Dental topography and diets of *Australopithecus afarensis* and early *Homo*

Peter Ungar*

*Department of Anthropology, University of Arkansas, Old Main 330, Fayetteville, AR 72701, USA*

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**Abstract**

Diet is key to understanding the paleoecology of early hominins. We know little about the diets of these fossil taxa, however, in part because of a limited fossil record, and in part because of limitations in methods available to infer their feeding adaptations. This paper applies a new method, dental topographic analysis, to the inference of diet from fossil hominin teeth. This approach uses laser scanning to generate digital 3D models of teeth and geographic information systems software to measure surface attributes, such as slope and occlusal relief. Because it does not rely on specific landmarks that change with wear, dental topographic analysis allows measurement and comparison of variably worn teeth, greatly increasing sample sizes compared with techniques that require unworn teeth. This study involved comparison of occlusal slope and relief of the lower second molars of *Australopithecus afarensis* (*n*=15) and early *Homo* (*n*=8) with those of *Gorilla gorilla gorilla* (*n*=47) and *Pan troglodytes troglodytes* (*n*=54). Results indicate that while all groups show reduced slope and relief in progressively more worn specimens, there are consistent differences at given wear stages among the taxa. Early *Homo* shows steeper slopes and more relief than chimpanzees, whereas *A. afarensis* shows less slope and relief than any of the other groups. The differences between the two hominin taxa are on the same order as those between the extant apes, suggesting similar degrees of difference in diet. Because these chimpanzees and gorillas differ mostly in fallback foods where they are sympatric, results suggest that the early hominins may likewise have differed mostly in fallback foods, with *A. afarensis* emphasizing harder, more brittle foods, and early *Homo* relying on tougher, more elastic foods.

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**Keywords:** Diet; Molars; Hominins; Dental functional morphology

**Introduction**

Diet is an important key to understanding the ecology of living primates (Fleagle, 1999). It should be expected, then, that changes in feeding adaptations played an important role in the origins and early evolution of our own tribe and genus. It is difficult to determine the extent of this role, however, because of our limited knowledge of early hominin diets. This is due in part to a limited fossil record, and in part to limitations in methods available to infer dietary adaptations from the
fossils we do have. The study described here examined early hominin dental functional morphology using a new technique, dental topographic analysis. Results suggest that *Australopithecus afarensis* molars have less occlusal slope and relief than chimpanzees or gorillas, whereas early *Homo* molars have values intermediate between those of the two extant apes. This implies differences in diet between the hominins, with early *Homo* having the potential to consume tough, deformable foods (i.e., those that resist crack propagation) more efficiently than could *A. afarensis*.

**Background**

Reconstructs of fossil primate diets are often based on studies of tooth shape. Researchers have recognized form–function relationships between dental morphology and diet for a long time, and have focused much attention on unraveling these relationships (e.g., Owen, 1840–1845; Gregory, 1922; Crompton and Sita-Lumsden, 1970; Kay and Hiiemae, 1974; Kay, 1975, 1977, 1978; Rosenberger and Kinzey, 1976; Maier, 1977, 1984; Kay and Hylander, 1978; Kinzey, 1978; Seligsohn and Szalay, 1978; Lucas, 1979). It is clear, for example, that primate folivores and insectivores have reciprocally concave, highly crested teeth adapted for shearing, whereas frugivores and hard-object specialists have rounder, flatter teeth adapted for crushing and grinding.

Kay and colleagues (Kay, 1978; Kay and Hylander, 1978; Kay and Covert, 1984) have recognized that comparisons of occlusal form between species require a quantitative approach. Their shearing quotient (SQ), for example, is calculated as a residual from a regression of the summed length of mesiodistal crests over the length of the occlusal table for a series of closely related species with a given type of diet. The higher the SQ, the longer the shearing crests relative to expectation of a species with that diet. The lower the SQ, the shorter the shearing crests relative to expectation. Comparative studies have confirmed that folivores and insectivores have higher SQs than closely related frugivores, and that among frugivores, hard-object specialists have the lowest SQ values (Anthony and Kay, 1993; Strait, 1993; Meldrum and Kay, 1997). Studies of SQ have been applied to a wide range of fossil primates, leading to important dietary inferences for many extinct species (e.g., Kay, 1977; Kay and Simons, 1980; Anthony and Kay, 1993; Strait, 1993; Williams and Covert, 1994; Ungar and Kay, 1995; Fleagle et al., 1996; Meldrum and Kay, 1997; Benefit, 2000).

While this approach has brought new insights regarding the diets of some fossil primate taxa, methodological limitations have prevented them from being broadly applied to infer early hominin diets. The problem is that shearing crests are measured as distances between cusp tips and the notches between cusps. Crest lengths change with attrition, and quickly become impossible to measure as cusp tips are obliterated by wear. Thus, SQ studies are limited to unworn teeth. Few, if any, early hominin taxa are well enough represented by unworn teeth to allow statistical comparisons with extant baseline series. There are, for example, fewer than 10 unworn M2s in the entire collection of published australopith teeth from South Africa (Ungar et al., 1999). The picture for early *Homo* is even bleaker, with no available unworn M2s of *H. habilis*, *H. rudolfensis*, or African *H. erectus*.

Despite these limitations, there are intimations in the literature that early hominins differed from one another in functional aspects of tooth shape (Kay, 1985). Grine (1981, 1984), for example, suggested that *Australopithecus africanus* cheek teeth have more occlusal relief than do those of *Paranthropus robustus*. This is consistent with the limited SQ results available (Ungar et al., 1999). In the latter study, the species average SQ for “ gracile” australopith M2s was found to be higher than the “robust” australopith average SQ value, though mean values for both taxa were lower than those of extant apes in the comparative baseline series. This suggests that neither species was well-suited to processing tough, deformable foods, and that *P. robustus* teeth would have been particularly adept at crushing brittle, inelastic items that are less resistant to crack propagation.

No SQ analyses have been published for any other early hominin species (again, in large part because of a lack of sufficient unworn teeth for
analysis). Nevertheless, significant variation among taxa would be expected given apparent differences in gross morphology. As Teaford and coauthors (Teaford et al., 2002: 153) recently wrote, “while it appears that *H. habilis* and *H. rudolfensis* had somewhat more occlusal relief than did the australopiths, this difference is difficult to assess given current methods for quantifying occlusal relief” (Fig. 1).

**Dental topographic analysis**

Dental topographic analysis offers a new approach to the quantification of occlusal relief that allows consideration of both worn and unworn teeth (Ungar and Williamson, 2000; M’Kirera and Ungar, 2003; Ungar and M’Kirera, 2003; Dennis et al., in press). A laser scanner is used to generate 3D points along the surface of a tooth, and these points are used in a geographic information system (GIS) to model and characterize that surface as a whole. Dental topographic analysis has the advantage over traditional SQ studies in that measurements do not rely on specific landmarks that erode with the onset of wear.

Recent studies of extant primate dental topography have shown this approach to be an
effective way to model and compare the shapes of variably worn molar teeth (Ungar and Williamson, 2000). Scoring teeth by wear stage allows direct comparisons of shape data among similarly worn specimens of different species. Such attributes as average surface slope, occlusal relief, and surface angularity or jaggedness have all been shown to differ between chimpanzees and gorillas when controlling for degree of gross tooth wear (M’Kirera and Ungar, 2003; Ungar and M’Kirera, 2003; see below). Further, a longitudinal study of changes in tooth shape in Alouatta palliata has shown that individuals of that species wear their teeth down in similar ways (Dennis et al., in press). Assuming the pattern holds for other taxa, this suggests that variably worn teeth of different individuals can be used to represent a species, a necessary prerequisite for studies of tooth shape changes with wear for fossil taxa.

**Paleontological applications**

While most early hominin species are not represented by enough unworn specimens of a given tooth type for SQ analysis, there are sufficient numbers of worn specimens of at least some taxa for dental topographic analysis. Australopithecus afarensis presents such a case. This taxon is one of the best represented Pliocene hominins, with well-dated specimens ranging from about 3.7 Ma at Laetoli to 3.0 Ma at Hadar (Drake and Curtis, 1987; Kimbel et al., 1994; Lockwood et al., 2000; see also Ward et al., 1999).

Australopithecus afarensis has been thought to have played a central role in early human evolution since it was first recognized (Johanson and White, 1979), with numerous researchers placing this species on the line leading ultimately to modern humans (see Strait et al., 1997, for review). While recent finds have led some to favor a more complex hominin phylogenetic tree featuring uncertain ancestor-descendant relationships (e.g., Leakey et al., 2001; Lieberman, 2001), A. afarensis remains important to studies of the evolution of human diet. Its occlusal morphology is conservative for early hominins, and its cusps lack the swollen, inflated appearance often seen in later australopiths (White et al., 1981). This species therefore offers a useful model for a generalized australopith from which the occlusal morphology of later hominins, including early Homo, might have been derived.

Studies of occlusal form in early African Homo species (H. rudolfensis, H. habilis, and H. erectus) might likewise provide new insights into the role that diet played in the origin and early evolution of our genus. As with earlier Pliocene hominins, temporal overlap between early Homo species makes it difficult to determine which may have given rise to modern humans. Fossils attributable to H. habilis and H. rudolfensis evidently date to between about 2.4 and 1.65 Ma (Wood, 1991, 1992, 1999; Hill et al., 1992; Bromage et al., 1995; Kimbel et al., 1996; Sherwood et al., 2002). These two species overlap with African H. erectus near the end of their temporal ranges, with the latter dating from at least 1.89 Ma to 660 ka (Wood and Van Noten, 1986; Feibel et al., 1989).

It is not possible at this time to evaluate form–function relationships for individual species of early Homo because of very limited sample size (see Wood, 1991). We might, however, combine H. habilis, H. rudolfensis, and early African H. erectus molars into a single early Homo sample for functional study. The justification for doing so is their evident closer evolutionary relationships with one another than with any known australopith species (Strait and Grine, 2001). While there are no unworn M2s available for early Homo, there are enough worn molars to evaluate differences between this taxon and earlier australopiths.

The study described here is the first quantitative analysis of worn early hominin occlusal morphology. A new technique, dental topographic analysis, is applied to available Australopithecus afarensis and early Homo M2s to examine functional aspects of tooth form. Results for these fossil taxa are compared both to one another and to data from an extant baseline series of chimpanzee and gorilla M2s. Documented differences in morphology, both between the early hominins and between the fossil taxa and the extant apes, offer new insights into the dietary adaptations of both A. afarensis and early Homo.
Materials and methods

Specimens used in this study

High resolution replicas of lower second molars (M2s) were prepared from original teeth of both extant and fossil specimens following conventional procedures. These teeth were chosen because SQ studies have shown that M2 occlusal morphology is very effective for distinguishing hominoids on the basis of their diets (Kay, 1977). Molds of undamaged occlusal surfaces were made using President’s Jet (Colte`ne-Whaledent Corp., Mawah, NJ) regular-body polyvinylsiloxane dental impression material. Casts were poured using Epotek 301 (Epoxy Technologies, Inc., Billerica, MA) epoxy and centrifuged prior to hardening to remove bubbles that would otherwise obscure occlusal morphology. Because laser scanners tend to have difficulty identifying surfaces of translucent epoxy, a pale pink pigment was added to the mix, and replicas were coated with a thin layer of Magniflux SKD-S2 Developer (Illinois Tool Works, Inc, Glenview, IL).

All available M2s of Australopithecus afarensis, Homo rudolfensis, H. habilis, and H. erectus housed at the National Museum of Ethiopia, National Museum of Kenya, National Museum of Tanzania, Transvaal Museum, and the University of the Witwatersrand Department of Anatomy were considered. Most specimens had to be excluded from analysis because taphonomic damage to the crown would affect measurements of surface topography. The list of fossil specimens included in this study is presented in Table 1 (n=15 for A. afarensis and n=8 for early Homo).

The comparative baseline series consisted of variably worn M2s of wild-shot Gorilla gorilla gorilla (n=47) and Pan troglodytes troglodytes (n=54) housed at the Cleveland Museum of Natural History. These taxa were chosen for comparison with the fossil species because these apes are closely related to the hominins, and have similar molar cusp patterns. Kay and Ungar (1997) note the importance of phylogenetic control when applying the comparative method to infer diet from molar morphology. As Kay and Covert (1984) have shown, for example, fundamental differences in tooth form between cercopithecoids and hominoids prevent direct comparison of these taxa. Likewise, autapomorphic traits can even make it difficult to compare closely related taxa. Such is the case with orangutans, which often have crenulations likely to affect average occlusal slope and relief, as well as morphological changes with molar wear.

On the other hand, chimpanzees and gorillas are appropriate for comparisons with early hominins. While early hominins probably did not eat the same exact foods consumed by living African apes, degrees of difference in occlusal morphology can be compared between taxa, potentially offering new insights into differences in mechanical properties of foods eaten by the fossil taxa (see Spears and Crompton, 1996; Kay and Ungar, 1997).

Gorilla gorilla gorilla and Pan troglodytes troglodytes are particularly useful baseline taxa for comparison because of the modest degree to which they differ in the material properties of the foods they consume. At sites where the two taxa are sympatric, such as Lopé, Gabon, chimpanzees and gorillas overlap considerably in their diets, but

Table 1
Specimens used in this analysis (all M2s)

| AL 128-23       | A. afarensis |
| AL 145-35       | A. afarensis |
| AL 188-1        | A. afarensis |
| AL 198-1        | A. afarensis |
| AL 207-13       | A. afarensis |
| AL 241-14       | A. afarensis |
| AL 266-1        | A. afarensis |
| AL 330-5        | A. afarensis |
| AL 333w-1a      | A. afarensis |
| AL 333w-27      | A. afarensis |
| AL 333w-57      | A. afarensis |
| AL 333w-60      | A. afarensis |
| AL 400-1a       | A. afarensis |
| AL 417-1a       | A. afarensis |
| LH 23           | A. afarensis |
| KNM-ER 806      | H. erectus  |
| KNM-ER 992      | H. erectus  |
| KNM-ER 1506     | H. rudolfensis |
| KNM-ER 1802     | H. rudolfensis |
| KNM-ER 3734     | Homo indet. |
| KNM-WT 15000    | H. erectus  |
| OH 16           | H. habilis  |
| OH 22           | H. erectus  |
they also differ, particularly at times of fruit scarcity. At such “crunch” times, gorillas fallback on tougher, more fibrous plant parts, such as leaves and stems, whereas chimpanzees continue to exploit available ripe, succulent fruits (Tutin et al., 1991; Remis, 1997). Differences in their molar topography reflect these differences in their diets (M’Kirera and Ungar, 2003; Ungar and M’Kirera, 2003).

Data acquisition and analysis

Data acquisition and analysis followed the dental topographic approach described in detail elsewhere (M’Kirera and Ungar, 2003; Ungar and M’Kirera, 2003; Dennis et al., in press). First, molar replicas were mounted on a horizontal platform approximating the occlusal plane. Specimens were then rotated about the mesiodistal and buccolingual axes using setscrews to maximize the occlusal surface in top view. Repeatability studies have shown most measurements of specimens oriented in this manner to be precise to within one percent (Ungar et al., 2002).

Specimens were then scanned using a modified Surveyor 500 laser scanner (Laser Design, Inc., Minneapolis, MN) with an RPS 150 rapid profile sensor. This instrument collects elevation data for a surface at fixed intervals in an \( x,y \) plane. The lateral and vertical resolutions of the instrument were both set to 25.4 µm for this study, producing a matrix of 1550 evenly spaced elevations, or \( z \)-values, for each 1 mm\(^2\) in the horizontal plane. Elevations were collected using two offset detectors to avoid missing data resulting from shadowing effects of steep cusps on adjacent low points. Resulting data were output as ASCII files containing lists of \( x,y,z \) coordinates representing the occlusal surface of each specimen.

These ASCII files were opened as data tables in ArcView 3.2 (ESRI Corp., Redlands, CA) with Spatial Analyst and 3D Analyst extensions. Tooth surfaces were interpolated using inverse distance weighting and cropped to include only the occlusal table (defined as the surface above a horizontal plane intersecting the lowest point on the talonid basin when the tooth is oriented as described above [Ungar and Williamson, 2000]). Average slope (in degrees) between adjacent elevations was then calculated for each surface. Further, ArcView was used to create a triangulated irregular network (TIN), which is a series of triangles connecting adjacent data points on each surface. The surface areas of these triangles were tallied to generate a 3D surface area value for the specimen. This value was then divided by the projected horizontal or 2D planimetric area calculated from the \( x,y \) point data and multiplied by 100 to give a dimensionless index of occlusal relief. Relief data included here for the chimpanzees and gorillas were first reported by M’Kirera and Ungar (2003).

Finally, molar replicas were scored for gross wear using Scott’s (1979) method. This method, commonly used with bioarchaeological samples (see Rose and Ungar, 1998), has also proven to be a repeatable, effective approach to characterizing molar wear of extant hominoids (M’Kirera and Ungar, 2003; Ungar and M’Kirera, 2003). Scores based on degree of faceting or dentine exposure of individual cusps were summed as described by Scott (1979). Specimens were arranged into six wear stages based on their Scott score values: 1) 5–9; 2) 10–14; 3) 15–19; 4) 20–24; 5) 25–29; 6) 30–34.

Both average slope and relief data were analyzed using SYSTAT 7.0 (Systat Software Inc., Richmond, CA). Data were rank-transformed to mitigate violation of assumptions required of parametric tests (Conover and Iman, 1981), and two-way ANOVAs with taxon and wear score as factors were conducted for slope and occlusal relief. This allowed assessment of the effects of taxon and degree of wear on each model, as well as the effects of interactions between the two factors. Bonferroni pairwise multiple-comparisons tests were used to determine sources of significant variation for taxon and wear stage differences. As stated above, small sample sizes for *Homo habilis, H. rudolfensis,* and African *H. erectus* made comparisons of these individual species impractical, so they were combined into a single early *Homo* sample for analysis.

It should be noted that combining the early *Homo* sample probably conflates dietary variation among individual species. Wood and Collard (1999) suggested, for example, that *Homo habilis*...
and *H. rudolfensis* retained large australopith-size molar teeth, and thus had a “mechanically more demanding” diet compared with *H. erectus*. While these assertions concerning tooth size have been challenged (McHenry and Coffing, 2000), and the functional significance of molar size differences among higher primates remains unclear (see Ungar, 1998), it would be best to consider species individually if sufficient samples of each become available in the future.

The approach presented here compares early hominin and extant ape specimens with similar degrees of faceting and dentine exposure. Statistical analyses were limited to specimens at wear stages represented by all species (2–4). The fossil hominin specimens all fell within wear stages 1–4, whereas the extant hominoids ranged from stages 2–5. This lack of complete overlap evidently reflects differences between taxa in enamel thickness. Notwithstanding methodological issues concerning the characterization of molar enamel thickness, researchers generally agree that early hominin molars have thicker enamel than do those of chimpanzees or gorillas (e.g., Grine and Martin, 1988). The approach presented here allows comparison of dental morphology between early hominin and extant ape specimens with similar degrees of faceting and dentine exposure. Still, given that enamel thickness can influence rate of wear (Dean et al., 1992), comparisons of specimens at a given wear stage does not necessarily imply comparisons of individuals at similar ages.

**Results**

Results are presented in Figs. 2 and 3 and Tables 2–4. While sample sizes for the fossil hominin taxa are small, two distinct patterns are evident. First, as with the chimpanzees and gorillas, *Homo* and *Australopithecus afarensis* each show decreases in both average occlusal surface slope and relief through successive wear stages. In other words, molar teeth of all four taxa became...
progressively flatter as they wore. Second, differences between early Homo and A. afarensis and between each hominin and the extant ape taxa are fairly consistent for both variables at given stages of wear. Gorilla gorilla specimens tend to have the steepest slopes and most relief, followed by early Homo, then Pan troglodytes, and finally A. afarensis, which has the flattest slopes with the least relief (Fig. 4). Early Homo slope and relief mean values are greater than those of A. afarensis in seven of eight cases (see Table 2). The slope and relief mean values for A. afarensis are smaller than those of G. gorilla in seven of eight cases, and smaller than those of P. troglodytes in all six cases. Finally, early Homo slope and relief mean values are smaller than those of G. gorilla in all six cases and larger than those of P. troglodytes in five of six cases.

Despite the small sample sizes, statistical analyses yielded results consistent with these observations. First, factorial ANOVAs on the ranked slope and ranked relief data both evinced significant variation in the models (Table 3). There is significant variation among the taxa and among the wear stages for both slope and relief models. Further, neither model showed a significant interaction between the two factors. In other words, degrees of difference between the taxa do not change significantly at different wear stages—differences between gorillas, chimpanzees, early Homo, and Australopithecus afarensis evidently remain consistent through the wear sequence.

Bonferroni multiple comparisons tests reveal the sources of significant variation. Comparing values among wear stages, the second wear stage has significantly steeper average slopes and relief than the fourth wear stage. In addition, the third wear stage shows significantly steeper slopes and marginally more relief than the fourth wear stage. Comparing values among taxa, as already
demonstrated elsewhere (M’Kirera and Ungar, 2003; Ungar and M’Kirera, 2003), *Gorilla gorilla* M2s have significantly steeper slopes and more occlusal relief than those of *Pan troglodytes*. Furthermore, early *Homo* molars have significantly less occlusal relief than those of *G. gorilla* and marginally significantly steeper slopes than those of *Australopithecus afarensis*. Finally, *A. afarensis* has significantly lower slope values and less occlusal relief than *G. gorilla*.

In sum, despite small sample sizes, there are trends evident in the data. First, there is a tendency for the molar teeth of all four taxa to become flatter with wear. Second, differences among the taxa remain about the same at all observed stages of wear. *Gorilla* M2s have the steepest slopes with

<table>
<thead>
<tr>
<th>Wear</th>
<th>Australopithecus</th>
<th>Gorilla</th>
<th>Homo</th>
<th>Pan</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean</td>
<td>SD</td>
<td>N</td>
<td>Mean</td>
<td>SD</td>
</tr>
<tr>
<td>A. Slope</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>37.89</td>
<td>–</td>
<td>1</td>
<td>–</td>
</tr>
<tr>
<td>2</td>
<td>32.01</td>
<td>6.154</td>
<td>4</td>
<td>37.75</td>
</tr>
<tr>
<td>3</td>
<td>25.46</td>
<td>3.810</td>
<td>7</td>
<td>36.29</td>
</tr>
<tr>
<td>4</td>
<td>25.21</td>
<td>2.450</td>
<td>2</td>
<td>32.13</td>
</tr>
<tr>
<td>5</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>27.53</td>
</tr>
<tr>
<td>6</td>
<td>32.05</td>
<td>–</td>
<td>1</td>
<td>32.14</td>
</tr>
</tbody>
</table>

| B. Relief |
| 1    | 150.61 | – | 1 | – | – | 152.14 | – | 1 |
| 2    | 139.34 | 6.206 | 4 | 163.86 | 9.411 | 7 | 154.06 | 18.627 | 2 |
| 3    | 129.29 | 13.641 | 7 | 164.88 | 9.279 | 10 | 143.08 | 8.770 | 3 |
| 4    | 135.30 | 9.155 | 2 | 152.51 | 14.309 | 14 | 131.86 | 10.074 | 2 |
| 5    | – | – | – | 142.35 | 6.734 | 13 | – | – | – |
| 6    | 169.90 | – | 1 | 139.39 | 3.619 | 3 | – | – | – |

Table 3
Analysis of slope data (data rank transformed)

A. Factorial ANOVA

<table>
<thead>
<tr>
<th>Effect</th>
<th>SS</th>
<th>df</th>
<th>MS</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Taxon</td>
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<td>3</td>
<td>7783</td>
<td>8.607</td>
<td>0.000</td>
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<tr>
<td>Wear class</td>
<td>15207</td>
<td>2</td>
<td>7603</td>
<td>8.409</td>
<td>0.000</td>
</tr>
<tr>
<td>Interaction</td>
<td>3708</td>
<td>6</td>
<td>618</td>
<td>0.683</td>
<td>0.663</td>
</tr>
<tr>
<td>Error</td>
<td>81385</td>
<td>90</td>
<td>904</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

B. Bonferroni multiple comparison tests

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Australopithecus</th>
<th>Gorilla</th>
<th>Homo</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Gorilla</em></td>
<td>52.295&lt;sup&gt;b&lt;/sup&gt;</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td><em>Homo</em></td>
<td>34.493&lt;sup&gt;a&lt;/sup&gt;</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td><em>Pan</em></td>
<td>19.172</td>
<td>–</td>
<td>–</td>
</tr>
</tbody>
</table>

| Wear stage | 2 | 3 |
| 3          | –17.645 | 3 |
| 4          | –41.358<sup>b</sup> | –23.713<sup>b</sup> |

<sup>a</sup>p<0.10.<br><sup>b</sup>p<0.05.

Table 4
Analysis of relief data (data rank transformed)

A. Factorial ANOVA

<table>
<thead>
<tr>
<th>Effect</th>
<th>SS</th>
<th>df</th>
<th>MS</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
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<td>3</td>
<td>15739</td>
<td>20.040</td>
<td>0.000</td>
</tr>
<tr>
<td>Wear class</td>
<td>6585</td>
<td>2</td>
<td>3292</td>
<td>4.192</td>
<td>0.018</td>
</tr>
<tr>
<td>Interaction</td>
<td>3912</td>
<td>6</td>
<td>652</td>
<td>0.830</td>
<td>0.550</td>
</tr>
<tr>
<td>Error</td>
<td>70685</td>
<td>90</td>
<td>785</td>
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</tr>
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</table>

B. Bonferroni multiple comparison tests

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Australopithecus</th>
<th>Gorilla</th>
<th>Homo</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Gorilla</em></td>
<td>52.342&lt;sup&gt;b&lt;/sup&gt;</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td><em>Homo</em></td>
<td>18.837</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td><em>Pan</em></td>
<td>9.555</td>
<td>–</td>
<td>–</td>
</tr>
</tbody>
</table>

| Wear stage | 2 | 3 |
| 3          | –13.397 | 3 |
| 4          | –28.144<sup>b</sup> | –14.747<sup>a</sup> |

<sup>a</sup>p<0.10.<br><sup>b</sup>p<0.05.
the most relief, followed by early Homo. Australopithecus afarensis teeth have the least relief and lowest slope values, and chimpanzee values fall between those of the two hominin taxa. As a final note, no study has yet assessed possible effects of size on average occlusal slope or relief. Nevertheless, because these data in no way sort by tooth or inferred body size, differences in occlusal slope and relief among taxa are clearly not allometric.

Discussion

Differences between primates in tooth crown shape have been related to differences in the mechanical demands of their diets (Kay, 1975; Lucas, 1979; Lucas and Teaford, 1994; Strait, 1997; Yamashita, 1998). As Spears and Crompton (1996) noted, dental morphology affects the nature, magnitude, and distribution of stress on food particles. Morphological differences between the molars of species considered in this study therefore should reflect differences in their diets.

Differences in occlusal morphology between chimpanzees and gorillas

The differences in occlusal morphology between chimpanzees and gorillas evidently relate to differences in the material properties of the foods they eat, particularly their fallback foods. Central African common chimpanzees are primarily frugivorous, with soft fruits reported to constitute 70–80% of their diets (Kuroda, 1992; Tutin et al., 1997). Fruit is also commonly consumed by western lowland gorillas, making up about half of the food species found in their fecal remains (Williamson et al., 1990; Nishihara, 1992; Remis, 1992;.)
Differences and similarities in food preferences are most obvious where these taxa are sympatric and have access to the same resources. At Lopé, Gabon, for example, dietary overlap is substantial, with gorillas reported to consume 73% of the food species eaten by chimpanzees (Tutin and Fernandez, 1985). Differences between the two taxa are notable at times of fruit scarcity though, when gorillas fall back on tougher, more fibrous foods (such as leaves and stems) than those eaten by chimpanzees (Tutin et al., 1991; Remis, 1997).

Several studies have shown that gorillas have longer shearing crests and steeper cusps than do chimpanzees (Kay, 1978; Hartman, 1986; Uchida, 1998). These occlusal differences clearly reflect differences in the mechanical demands of their diets. Tougher fallback items taken by gorillas require long tooth–tooth contact times, and steep planes of contact for shearing and slicing (Kay and Hiiemae, 1974; Lucas, 1979; Strait, 1997; Uchida, 1998). Flatter surfaces of chimpanzee molars are better suited to crushing and grinding, and extracting juices from fruit pulp. Given analogies between shearing crest length and occlusal relief and between cusp steepness and crown slope, data presented here likewise reflect reported differences in diet between these two taxa (M’Kirera and Ungar, 2003; Ungar and M’Kirera, 2003). In sum, more occlusal relief and steeper cusps suggest efficiency in fracturing tougher, more deformable foods, whereas less occlusal relief and less steep cusps suggest efficiency in fracturing brittle, less deformable foods.

It should be reiterated that differences in occlusal morphology between P. t. troglodytes and G. g. gorilla evidently reflect differences in fallback resources rather than preferred foods. While both taxa evidently prefer soft fruits when available, differences in occlusal morphology apparently allow the gorillas to take advantage of fallback foods that are less accessible to the chimpanzees. The idea that occlusal differences can relate to important secondary foods rather than more commonly consumed preferred items is not new. Kinzey (1978) noted, for example, that while Callitrichus moloch and C. torquatus are both primarily frugivorous, the former have longer shearing crests for slicing leaves and the latter have larger talonid basins for crushing insect chitin. He reasoned that dental morphology therefore reflects adaptations not only to primary foods, but also to less frequently eaten but still critical ones.

As an aside, it can be noted that mountain gorillas (Gorilla gorilla beringei) are regularly reported to consume more leaves, stems and other fibrous foods year-round than western lowland gorillas (Watts, 1984, Doran et al., 2002). Many mountain gorillas live in higher altitude forests with fewer available fruit species. Differential fruit availability, rather than food preference, might then explain diet differences between the G. g. beringei and G. g. gorilla subspecies. This is consistent with observations that mountain gorillas at sites with greater fruit availability consume more fruit (McNeilage, 2001; Robbins and McNeilage, 2003). While food preferences can be difficult to assess, it might therefore be that mountain gorillas at “marginal” sites perpetually fallback on more fibrous, less desirable foods. If so, gorilla occlusal morphology would facilitate the dietary flexibility necessary to allow this.

Dental topography and early hominin diets

Relationships between tooth morphology and diet in chimpanzees and gorillas provide a good comparative baseline for inferring aspects of diet in early hominins. The dental topography data for Australopithecus afarensis and early Homo can be interpreted in this context, and results compared with those from previous studies on the diets of these fossil taxa.

Australopithecus afarensis

Several workers have noted that Australopithecus afarensis had smaller incisors than extant chimpanzees, but larger molar teeth (McHenry, 1988; Picq, 1990; Teaford and Ungar, 2000; Wood and Richmond, 2000). According to conventional wisdom, dental allometry, taken with evidence of thick tooth enamel and thick mandibular corpora, suggest intensive mastication without extensive incisal preparation. Researchers have suggested, following these lines of evidence, a diet that included nuts, seeds, and underground storage
organs. It has been emphasized, however, that *A. afarensis* probably had a mixed forest-savanna resource adaptation rather than a hard-object specialization. These hominins would probably still have preferred soft, sugar-rich fruits, but would have been able to make better use of hard, brittle resources as fallback foods given seasonal availability of favored items (Picq, 1990; Teaford and Ungar, 2000; Ungar and Teaford, 2001; see Conklin-Brittain et al., 1998). Ryan and Johanson (1989) also proposed a mixed adaptation for *A. afarensis* based on dental microwear features on their anterior teeth. This suggested to them the consumption of both closed forest plants and open savanna foods, such as seeds, roots, and rhizomes.

Results presented here for *Australopithecus afarensis* indicate less crown relief and less sloping occlusal surfaces at given stages of wear than in either gorillas or chimpanzees. This implies more efficient fracture of brittle, less deformable foods but less efficient fracture of tough, more deformable foods. The average degrees of difference between chimpanzees and *A. afarensis* in occlusal slope and relief are certainly no more, and likely even less than that between the chimpanzees and gorillas. Given that the extant ape diets differ mostly in fallback foods, it is reasonable to suggest that the *A. afarensis* diet may also have differed from that of chimpanzees largely in fallback resources, which could have included more hard, brittle items. This is consistent with dietary reconstructions of Ryan and Johanson (1989) and Picq (1990).

Early Homo

There is less consensus concerning the dietary adaptations of early *Homo* in the literature than there is for *Australopithecus afarensis*. Several models have stressed changing resources associated with spreading savannas around the time of the Plio-Pleistocene boundary (see Cerling, 1992; Behrensmeyer et al., 1997; Potts, 1998). Many have suggested an increase in vertebrate tissue consumption based largely on the longstanding assumed relationships between Oldowan tools, evidence of butchery, and fossils of early *Homo* (e.g., Leakey et al., 1964). Physiological models and ethnographic/ethological analogy have been cited in support of this scenario (Milton, 1987; Aiello and Wheeler, 1995; Stanford and Bunn, 2001, and references therein). Others have suggested that savanna plants (especially their underground storage organs, or USOs) rather than animals provided keystone resources for early *Homo*, particularly *H. erectus* (O’Connell et al., 1999; Wrangham et al., 1999).

The fossil remains of early *Homo* have, however, provided little concrete evidence one way or the other. Some have suggested that early *Homo*, especially *H. habilis* and *H. rudolfensis*, had relatively large incisors, implying increased consumption of foods requiring incisal preparation compared with many australopiths (Jolly, 1970; Teaford et al., 2002). Others have suggested that reduced molar size in early *Homo*, compared with australopiths, indicates the consumption of a mechanically less demanding diet—though there is no consensus concerning whether this size decrease began with *H. habilis* and *H. rudolfensis* or with early African *H. erectus* (Wood and Collard, 1999; McHenry and Coffing, 2000). Scenarios suggesting consumption of a mechanically less demanding diet may receive some support from observations that early *Homo*, especially *H. erectus*, had thinner molar enamel than most australopiths (see Beynon and Wood, 1986).

If the small samples considered here are representative of their taxa, dental topographic analysis indicates that early *Homo* is intermediate between chimpanzees and gorillas in slope and occlusal relief, and therefore, was probably intermediate in the fracture properties of the foods to which it was adapted. Early *Homo* could have more efficiently fractured tough, plant foods than could chimpanzees, or for that matter, *A. afarensis*. Thinner enamel in early *Homo* would also be consistent with the consumption of tougher foods, as sharp edges at the sites of dentin exposure with wear would improve shredding and slicing efficiency (Kay, 1981; Ungar and M’Kirera, 2003).

What sorts of tough foods might have been available to early *Homo*? Research on mechanical properties of foods that would have been available to early hominins is very limited. Nevertheless, tubers, especially larger ones (Baritelle and Hyde,
are often fairly brittle, whereas mammalian soft tissues tend to be tough and elastic (Lucas and Peters, 2000). Thus, meat seems more likely to have been a key tough-food resource for early Homo than would have USOs. It has also been noted that USOs are of limited nutritional value (Schoeninger et al., 2001), and so would not have made very good keystone resources.

Increased occlusal relief and steeper sloped cusps yield sharper cutting surfaces that would give animal tissues less of an opportunity to stretch and absorb energy, thereby thwarting the major toughening mechanism. Thus, increased consumption of animal products may have played a role in the dental adaptations of the earliest members of our genus. Indeed, researchers have considered hunting and meat eating to be key elements in human evolution since the time of Darwin (1871).

If so, it may be argued that environmental change during the Plio-Pleistocene provided early Homo with the motive, and technological innovation offered them the opportunity for a new dietary adaptation that included more meat than eaten by their hominin predecessors. Cerling (1992) noted that following 2.5 Ma, C4 grasslands spread across East Africa, concomitant with periodic fluctuations in climate (Behrensmeyer et al., 1997; Potts, 1998). Conventional wisdom associates adaptive radiations of both Paranthropus and Homo with these environmental changes (Stanley, 1992; De Menocal, 1995; Vrba et al., 1995). This suggests an increasingly mosaic environment that would have included fewer C3 foods and more savanna resources, including larger-bodied ungulates.

It is also compelling that the earliest evidence of stone tool manufacture and animal processing (Semaw et al., 1997, 2003; De Heinzelin et al., 1999) are found in deposits dated to about 2.5 Ma, roughly coincident with the first appearance of Homo (Hill et al., 1992; Bromage et al., 1995; Kimbel et al., 1996; Suwa et al., 1996; Wood, 1999; Sherwood et al., 2002). Further, most sites yielding stone tools and bones modified by early hominins postdate 2.0 Ma (Blumenschine and Masao, 1991), with the earliest large concentrations roughly coincident with the appearance of African Homo erectus (Feibel et al., 1989; Wood, 1991).

Differences between the hominins

The teeth of Australopithecus afarensis have been said to present a “primitive morphological composite that parallels extant and Middle Miocene apes” (White et al., 1981: 466; see also Picq, 1990). White and coauthors (White et al., 1981) note, for example, that the lower molar cusps of A. afarensis lack the swollen, inflated appearance often seen in later australopiths, such as A. africanus and Paranthropus spp. The post-canine dentition of A. afarensis may therefore present a generalized australopith morphotype from which early Homo occlusal morphology could have been derived.

Dental topographic differences between Australopithecus afarensis and early Homo are of about the same magnitude as differences between Pan troglodytes troglodytes and Gorilla gorilla gorilla. As noted above, these chimpanzees and gorillas overlap considerably in diet, but do differ somewhat, particularly in fallback resources consumed during seasonal crunch times. Differences in diet between A. afarensis and early Homo may likewise have been mostly in fallback resources.

Raymond Dart’s ideas concerning predatory nature of hominins were predicated on observations that savanna baboons fallback on hunting during harsh dry seasons when preferred resources are unavailable. He wrote “baboons anywhere become hunting mammals under the pressure of seasonal or environmental need” (Dart, 1953: 215). Perhaps, then, the transition to Homo may have involved a shift toward the use of meat as a fallback resource given more open or variable environments. Hopefully, other approaches to the reconstruction of diet, such as bone and tooth chemistry analyses, will provide further evidence with which to evaluate this hypothesis.

Caveats

Such hypotheses must, however, be tempered by the acknowledgement that, while a great deal of research has focused on the paleoenvironmental context of the Plio-Pleistocene hominins (Cerling, 1992; contributions in Vrba et al., 1995; Behrensmeyer et al., 1997; Potts, 1998; Sept, 2000), we cannot know the full complement of foods
available in the past, let alone infer their material properties. Furthermore, we cannot attribute the earliest stone tools and cut-marked bones to early Homo with complete confidence given the presence of both Australopithecus garhi (Asfaw et al., 1999) and Paranthropus aethiopicus (Walker et al., 1986) in East Africa at about 2.5 Ma. Nor can we attribute the first large concentrations of these archaeological remains to a specific hominin taxon, given the contemporaneity of H. habilis, H. rudolfensis, and Paranthropus boisei. Still, it is reasonable to assume that early Homo in Africa ate vertebrate tissues given Plio-Pleistocene archaeological evidence in Eurasia, where no other hominin species have so far been found (e.g., Dennell et al., 1988; Gabunia and Vekua, 1995). Most would, likewise, agree that H. rudolfensis and H. habilis probably also made and used Oldowan tools to process animal tissues.

Tool use introduces another possible confounding variable for interpreting dental morphology in early Homo. Most tools made by non-human primates and other animals are used for food acquisition and processing (e.g., Hunt, 1996; Fox et al., 1999; Whiten et al., 1999). If early Homo became increasingly reliant on tools (Oakley, 1962), selective pressures on their jaws and teeth may have changed along with properties of foods as they were altered by preparation (Brace et al., 1991). If selective pressures changed accordingly, this could make it even more difficult to use form–function relationships to reconstruct the diets of these hominins.

Conclusions

In sum, dental topographic analysis of Australopithecus afarensis and early Homo add to our understanding of the dietary adaptations of these taxa. First, it is clear that, as with results for chimpanzees and gorillas, average cusp slope and occlusal relief decreased in both fossil taxa as their molar teeth wore down. It is also clear that differences between taxa are about the same at given wear stages, suggesting that variably worn fossil teeth can be included in functional analyses. Results presented here indicate that, at given wear stages, early Homo teeth have more occlusal relief than chimpanzees and less than gorillas, whereas A. afarensis molars have less occlusal relief than the other taxa studied. This suggests that early Homo was capable of more efficiently consuming tough, elastic foods than are chimpanzees or than was A. afarensis. In contrast, A. afarensis was well suited to crushing hard, brittle foods. Differences between the hominins are similar in degree to those between the extant African apes, suggesting that A. afarensis may have taken harder, more brittle fallback foods, whereas early Homo may have relied more on tough fallback resources, perhaps including meat.

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