



## Microwear textures of *Australopithecus africanus* and *Paranthropus robustus* molars in relation to paleoenvironment and diet

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### ABSTRACT

The importance of diet in primate ecology has motivated the use of a variety of methods to reconstruct dietary habits of extinct hominin taxa. Dental microwear is one such approach that preserves evidence from consumed food items. This study is based on 44 specimens of *Australopithecus africanus* from Makapansgat and Sterkfontein, and 66 specimens of *Paranthropus robustus* from Swartkrans, Kromdraai and Drimolen. These samples enable examination of potential differences between the two assemblages of *A. africanus*, and among the various assemblages of *P. robustus* in relation to the paleoenvironmental reconstructions that have been proffered for each fossil site. Sixteen microwear texture variables were recorded for each specimen from digital elevation models generated using a white-light confocal profiler. Only two of these differ significantly between the Makapansgat and Sterkfontein samples of *A. africanus*. None of the microwear texture variables differs significantly among the samples of *P. robustus*. On the other hand, *P. robustus* has significantly higher values than *A. africanus* for 11 variables related to feature complexity, size, and depth; *P. robustus* exhibits rougher surfaces that comprise larger, deeper features. In contrast, *A. africanus* has smoother, simpler wear surfaces with smaller, shallower and more anisotropic features. As for possible habitat differences among the various sites, only a relatively small number of subtle differences are evident between the specimens of *A. africanus* from Makapansgat and Sterkfontein, and there are none among the specimens of *P. robustus* from various deposits. As such, it is reasonable to conclude that, while subtle differences in microwear textures may reflect differences in background habitats, the wear fabric differences between *P. robustus* and *A. africanus* are most reasonably interpreted as having been driven by dietary differences.

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### 1. Introduction

Diet is central to nearly every aspect of primate ecology and behavior. The seasonal availability, the type and quality, and the physical characteristics of foods impact a variety of species attributes including mobility patterns, social organization and population size, as well as a myriad of postcranial and craniodental morphologies that may be related to their procurement, ingestion, mastication and digestion (Chivers et al., 1984; Fleagle, 2013; Strier,

2016). As such, determining diet has been of paramount importance to paleoanthropologists, whereby a variety of methods have been applied in attempts to reconstruct the dietary habits of fossil hominin taxa. Particularly prominent are biomechanical models that seek to relate morphology to diet (see Grine and Daegling, 2017, for a review). However, craniodental morphologies may inform more about what an extinct species was capable of eating, and perhaps more about its phylogenetic history than the constitution of its diet. Unfortunately, as noted by Ross and Iriarte-Diaz (2014), most biomechanical studies have neglected any consideration of phylogeny. While the low, bulbous and thickly-enameled cusps of *Paranthropus* molars are suboptimal for shredding displacement-limited (i.e., tough) foods such as fibrous sedges,

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these teeth can also be viewed as a biological entity that is contingent not only upon a range of possible functions, but also the dentition of its predecessors (Ungar and Hlusko, 2016). What is required to move beyond the problems inherent in biomechanical inferences is direct evidence left by the foods that were actually (rather than hypothetically) consumed during an individual's lifetime (Grine et al., 2012). Such direct evidence can take the form of dental microwear and the biogeochemistry of tooth enamel (especially its stable light isotope ratios; Grine et al., 2012). In contrast to biomechanical and adaptationist models of craniodental evolution, isotope chemistry and microwear preserve nongenetic signals that are directly related to an individual's diet rather than its evolutionary heritage. These signals may be at odds with inferences derived from ecomorphological or taxonomic approaches to paleontology, as has been demonstrated by studies of fossil artiodactyls, perissodactyls and rodents from South African Plio-Pleistocene deposits (Lee-Thorp and van der Merwe, 1993; Lee-Thorp et al., 1994; Sponheimer and Lee-Thorp, 1999; Sponheimer et al., 1999, 2001; Hopley et al., 2006; Schubert et al., 2006; Steininger, 2011). Indeed, according to Sponheimer et al. (2001:328), “carbon isotope studies have shown that 25% or more Pliocene taxa had diets different from those reported (or assumed) in the literature.”

### 1.1. Dental microwear and diet

Distinctive microwear texture patterns on molar occlusal surfaces are associated with varying angles of contact between opposing teeth and whatever is between them (Gordon, 1982, 1984). As in vitro experimental studies have confirmed, a steep angle of approach (i.e., crushing) causes pits and high surface complexity, whereas a shallow angle (i.e., shearing) causes scratches and high texture anisotropy (Gügel et al., 2001; Hua et al., 2015). In other words, the principal connection between microwear pattern and diet evidently comes from food fracture properties, given that hard foods are crushed, and tough ones are sheared, rather than from attributes of the abrasives that cause microwear per se. This explains the decoupling of gross wear and microwear by Karme et al. (2016), who found that rate of dental tissue loss depends largely on diet abrasiveness, but that differences in gross wear rate need not correspond with differences in microwear patterning.

Indeed, studies of animals known to feed on different diets affirm the usefulness of dental microwear by demonstrating that intraspecific variations reflect seasonal differences in diet (Merceron et al., 2010; Calandra and Merceron, 2016), and the presence/absence of specific food items in the diet (Mainland, 2003; Daegling et al., 2011; Schulz et al., 2013). Thus, while the interpretation of such differences can be complicated (Karme et al., 2016; Ramdarshan et al., 2016), and grit can certainly cause dental microwear (Petersen, 1977; Puech and Prone, 1979; Teaford and Walker, 1983; Teaford and Lytle, 1996; King et al., 1999; Sanson et al., 2007; Lucas et al., 2013; Hoffman et al., 2015), basic diet differences are not swamped by the presence of grit in the diet (Ungar et al., 2016; Merceron et al., 2016, 2017). In fact, diet-microwear associations hold when comparing a broad variety of mammalian species from a wide array of environmental settings (Teaford and Walker, 1984; Teaford, 1985; Robson and Young, 1986; Teaford and Oyen, 1989; Van Valkenburgh et al., 1990; Strait, 1993; Mainland, 1998; Ward and Mainland, 1999; Silcox and Teaford, 2002; Rivals and Semperebon, 2006). Those species that eat hard foods tend to have more pitting, and those that eat tougher foods tend to have more scratches on their molar surfaces. Moreover, recent microwear texture analyses have affirmed the distinction between tough- and hard-food feeders, with a very wide array of taxa having been examined, including rabbits (Schulz et al., 2013), bats (Purnell et al., 2013), antelopes (Ungar et al., 2007; Scott, 2012),

bears (Donohue et al., 2013), deer (Merceron et al., 2010), armadillos and sloths (Haupt et al., 2013), dogs, hyenas, and cats (Schubert et al., 2010; Ungar et al., 2010a; DeSantis et al., 2012; Stynder et al., 2012), primates (Scott et al., 2009, 2012; Percher et al., 2017), and marsupials (Prideaux et al., 2009). Mammals that more often consume hard, brittle foods tend to have higher average microwear surface texture complexity, and those that more often shear or slice tough items have more surface anisotropy.

### 1.2. Microwear and diet among South African australopiths

The study of occlusal microwear among the South African australopiths was initiated some 40 years ago on 7 deciduous molars of *Australopithecus africanus* and 11 of *Paranthropus robustus* (Grine, 1977, 1981, 1984). That qualitative assessment of scanning electron microscope (SEM) images concluded that the “wear scratches on the teeth of the ‘robust’ individuals are more randomly oriented” (Grine, 1977:158), “the degree of scratching, the numbers of pits and the degree of pitting on the Phase I facets of many of the ‘robust’ australopithecine molars are greater than on any of the ‘gracile’ australopithecine teeth,” and “the Phase II facets of the ‘robust’ molars tend to be more heavily pitted than the homologous surfaces on the ‘gracile’ teeth” (Grine, 1981:217).

The first examination of permanent molar microwear in these taxa entailed a quantitative assessment of SEM images of Phase I and Phase II facets of maxillary second molars (Grine, 1986; Table 1). Although this limited the sample to 10 specimens of *A. africanus* and 9 of *P. robustus*, the study was restricted to the M<sup>2</sup> because this mitigated any problems that might have been associated with different molar positions (Gordon, 1982, 1984), and because most of the comparative microwear data that had been published for extant primates had been recorded for this tooth position (Teaford and Walker, 1984; Teaford, 1985). That analysis included a tally of the number of microwear features—pits and scratches—exhibited over a field of 0.5 mm<sup>2</sup>, wear scratch orientation (i.e., degree of anisotropy), and feature dimensions (scratch breadth, pit length and pit breadth). It was found that, for molars of *P. robustus*, the scratches displayed greater directional heterogeneity, wear features were more numerous with a higher proportion of pits, and that the pits tended to be larger. This led to the conclusion that the teeth of *Paranthropus* were used for “more crushing and grinding” than those of *Australopithecus* (Grine, 1986:804). Analysis of comparative data for extant primates suggested that “the diet of *Paranthropus* consisted of hard food objects, whereas *Australopithecus* subsisted on a softer frugivorous and/or folivorous regimen” (Grine, 1986:819).

In view of uncertainties relating to the definition and measurement of individual wear features, Grine and Kay (1988)

**Table 1**  
Maxillary molars of *Australopithecus africanus* and *Paranthropus robustus* employed in microwear studies by Grine (1986) and Scott et al. (2005).

<i>Australopithecus</i>		<i>Paranthropus</i>	
Specimen	Tooth <sup>a</sup>	Specimen	Tooth <sup>a</sup>
Sts 12	LM <sup>2</sup>	SK 13	RM <sup>2</sup>
Sts 17	RM <sup>2</sup>	SK 16	LM <sup>2</sup>
Sts 22	LM <sup>2</sup>	SK 42	RM <sup>2</sup>
Sts 28	RM <sup>2</sup>	SK 48	RM <sup>2</sup>
Sts 30	RM <sup>2</sup>	SK 49	RM <sup>2</sup>
Sts 31	LM <sup>2</sup>	SK 834	RM <sup>2</sup>
Sts 52	LM <sup>2</sup>	SK 837	RM <sup>2</sup>
Sts 53	LM <sup>2</sup>	SK 877	RM <sup>2</sup>
Sts 61	RM <sup>2</sup>	TM 1517	LM <sup>2</sup>
TM 1511	LM <sup>2</sup>		

<sup>a</sup> Abbreviations: L = left; R = right.

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