Dental microwear texture analysis and diet in the Dmanisi hominins

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ABSTRACT

Reconstructions of foraging behavior and diet are central to our understanding of fossil hominin ecology and evolution. Current hypotheses for the evolution of the genus Homo invoke a change in foraging behavior to include higher quality foods. Recent microwear texture analyses of fossil hominin teeth have suggested that the evolution of Homo erectus may have been marked by a transition to a more variable diet. In this study, we used microwear texture analysis to examine the occlusal surface of 2 molars from Dmanisi, a 1.8 million year old fossil hominin site in the Republic of Georgia. The Dmanisi molars were characterized by a moderate degree of surface complexity (Asfc), low textural fill volume (Tfv), and a relatively low scale of maximum complexity (Smc), similar to specimens of early African H. erectus. While caution must be used in drawing conclusions from this small sample (n = 2), these results are consistent with continuity in diet as H. erectus expanded into Eurasia.

Introduction

The origin of the genus Homo in the early Pleistocene is generally thought to reflect an evolutionary shift in foraging behavior and diet. Earlier Pliocene hominins appear to have subsisted predominantly on unprocessed plant foods, with Australopithecus species relying on their large, thick-enameled molars to break down hard or tough, low-quality foods (Conroy, 2005; Ungar et al., 2010). The decrease in tooth size and enamel thickness and increase in occlusal surface relief in early members of the genus Homo, along with the appearance of stone tools and cut marks on herbivore fossils in the early Pleistocene, suggest a change in hominin diets. The expansion of hominins into Eurasia at around 2 mya further suggests that this change in diet might have been an integral part of the ecological flexibility typical of Pleistocene early Homo.

Different models have been proposed to link these foraging changes to the origin of our genus. Traditional reconstructions have typically emphasized the importance of meat in the diet and the adoption of hunting and scavenging into the hominin foraging repertoire. While they vary somewhat in their focus, these carnivory-based models generally propose that the addition of meat as a significant portion of the diet in early Homo increased energy availability while simultaneously increasing selection pressure for improved ranging and cognitive abilities related to cooperative hunting and scavenging and stone tool manufacture (Washburn, 1963; Lee and DeVore, 1968; Isaac, 1971; Shipman and Walker, 1989; Aiello and Wheeler, 1995; Daegling and Hylander, 2000; Stanford and Bunn, 2004; Bramble and Lieberman, 2004; Pontzer, 2006; Pontzer et al., 2010). Some of these models have suggested that the addition of meat to the hominin diet was key to the increase in brain size and behavioral sophistication evident through the Pleistocene (Shipman and Walker, 1989; Speth, 1989; Aiello and Wheeler, 1995).

Alternative models have downplayed the importance of hunting and scavenging, and have instead implicated other dietary shifts in the origin of the genus Homo. O’Connell and others (O’Connell et al., 1999, 2002) have proposed that the behavioral and anatomical changes evident in early Homo reflect an increased dietary focus on underground storage organs (e.g., roots and tubers) as a food source. Wrangham and others (Wrangham et al., 1999; Wrangham and Conklin-Brittain, 2003; Carmody and Wrangham, 2009) have argued that cooking was the key event underpinning the origin and evolution of our genus. All of these models propose that dietary changes had profound effects on the social ecology of early Homo (O’Connell et al., 1999; Wrangham et al., 1999).

While both traditional and alternative models rely heavily on anatomical and archeological evidence for dietary shifts, measurements of tooth wear have suggested a more complex view
of *Homo* foraging behavior. Analyses of molar occlusal microwear have shown that African specimens assigned to early *Homo* differ from their australopith predecessors in their wear pattern and cusp morphology (Ungar et al., 2006). But these differences suggest a broader diet for early *Homo*, not one that is necessarily focused on meat, underground storage organs, or any singular food source (Ungar et al., 2006). Based on these and other data, Ungar and colleagues (Ungar et al., 2006) have argued that the defining adaptive dietary feature in early *Homo* was its versatility, a trait that proved evolutionarily advantageous in the fluctuating environments experienced through the early Pleistocene (Ungar et al., 2011).

In this paper, we examine tooth wear in hominin molars from the site of Dmanisi. We used microwear texture analysis, a method that has been shown to be effective in distinguishing diet properties both within and between species (Ungar et al., 2003; Scott et al., 2005, 2006; Ungar and Scott, 2009; Mercer et al., 2010). The Dmanisi hominins, typically assigned to *Homo erectus* (Gabunia and Vekua, 1995; Vekua et al., 2002; Rightmire et al., 2006; Lordkipanidze et al., 2007), retain a number of primitive traits for the genus, including a relatively small brain, small stature, and primitive metatarsal morphology (Rightmire et al., 2006; Pontzer et al., 2010). Nonetheless, these hominins are associated with Oldowan-style stone tools and cut marks on herbivore long bones, suggesting some degree of hunting or scavenging behavior in this population (Lordkipanidze et al., 2007).

Dated to 1.8 mya (Lordkipanidze et al., 2007), Dmanisi is the oldest hominin fossil locality outside of Africa. We compared microwear texture data for the Dmanisi hominins to previously published data for other early hominins, including *Australopithecus afarensis*, *Australopithecus africanus*, *Homo habilis* and African *H. erectus* (Ungar et al., 2011). Similarity in occlusal texture among African and Dmanisi specimens would be consistent with the hypothesis that the dietary strategy of *H. erectus* remained relatively consistent as the species expanded into Eurasia.

**Methods**

**Sample**

Two right lower second molars from Dmanisi were examined (Fig. 1). One molar was from the D211 mandible (Gabunia and Vekua, 1995), the other was from the D2735 mandible associated with the D2700 cranium (Vekua et al., 2002). Both molars were in full occlusion at the time of death but are only slightly worn, with no exposed dentin. Molar surfaces from the large D2600 mandible were not included in this analysis due to their extreme wear and resulting lack of sufficient preserved occlusal enamel (Gabunia et al., 2002). Unlike many specimens from eastern Africa, which are often surface collected, the fossils at Dmanisi are the product of subsurface excavation. The sediments from which the Dmanisi molars were recovered consist largely of volcanic ash, and some volcanic particles are certainly hard enough to scratch enamel (Riede and Wheeler, 2009), but based on established criteria (Teaford, 1988; King et al., 1999), there was no evidence in the Dmanisi sample of postmortem abrasion. Thus, the only way volcanic particles from the environment (such as dust or soil) could have contributed to the microwear features measured here was if the hominins ingested food items coated with them (e.g., Riede and Wheeler, 2009).

**Preparing casts**

High-resolution epoxy casts were made from molds of original fossils using methods described in detail previously (Grine and Kay, 1987; Teaford and Oyen, 1989; Ungar, 1996). The teeth examined had never been treated with a preservative, and thus tooth surfaces were merely cleaned using cotton swabs soaked in acetone to remove any dirt on the surface. After cleaning, a mold of the tooth row was made using President’s Jet regular body polyvinylsiloxane dental impression material (Coltène/Whaledent Corp., Mawah, NJ), and allowed to de-gas before casting. Replicas were then poured into these molds using Epotek 301 (Epoxy Technologies, Inc., Billerica, MA), a high-resolution epoxy resin and hardener.

**Surface data collection**

Texture analysis data collection has been described in detail elsewhere (e.g. Ungar et al., 2003; Scott et al., 2005, 2006; Ungar and Scott, 2009). Facet 9 of each specimen was scanned using a Sensofar Plµ white-light scanning confocal profiler (Solarius Development Inc., Sunnyvale, CA) with a 100× objective lens. Point clouds were generated for each surface examined with a lateral sampling interval of 0.18 μm, a vertical resolution of 0.005 μm, and a field of view of 102 × 138 μm. Four adjoining areas were scanned for each specimen for a total work envelope of 204 × 376 μm. The scans were then normalized and leveled using Solarmap Universal software (Solarius Development Inc.). Identifiable defects, which for the Dmanisi scans consisted only of dust particles, were excluded from analysis by applying the thresholding and erase defect features in Solarmap. The four adjoining scans for each specimen were then analyzed using Toothfrax (Surfract Corp., Worcester, MA) and SFrax scale-sensitive fractal analysis software packages.

**Scale-sensitive fractal analysis**

Scale-sensitive fractal analysis is based on the principle that apparent surface texture changes with scale of observation. Surfaces that appear to be smooth at coarse scales may be rough when observed at finer scales. These changes in surface texture can be measured using surface profiles by length-scale analysis, or by examining two- to three-dimensional surfaces using area-scale and volume-fill analyses. Several texture variables relevant to microwear studies have been identified (Ungar et al., 2003; Scott et al., 2005, 2006). Here we present data for five of these variables: complexity, anisotropy, scale of maximum complexity, textural fill volume and heterogeneity. The individual values reported are medians of the four collected scans, following Scott et al. (2006). As the microwear texture variables used in this study have been previously described in detail (Ungar et al., 2003, 2007, 2008; Scott et al., 2005, 2006), they are summarized briefly here. Complexity (Asf) Area-scale fractal complexity reflects change in the roughness of the enamel surface measured at different scales. Complexity is calculated as the slope of the steepest part of a curve.
of relative area over a range of scales. Overlapping pits and scratches of varying sizes would result in higher values for \( Asfc \). Complexity has been used to distinguish taxa that eat hard-brittle (also called “stress-limited”; Lucas, 2004) foods, such as some fruit seeds, from those that consume tough (also called “displacement-limited”) foods, including many leaves or meat.

Scale of maximum complexity (\( Smc \)) Previous studies have suggested that the range of scales over which \( Asfc \) is calculated may be informative (Scott et al., 2005, 2006). The \( Smc \) is the steepest part of the curve used to calculate \( Asfc \). Surfaces with greater \( Smc \) values tend to have less wear at very fine scales and/or more wear at coarse scales. For example, a surface characterized by large pits and very few fine scratches would have a high values for \( Smc \).

Anisotropy (\( epLsar \)) Length-scale anisotropy measures the directionality of surface texture by examining the orientation of surface roughness. Relative lengths of profiles sampled across a surface at given orientations can be defined as vectors, here calculated at 5° intervals using 1.8 \( \mu m \) line segments. Anisotropy is calculated as the length of the mean vector. Surfaces characterized by scratches all running the same direction would have high \( epLsar \) values. Tough object feeders tend to have the highest \( epLsar \) values. Tough object feeders tend to have high \( epLsar \) values. Tough object feeders tend to have high \( epLsar \) values. Tough object feeders tend to have high \( epLsar \) values.

Textural fill volume (\( Tfv \)) The volume-filling algorithm fills the surface with square cuboids of different volumes. Textural fill volume is calculated as the difference in volume for fine cuboids with 2 \( \mu m \) faces and larger cuboids with 10 \( \mu m \) faces. A surface dominated by moderate-sized, deep features would have a high value for \( Tfv \).

Heterogeneity (\( HAfsc \)) This variable is measured as variation in complexity across a surface. Each scan is divided into 9 × 9 subregions and \( Asfc \) is calculated for each using the auto-split function in Toothfrax. Heterogeneity is then calculated as the median absolute deviation of \( Asfc \) divided by the median for \( Asfc \).

Results

Previous studies of hominin microwear textures have reported significant differences between \( A. afarensis \), \( A. africanus \), \( H. habilis \) and African specimens of \( H. erectus \) (Scott et al., 2005; Ungar and Scott, 2009; Ungar et al., 2010, 2011), with most differences recorded in \( Asfc \), \( Smc \), and \( Tfv \). The two Dmanisi specimens both have moderate values for \( Asfc \), as reported for African \( H. erectus \) and \( A. africanus \). The Dmanisi molars also show low values for \( Smc \), like those reported for African \( H. erectus \), and have relatively low \( Tfv \) values compared to the other hominins, again, similar to those of African \( H. erectus \). When compared to the data for the other hominins, the specimens from Dmanisi plot within the 25–75th percentile region of those previously reported for African \( H. erectus \) for all five microwear texture components examined (Fig. 2). One or both of the Dmanisi specimens fall outside of the 25–75th percentile regions for one or more of the texture components reported for other hominin species (Fig. 2). However, the small sample size of the Dmanisi sample prevents meaningful statistical testing, and warrants caution in interpreting these results.

Figure 2. Five measures of microwear texture analysis in Dmanisi samples (dotted lines) compared to African hominin samples. This figure is modified from Ungar et al. (2011) with data for the other hominins reported therein. Shaded boxes indicate the 25–50th and 50–75th percentile ranges, whiskers indicate 0–25th and 75–100th percentile ranges excluding outliers (○) and extreme values (*). See text for further details.
Discussion

Wear patterns preserved in tooth enamel provide one of the few direct indicators of diet in fossil species. Compared to available data from a broad range of Plio-Pleistocene hominins, the surface texture values for the lower molars from Dmanisi all fall within the range of variation for *H. erectus* specimens from lower Pleistocene sites in Africa (Fig. 2). The Dmanisi and African *H. erectus* specimens evince moderate surface complexity and low values for both scale of maximum complexity and textural fill volume. These suggest a diet in the days or weeks before death that varied, with no consistent pattern of consumption of foods that were especially hard or tough. However, it must be noted that the microwear texture data for the Dmanisi molars fall within the range of variation seen in some of the other hominin species, and a larger sample is necessary to compare the Dmanisi sample with others with any statistical power.

The fact that *H. erectus* specimens from Dmanisi fall within the range of those from Africa suggests similar food fracture properties; this accords well with archeological evidence and indirect anatomical evidence suggesting similarity in foraging behavior. Like early *H. erectus* in Africa, the Dmanisi hominins are associated with an Oldowan-style stone tool assemblage (Gabunia and Vekua, 1995; Lordkipanidze et al., 2007). While these tools may have had a diversity of uses, the cut marks on herbivore long bones in both Dmanisi and at some early Pleistocene sites in Africa indicate that hominins in both populations were engaged in some form of hunting or scavenging. The Dmanisi hominins also exhibit two postcranial features associated with increased cursoriality, a rigid longitudinal foot arch and increased hind limb length, which are typical of *H. erectus* and may be related to foraging behavior (Pontzer et al., 2010).

As discussed above, most current models for the origin of the genus *Homo* emphasize the importance of a particular food, such as underground storage organs or meat, as the critical factor in the evolution of the genus. Recent analyses of molar surface texture suggest that early *Homo*, and especially African *H. erectus*, adopted a broader diet — or at least, a diet more variable in its mechanical properties — than many australopithecines (Ungar et al., 2006, 2010, 2011). An increase in breadth suggests that dietary versatility, rather than a focus on any particular food type, was a defining characteristic of the diet in early *Homo*, or at least in *H. erectus*. African specimens of early *Homo* do not exhibit the deep microwear pits found in some South African “robust” australopithecines and associated with the consumption of hard-brittle foods (Grine, 1986; Ungar et al., 2006). Instead, dental wear patterns in early *Homo* are unremarkable, and the teeth are relatively small with more occlusal relief, suggesting a diet that included easily fractured, softer plant foods such as ripe fruits and possibly tougher foods. The Dmanisi specimens examined here are consistent with this dietary reconstruction and the notion that the dietary strategy of early African *H. erectus* remained relatively unchanged as the genus expanded into Eurasia in the early Pleistocene. More samples from Dmanisi and other sites outside of Africa are needed to test this hypothesis and the prediction that these hominins had the dietary variability apparent in early African *H. erectus* (Ungar et al., 2006).

Larger issues in reconstructing the diet of early *Homo* remain unresolved. While cusp morphology in *H. erectus*, including the specimens from Dmanisi, is consistent with the consumption of tough, fracture resistant foods such as meat or some underground storage organs, the relative importance of these foods — or others — remains difficult to assess. Further, it remains unclear whether the food properties for which the teeth of early *Homo* are the most effective represent preferred or fallback foods, especially given the very small sample sizes available for microwear analysis. Additional techniques for directly assessing diet, such as analysis of isotopic signatures in preserved enamel, as well as an increased number of fossil specimens, may ultimately help us resolve these issues. Until then, reconstructions of diets of early members of our genus must continue to integrate craniodental evidence with archeological remains in order to generate the most complete picture possible of foraging behavior in early *Homo*.

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References


