and the other taxa (*Anapithecus, Dryopithecus* spp., and *Pliopithecus* sppi) were evidently soft-fruit eaters. This range of variation exceeds that among living hominoids and offers insights into the adaptive radiations of pliopithecids and hominoids during the late Miocene.[37]

noted that "gracile" australopithecine cheek teeth show more occlusal relief than do those of "robust" early hominids, although *Australopithecus* still shows much less shearing emphasis than does any living folivorous ape.

While studies of shearing crest length accurately predict diet for many living primate groups, it should be noted that, as with incisor size comparisons, SQ values cannot be compared directly among higher-level taxa. For example, while shearing quotient accurately tracks diet in cercopithecoids or hominoids, Old World monkeys have relatively longer shearing crests than apes do when diet is controlled for.[41] Therefore, phylogeny also plays an important role in determining crest length. As with studies of tooth size, morphology should be interpreted within the context of phylogeny.

Kay and Ungar[27] have recently suggested an additional twist to this phenomenon when examining the fossil record. Although the molars of early Miocene apes show a substantial range of morphological variation (about equal to that of living apes), this range is downshifted from that of modern hominoids. Just as extant hominoids have less well-developed shearing crests than do cercopithecoids as a whole, these early Miocene apes have less well-developed shearing crests than do extant hominoids or, for that matter, middle to late Miocene European catarrhines. Interestingly, the shift toward longer crests seems to have occurred independently in middle to late Miocene hominoids and pliopithecids. Because this trend evidently cross-cuts phylogenetic boundaries, we may be looking at a temporal rather than a phylogenetic phenomenon, perhaps related to competition with evolving Old World monkeys or some other factor.

Dental Biomechanics

Since the 1980s, workers have begun to develop biomechanical models of primate dental morphology by considering idealized shapes for teeth designed to break down foods with given mechanical properties.[29,42] Strait[39] recently reviewed this topic in Evolutionary Anthropology. The basic idea is that natural selection dictates that pri-

mate tooth shape should reflect the mechanical properties of foods: occlusal morphology should be well-suited to break down the foods that primates eat habitually. As Spears and Crompton[42] note, dental morphology affects the nature, magnitude, and distribution of stress on food particles. Thus, an understanding of the mechanisms of food "failure" (fracturing or crack propagation), should make it possible to predict the most efficient tooth morphology for breaking down a food item having given material properties.

Dental biomechanics researchers point out that "crush," "grind," and "shear" all denote different types of food fracture, each of which can be complex. Lucas and Teaford,[29] for ex-

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ample, prefer to think of food breakdown in mechanical terms such as strength, or the stress necessary to cause a structure to start to fracture or permanently deform, and fracture toughness, or the resistance to propagation of a crack. The tooth form best suited to fragment a given food item depends on the strength and fracture toughness of that item.

Work to assess relationships between food properties (rather than general food categories) and actual tooth shape is now beginning. Strait,[15] for example, has found that faunivorous mammals that eat soft moths, caterpillars, and worms have longer shearing crests than do those that habitually consume hard-shelled beetles.

Yamashita[43] has recently extended this line of work by examining the hardness and shear strength of foods eaten by five Malagasy primate taxa. While many of her individual predictions for shearing crest lengths do not hold, this approach does appear be a promising means of allowing us to test hypotheses concerning relationships between tooth shape and food properties and, ultimately, to understand dental design.

DENTAL WEAR

Studies of Gross Tooth Wear

Many dental anthropologists have considered the dietary implications of gross tooth wear in prehistoric human populations,[44] but comparatively little work has been done to assess the functional implications of gross tooth wear in nonhuman primates. That which has been done focused on wear gradients, unusual patterns of wear, and the extent and inclination of wear facets on molar teeth. Meikle,[45] for example, noted that *Theropithecus* shows substantial wear gradients between anterior and posterior cheek teeth, suggesting rapid wear and a highly abrasive diet. Further, Teaford[46] compared wear gradients between species of primates, noting that macaques show steeper wear gradients than langurs do. He suggested that such differences might be related to diet.

Other workers have identified unusual patterns of wear on teeth, which they have related to diet and tooth use. For example, Kilgore[47] suggested that approximal grooves between the incisors of Gombe chimpanzees might relate to stripping foods such as the husks of palm fronds. Approximal grooves have been reported for several fossil hominid taxa, and have been explained by a variety of causes, from hydrolic patterns of grit-laden saliva[48] to toothpick use.[49]

Other workers have examined wear facet inclination and extent. Butler[50] noted that teeth preserve attritional facets as the result of tooth-to-tooth contact, and that these facets record a small part of jaw movement. Grine[51] further pointed out that facet inclination indicates whether teeth contact one another steeply, as in shearing, or head-on, as in crushing. He also ar-
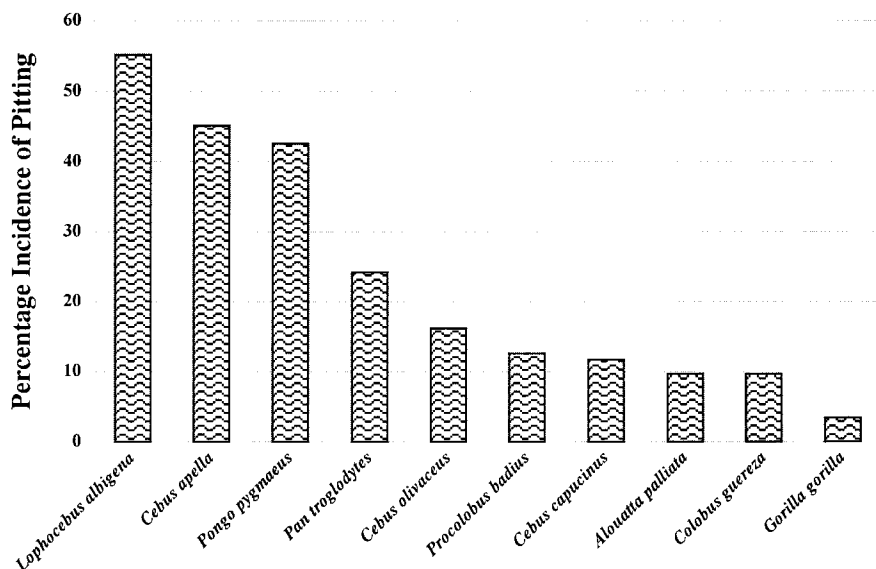
Figure 5. Dental microwear molar pit percentages for various extant primates having known differences in diet (based on data reported by Teaford[64]).

gued that the sizes of Phase II versus Phase I facets evince the relative importance of grinding and shearing in early hominids. Janis[52] extended this line of reasoning, looking at the relative extent of each wear facet associated with crushing or shearing behaviors. She found, for example, that the seed-eater *Colobus satanus* has larger crushing facets than does the more folivorous *C. guereza,* which has larger shearing facet areas for a given degree of wear.[52] Studies of this sort may have value for inferring the diets of fossil primates, but more quantitative work needs to be done on gross tooth wear in living primates to realize that potential.

Studies of Microscopic Tooth Wear in Extant Primates

Many studies have explored the functional implications of microscopic patterns of tooth wear (dental microwear). Phillip Walker[53] can be credited with the first effort to associate microscopic wear on nonhuman primate teeth with diet. As a result of his light microscopic examination of the incisors of a series of living cercopithecoids, he related differences among taxa to differences in ingestive behaviors and feeding substrate.

Teaford and Alan Walker[54] were the first to conduct a quantitative study of molar microwear in a variety of primate species with known differences in diet. Using scanning electron microscopy to examine tooth surfaces, these workers quantified feature densities and dimensions on homologous facets of homologous teeth at a fixed magnification of 500×. They found that frugivores (*Lophocebus, Cebus, Pongo,* and *Pan*) had higher ratios of microscopic pits to scratches than did folivores (*Colobus, Gorilla, Alouatta*). Further, among frugivores, hard-object specialists (*Lophocebus* and *Cebus apella*) had the highest relative frequencies of pits (Fig. 5). Teaford[55,56] confirmed these microwear-diet associations in subsequent studies of both Old World and New World monkeys. He and his coauthors have even identified intraspecific differences microwear patterns in *Cebus olivaceus*[57] and *Alouatta palliata*.[58] They found that these differences reflect seasonal and ecological zone differences in diet, but are not of a magnitude that obscures differences between species.

Quantitative work has also progressed on examinations of microwear on incisor teeth and their relation to feeding behavior. For example, the incisors of *Cebus olivaceus* have higher densities of microwear features than do the incisors of *Alouatta seniculus*.[59] Because capuchins use their incisors more in ingestion than do howler monkeys, microwear density can be related to degree of anterior tooth use on abrasive foods. Further work with Sumatran anthropoids (*Hylobates lar, Ma-*

caca fascicularis, Pongo pygmaeus, and *Presbytis thomasi*) has confirmed this association and suggested not only that incisor microwear orientation can be related to processing techniques, but that microwear feature size may be related to the sizes and shapes of dietary abrasives (see Box 2).[60]

Dental microwear has now been examined for about thirty genera of extant primates from all major groups.[59-64] Work is continuing to delineate the processes of microwear formation and to tease apart variables that can affect microwear formation.[65–67]

PALEONOTOLOGICAL APPLICATIONS TO DENTAL MICROWEAR ANALYSIS

Associations between aspects of diet and microwear in living primates have also been used to infer the diets of fossil primates. Several of these studies have focused on hominids. For example, Walker[9] suggested that microwear on the cheek teeth of East African early hominids resembled that on corresponding teeth of living frugivores such as mandrills, chimpanzees, and orangutans. Similarly, Ryan and Johanson[68] compared incisor microwear in *Australopithecus afarensis* and extant primates and proposed that these early hominids show a mosaic of gorilla and baboon-like features indicative of the use of incisors to strip gritty plant parts such as seeds, roots, and rhizomes. In addition, Grine[51,69] suggested that among South African early hominids, *Australopithecus africanus* molars had more striated occlusal facets, whereas *Paranthropus robustus* molars had more heavily pitted surfaces. This suggests that the "robust" australopithecines consumed small, hard objects, whereas the "gracile" forms ate softer foods such as fruits and immature leaves. Ungar and Grine[83] also found evidence for incisor microwear density differences between these hominids, implying that *Australopithecus* used its front teeth more during the ingestion of abrasive foods than did *Paranthropus.*
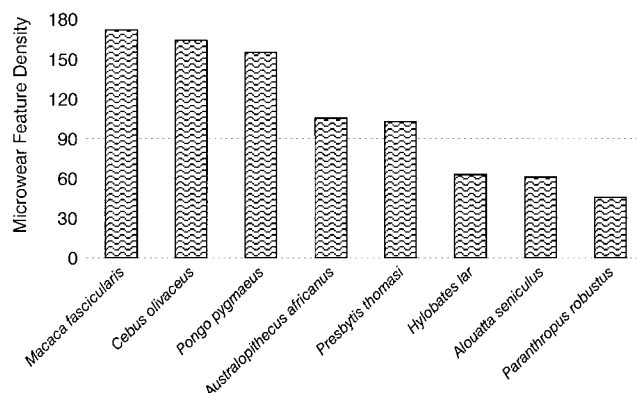
Microwear studies are also now used to infer the diets of other fossil primates, including species from every epoch in which true primates are known. For example, Strait[39] has ex-

Box 2. Incisor Microwear and Paleobiological Inference

Most quantitative studies of dental microwear have focused on molar teeth, which have been very useful for inferring food preferences of early hominids and other fossil primates. Incisor microwear can also provide important insights, into the ingestive behaviors of extinct forms. The inference of ingestive behaviors from microwear on fossil incisors requires an understanding of the relationships between front tooth use and microwear in living primates. A study of Sumatran anthropoids provides an example.

Ingestion is an important aspect of feeding behavior. Primates differ in the ways they acquire and prepare foods for consumption. This provides one way that sympatric species can partition their niches. For example, gibbons at the Ketambe Research Center on Sumatra use their incisors less than do sympatric macaques, orangutans, and langurs, both for food acquisition and processing.[82] Gibbons typically procure foods (e.g., the fruits of *Sapium baccatum*) with their hands and place them in their mouths without incisor use; macaques, langurs, and orangutans more often nip foods from the branch with their front teeth. Further, gibbons often do not use their front teeth when consuming fruits (e.g., *Mallotus sphaerocarpus*), whereas other sympatric primates often use their incisors to break through tough fruit skins or hard husks. Such differences in ingestive behaviors can be explained both by dietary differences and other aspects of each primate's biology and ecology.

Incisor microwear studies also show significant differences among these taxa, including lower densities of microwear for gibbons than for the other species. This suggests that microwear density relates to degree of incisor use during the ingestion of abrasive foods. An association between feature density and degree of incisor use is supported by a study of platyrrhines that showed higher densities of incisor microwear for Venezuelan capuchins than for howler monkeys.[59] The capuchins evidently use their front teeth more to prepare abrasive foods than do sympatric red howlers—again, even when considering individual food items such as the palm fruits *Copernicia tectorum.*

Other differences in incisor microwear patterns can also yield important insights into ingestive behavior differences. For example, high incidences of horizontally oriented scratches are consistent with observations that orangutans often strip foods laterally across the mouth.[82]

We can make use of these and other associations between anterior tooth use and incisor microwear to infer fossil primate feeding behaviors. Many researchers have argued, on the basis of differences in the shapes of their skulls and the sizes of their front teeth, that *Australopithecus africanus* and *Paranthropus robustus* differed in their ingestive behaviors.[2] Incisor microwear provides a unique opportunity to test this hypothesis using evidence of actual tooth use rather than evidence from inferred adaptations. A study by Ungar and Grine[83] showed that "gracile" australopithecines had higher densities of microwear features on all incisor surfaces examined than did "robust" forms. Microwear evidence therefore corroborates the theory that *Australopithecus* used their front teeth more to ingest abrasive foods than did *Paranthropus.*

Microwear density averages on the incisors of these hominids can be compared with those for living primates. While differences in the abrasives available in different environments may make it difficult to infer actual degrees of incisor use for the fossil species,[66] we can get some idea of the magnitude of differences between extinct taxa. For example, the degree of difference in incisor use between *Australopithecus* and *Paranthropus* was probably on the same order of magnitude as that between living gibbons and orangutans, or between capuchins and howler monkeys.

Average number of microwear features on the maxillary central incisor labial surfaces of various primate taxa. Counts are per field of view (=0.125 mm²) on micrographs taken at 200× magnification. Data from Ungar[60,85] and Ungar and Grine.[83]

amined dental microwear in several small-bodied Eocene omomyids. Her results suggest that these primates were mostly "hard-object" generalists. Further, Teaford, Maas, and Simons[70] have recently examined molar microwear in Oligocene catarrhines, including *Aegyptopithecus, Parapithecus,* and *Apidium.* Their evidence suggests that these primates were mostly frugivorous, though there were some differences among these forms.

As for Miocene primates, researchers have examined the Asian genera *Gigantopithecus* and *Sivapithecus;*[54,71] the African forms *Dendropithecus, Micropithecus, Proconsul, Prohylobates,* and *Rangwapithecus;*[72,73] and the Euro-

pean taxa *Anapithecus, Dryopithecus, Oreopithecus, Ouranopithecus,* and *Pliopithecus*[74] (See Figure, Box 1). Molar pit percentages suggest a broader variety of food preferences than is seen in living apes, ranging from hard-object feeding (e.g., *Ouranopithecus*) to soft-fruit frugivory (e.g., *Gigantopithecus, Sivapithecus, Dendropithecus, Proconsul, Anapithecus, Dryopithecus,* and *Pliopithecus*) to diets including more leaves (e.g., *Rangwapithecus* and *Oreopithecus*).

Workers have also studied microwear patterns on the molars of Plio-Pleistocene cercopithecoids such as *Cercocebus, Cercopithecoides, Colobus, Papio, Paracolobus, Rhinopithecus,* and *Theropithecus,*[75,76] many of which, but not all, show patterns comparable to modern analogs. For example, the colobine *Cercopithecoides* shows microwear on its nonocclusal surfaces that is consistent with terrestrial feeding, a scenario supported by its locomotor skeleton. Finally, workers have even begun to apply dental microwear techniques to the study of dietary diversity in subfossil primates from the late Pleistocene of Madagascar.[77]

DISCUSSION

Differences among living primates in tooth size, morphology, and wear have all been related, to some degree, to differences in diet or tooth use. Further, fossil primates vary in patterns of dental wear, and in the sizes and shapes of their teeth. Therefore, dental evidence should be of some value in reconstructing the feeding adaptations of past primates. Still, there are limits to what this evidence can currently tell us.

Function, Phylogeny and Clues From Dental Microwear

One major "wrench in the works" for any study of adaptation is the difficulty of separating the confounding effects of phylogeny from function. The sizes and shapes of primate teeth are clearly influenced by both factors. For example, while incisor size differences between closely related anthropoid species can evidently be explained by differences in anterior tooth use, platyrrhines have relatively
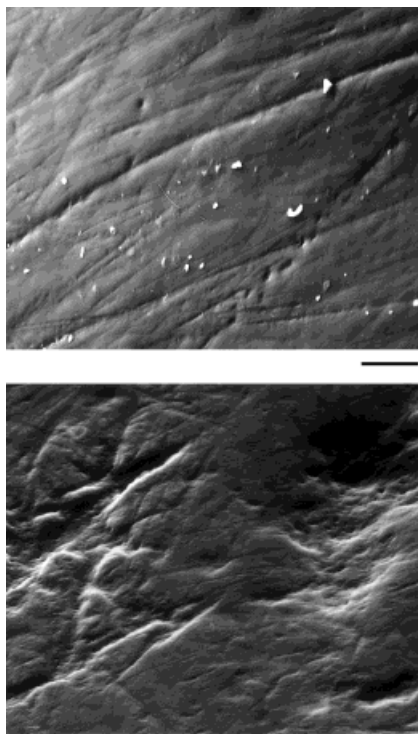

Figure 6. Electron micrographs of second molar Phase II wear facets of two apes from the late Miocene of Europe, *Oreopithecus bambolii* (top) and *Ouranopithecus macedoniensis* (bottom). Note the differences in patterns of scratches and pits. Scale bars = 25 μm.

smaller incisors than do catarrhines when diet is controlled for.[22] Similarly, among closely related primates "folivores have longer molar shearing crests than do frugivores, but cercopithecoids have longer shearing crests than do hominoids, independent of dietary differences.[41] These results suggest that morphological specializations related to dietary differences evolved in similar directions, but from different starting points. In the case of incisor size, the common ancestor of extant catarrhines had larger front teeth than did the first platyrrhines.

So can we directly relate differences in tooth size and shape to dietary differences in distantly related fossil taxa or those with unknown phyletic affinities? Perhaps not. The comparative method depends on direct comparison of fossil tooth size or shape with that of an appropriate neontological baseline series. We can gain some control over phylogenetic effects by comparing fossil species with extant taxa from the same adaptive radiation. When trying to infer diet, it is more

appropriate to compare the dental anatomy of a fossil Old World monkey to that of a series of extant cercopithecoids than to that of a series of extant platyrrhines. Still, basal taxa or those of uncertain phylogenetic affinities present a real problem.

Can we hope to know anything about the diets of basal taxa or fossil primates with uncertain phyletic affinities? Perhaps. Kay and Ungar[27] recently suggested one possible approach. If, as stated, diet-related morphological differences evolve in similar ways from different starting points, the amount

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of variation in such attributes among groups of primates can still be compared directly. For example, early Miocene catarrhines from East Africa show a range of shearing crest development similar to that of extant hominoids, although living apes generally have longer crests than do these fossil forms. It is likely that those early Miocene taxa with the longest crests (e.g., *Rangwapithecus*) were more folivorous than those with shorter crests, even though SQ values for these fossil species fall within the range of extant frugivorous hominoids. As Ungar and Kay[37] suggest, where a group of fossils
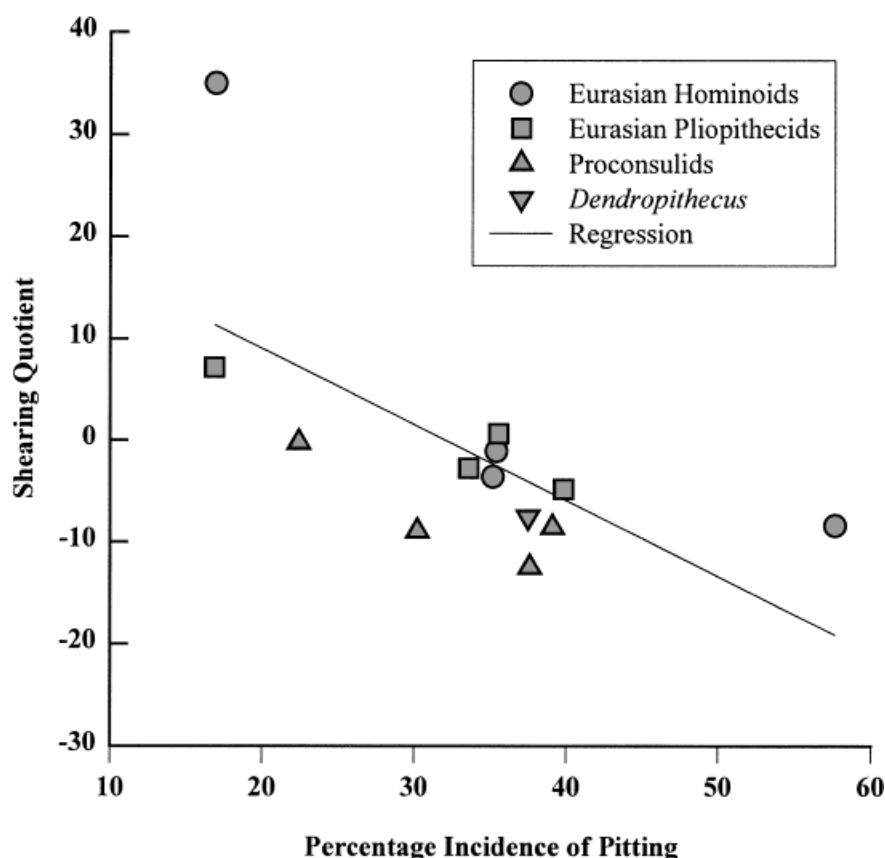
Figure 7. Regression of shearing quotient and dental microwear molar pit percentages for various Miocene catarrhine taxa (symbols represent taxa). Each symbol represents averaged values for one species. Data from[72] and work in progress by the author, Mark Teaford, and Richard Kay.

shows a greater range of shearing crest values than does an extant comparative baseline series, the fossils probably had a greater range of dietary adaptations.

Unfortunately, it is difficult to test such ideas without some clue to diet that does not depend on identifying a morphological starting point. Fortunately, dental microwear may provide one such clue. Microwear pit percentages and SQ values can both be used to separate folivores from frugivores and, among frugivores, hard-object from soft-object feeders. For example, because *Rangwapithecus* has low microwear pit percentages, it is likely that the range of SQ values for extant apes has been shifted upward as compared with the early Miocene forms.

In fact, a rank correlation test indicates that SQ and pit percentage values for fossil Miocene catarrhines covary significantly.[72] Early Miocene African forms fall below a least-squares regression line, indicating that these species have relatively lower shearing crest values for a given pit percentage (Fig. 7). This is consistent with the interpretation that the early Miocene African forms as a group had shorter shearing crests than did later Eurasian apes. This may suggest an evolutionary trend (or trends) towards longer crests in later apes, independent of diet. Perhaps, then, microwear can help separate function from phylogeny, even among fossil primates.

Other Limits on Dental Evidence for Primate Diets

Other limits of dental evidence suggest future avenues of research for paleobiologists. First we must have a better handle on the mechanics of food breakdown and how they relate to the sizes and shapes of primate teeth. Why is it that among cercopithecoids folivores have smaller molars relative to body size than do frugivores, whereas the reverse is true for other primates? Further, while the lengths of shearing crests are good predictors of diet when considering unworn molar teeth, how does wear figure into the equation? Wear can have a dramatic effect on tooth morphology. We need to understand how this affects tooth function and the efficiency with which different sorts of foods are eaten.

We also must get a better grasp on primate diets and tooth use. Many primate species have a strong preference for certain staples, but most take a diverse array of foods.[78] During my first couple of weeks at the Ketambe Primate Research Center in Sumatra, for example, I saw that colobines ate

Why is it that among cercopithecoids folivores have smaller molars relative to body size than do frugivores, whereas the reverse is true for other primates? Further, while the lengths of shearing crests are good predictors of diet when considering unworn molar teeth, how does wear figure into the equation?

mostly fruit, whereas macaques focused on immature leaves! I was nearly ready to pack my bags and go home when this pattern reversed itself. Categorizing primates as "frugivores" and "folivores" may be masking considerable variation in diet and tooth use.

Other sorts of differences in feeding behaviors may also have important implications for the study of dental evidence of diet. For example, many workers have reasoned that fruits require more incisal preparation than leaves do, so that frugivorous primates would have larger incisors than folivores. Naturalistic study has demonstrated that this need not be the case.

Lar gibbons are fruit specialists, but they tend to consume smaller fleshy fruits that require little if any incisal preparation—and they have relatively small incisors.[25]

It is also important to note that teeth can be adapted to foods other than those most frequently eaten if those foods are important dietary resources.[32] Such factors need to be taken into account if the resolution of our dietary reconstructions for fossil primates is to improve. Still, we can take some consolation in the knowledge that primates do show tendencies. Sussman[79] has identified species-specific dietary adaptations wherein primates of a given species in different forests tend to eat similar sorts of foods even when the same plant taxa are not available in each.

Finally, we need a better understanding of dental microwear. For example, we need to work on isolating the many factors that affect wear, such as the underlying structure of tooth enamel.[65] We must also appreciate that individual microwear features can be obliterated rather quickly, which means that microwear on an individual tooth gives information only on diet representing at most a few days.[81] Although there are certainly limits to what microwear can tell us, many of the difficulties associated with this approach can probably be obviated with good comparative baseline analyses and large fossil samples.

SUMMARY AND CONCLUSIONS

What, then, can dental evidence tell us about the diets and feeding behaviors of fossil primates? That depends on what dental evidence can tell us about the diets and feeding behaviors of living primates. If we can control for phylogeny, incisor size seems to reflect degree of front tooth use in ingestion, at least in anthropoids. Incisor microwear also provides information about feeding behaviors, such as degree of front tooth use and directions in which foods are pulled across the front of the mouth during ingestion. Such information may provide important clues to feeding adaptations and perhaps even niche separation in primate communities if the fossil record is detailed enough to document sympatry. We can feel reasonably confident in our reconstruc-

tions when incisor size and anterior dental microwear evidence lead to similar conclusions.[83]

As for molar morphology and microwear, these can give important clues to the material properties of foods habitually eaten by primates. Long molar crests and high densities of molar microwear scratches reflect tough foods, such as leaves. In contrast, bunodont molars and high frequencies of microwear pits are consistent with brittle, "harder" foods, such as nuts. Soft fruits are of intermediate fracture toughness, and are reflected in an intermediate molar morphology and microwear pit percentage. As with ingestive behavior inferences, reconstructions of food properties are most robust when microwear and shearing quotients suggest similar diets.[74]

There is probably a lot that we cannot know. Still, further comparative study will likely allow us to learn more. Also, other lines of evidence for diet should be considered and incorporated into reconstructions. Such lines include dental evidence, such as enamel thickness and structure as well as nondental studies of, for example, cranio-mandibular remains and bone chemistry.

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