Premolar microwear and tooth use in *Australopithecus afarensis*

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A B S T R A C T

The mandibular third premolar (P_3) of *Australopithecus afarensis* is notable for extensive morphological variability (e.g., metaconid presence/absence, closure of the anterior fovea, root number) and temporal trends in crown length and shape change over its 700 Ka time range. Hominins preceding *A. afarensis* have unicuspid, mesiodistally elongated P_3s with smaller talonids, and subsequent australopiths have bicuspid, more symmetrically-shaped P_3 crowns with expanded talonids. For these features, *A. afarensis* is intermediate and, thus, evinces the incipient stages of P_3 molarization. Here, we examine *A. afarensis* P_3 Phase II microwear and compare it with that of *Australopithecus africanus* and *Cercocebus atys*, an extant hard-object specialist, to assess whether the role of the P_3 in food processing changed over time in *A. afarensis*. Premolar Phase II microwear textures are also compared with those of the molars to look for evidence of functional differentiation along the tooth row (i.e., that foods with different mechanical properties were processed by separate regions of the postcanine battery). Microwear textures were also examined along the mesial protoconid crest, the site of occlusion with the maxillary canine, of the *A. afarensis* P_3 and compared with the same region in *Pan troglodytes* to determine whether microwear can be useful for identifying changes in the occlusal relationship between the P_3 and maxillary canine in early *Australopithecus*. Finally, temporal trends in P_3 Phase II and mesial microwear are considered. Results indicate that 1) both the P_3 and molar Phase II facets of *A. afarensis* have less complex microwear textures than in *A. africanus* or *C. atys*; 2) *A. afarensis* P_3 and molar Phase II textures differ, though not to the extent seen in taxa that eat hard and tough items; 3) microwear along the *A. afarensis* mesial protoconid crest is clearly distinct from that of the *P. troglodytes*, indicating that there is no honing equivalent in *A. afarensis*; and 4) there is little evidence of change over time in *A. afarensis* P_3 microwear on either the mesial or Phase II facet. In sum, these results provide no evidence that *A. afarensis* routinely loaded either its premolars or molars to process hard objects or that *A. afarensis* P_3 function changed over time.

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Introduction

Plio-Pleistocene hominin craniodental variation is usually thought to reflect dietary differentiation over time in response to changing environmental conditions (e.g., Robinson, 1954; Du Brul, 1977; Leakey et al., 2001; Kimbel, 2007; Wood and Lonergan, 2008; White et al., 2009; Ungar and Spoonheimer, 2011). Numerous lines of evidence have been used to infer hominin feeding behavior and ecology, including comparative anatomy (e.g., Grine, 1981; Kay, 1985; Hylander, 1988; Daegling and Grine, 1991),

finite element modeling (e.g., Macho et al., 2005; Strait et al., 2009, 2010), dental microwear (e.g., Grine, 1977, 1981; Puech, 1979; Walker, 1981; Ungar et al., 2006, 2008, 2010; Grine et al., 2006a, 2006b; Ungar and Spoonheimer, 2011), enamel stable isotopes (e.g., Lee-Thorp et al., 1994, 2010, 2012; van der Merwe et al., 2003, 2008; Cerling et al., 2011b; Ungar and Spoonheimer, 2011), paleo-climate proxies (e.g., DeMenocal, 2004), and paleohabitat data (e.g., Reed, 1997, 2008; Bobe, 2006; Cerling et al., 2011a). While hominin species almost certainly differed from one another in diet, it has proven difficult to associate the appearance of individual anatomical features with specific dietary transitions. As teeth are intimately linked to food processing, they are among the most likely structures to show such associations and, in particular, changes in hominin tooth size and shape almost certainly reflect adaptations

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to different dietary regimes. This study uses dental microwear texture analysis of the mandibular third premolar (P$_3$) to evaluate functional explanations for changes in P$_3$ crown shape in the early hominin species *Australopithecus afarensis*.

The hominin genera *Australopithecus* and *Paranthropus* are noted for a craniodental morphology that includes reduced, non-honing canines, postcanine megadontia, thickly enameled post-canine teeth, large areas of origin for the temporalis and masseter muscles, robustly built mandibles, and features associated with the buttressing of the face (Robinson, 1956; Grine, 1985; Wood and Uytterschaut, 1987; Suwa, 1988, 1990; Suwa et al., 1996; White et al., 2000, 2006; Ward et al., 2001, 2010; Kimbel et al., 2004; Kimbel, 2007; Wood and Constantino, 2007; Wood and Lonergan, 2008; Kimbel and Delezene, 2009; Strait et al., 2009, 2010; Berthaume et al., 2010; Villmoore and Kimbel, 2011). This suite of features is often thought to be associated with the production of high occlusal forces and resistance to masticatory stress, hypothesized to be an adaptation for processing hard food objects (i.e., those with stress-limited defenses) (Ward et al., 1999; Teaford and Ungar, 2000; Wood and Richmond, 2000; Walker, 2002; Macho et al., 2005; Suwa et al., 2009; Strait et al., 2009, 2010; Constantino et al., 2010, 2011; Ungar, 2011). Craniomandibular robusticity shows a morphocline of expression from least robust in *Australopithecus anamensis* and *A. afarensis*, to more robust in the younger *Australopithecus africanus* and, finally, to most robust in the genus *Paranthropus* (e.g., White et al., 1981; Ward et al., 1999, 2001; Teaford and Ungar, 2000; Wood and Constantino, 2007). Because extant apes, *Ardipithecus*, and *Sahelanthropus* lack post-canine megadontia and have generally more gracile cranial and mandibular features (Brunet et al., 2002, 2005; Wood and Lonergan, 2008; Suwa et al., 2009), the evolution of *Australopithecus* has been hypothesized to represent a shift into a new dietary niche that included mechanically challenging foods — tough, abrasive, or hard (Ward et al., 1999, 2001; Teaford and Ungar, 2000; Wood and Richmond, 2000; White et al., 2000, 2006; Walker, 2002; Macho et al., 2005; Constantino et al., 2010).

Molar microwear in extant primates has been shown to reflect differences in the fracture properties of foods (e.g., Teaford and Walker, 1984; Teaford, 1985, 1993; Teaford and Robinson, 1989; Walker and Teaford, 1989; Teaford and Glander, 1996; Daegling and Grine, 1999; King et al., 1999; Nystrom et al., 2004). Molar Phase II wear surfaces have usually been the focus of such studies, as they are formed either during 'puncture-crushing' or at the end of the 'power stroke' of chewing. Based on such work, extant hard-object-feeding primates have been shown to exhibit microwear textures that are complex (i.e., vary in roughness with scale of observation), while folivorous taxa, which feed on tough foods, usually have less complex but more anisotropic wear textures (Ungar et al., 2007; Scott et al., 2012). Indeed, Scott et al. (2012) demonstrated that there is little overlap in Phase II surface complexity between hard object and tough/soft object feeding primates, which provides a useful baseline for inferring the mechanical properties of foods consumed by extinct primates (e.g., Merceron et al., 2009; Scott et al., 2009; Ungar and Spoonheimer, 2011). Interestingly, the assumption that hard objects were commonly eaten by *all* early hominins has not been confirmed by molar microwear analyses. Instead, as evidenced by complex textures for some individuals, they were likely eaten at least occasionally by some populations (i.e., *Paranthropus robustus*) and not by others (i.e., *Paranthropus boisei*) (Scott et al., 2005; Ungar et al., 2008, 2010; Ungar and Spoonheimer, 2011). With respect to the earlier *Australopithecus* species, conventional feature-based molar microwear studies suggested no evidence for hard-food consumption across the 1.2-million-year span of *A. afarensis* and its putative ancestor, *A. anamensis* (Grine et al., 2006a, b). Texture

analysis results are consistent with this, as neither *A. anamensis* nor *A. afarensis* have high complexity Phase II molar surfaces (Ungar et al., 2010). Indeed, the three eastern African early hominin taxa (*A. anamensis*, *A. afarensis*, *P. boisei*) have molar wear textures that are significantly less complex than those observed in extant primate hard-object feeders (Daegling et al., 2011; Scott et al., 2012). This suggests that the origin and elaboration of masticatory robusticity and megadontia may not reflect a specialized hard-object diet (Ungar et al., 2008, 2010; Ungar, 2011; Ungar and Spoonheimer, 2011), but instead may reflect a complex combination of an abrasive diet including food items with variable material properties.

Still, *A. anamensis* and *A. afarensis* have been purported to have made the initial incursion into a hard-object feeding niche (Ward et al., 1999, 2001; Teaford and Ungar, 2000; Wood and Richmond, 2000; White et al., 2000, 2006; Walker, 2002; Macho et al., 2005; Constantino et al., 2010). Within this hypothesized anagenetic lineage, which spans ca. 4.2 to 3.0 Ma (Kimbel et al., 2006), the P$_3$ shows a dramatic morphological transformation from a mesiodistally elongated, asymmetric, and unicuspid tooth in early *A. anamensis* to a shorter, more symmetric, and often bicuspid form in *A. afarensis* (Coppens, 1977; White, 1977, 1980; Johanson et al., 1982; Olson, 1985; Kimbel et al., 1985; Leonard and Hegmon, 1987; Suwa, 1990; Ward et al., 1999, 2001; Kimbel et al., 2006; Kimbel and Delezene, 2009; Delezene and Kimbel, 2011). Across the 700 Ka time range of *A. afarensis*, the P$_3$ crown reduced in mesiodistal length and its shape changed to become more symmetrical (Lockwood et al., 2000; Delezene and Kimbel, 2011). While the *A. afarensis* P$_3$ sample is noted for its variable expression of several derived features (e.g., presence of a protoconid, anterior fovea closure, incipient talonid expansion, symmetrical crown), the geologically younger *A. africanus* consistently expresses all of these derived features (Suwa, 1990). Thus, the pattern of anatomical differences in the P$_3$ crowns between the early australopiths, *A. anamensis* and *A. afarensis*, and *A. africanus* may in fact track the pattern of overall masticatory robusticity, making it tempting to hypothesize that P$_3$ molarization is an adaptation to a mechanically challenging diet. However, the precise functional implications of such changes remain unknown.

While the expansion of the distal P$_3$ crown is obvious in early *Australopithecus*, the mesial portion of the crown also underwent a dramatic transformation. Notably, the principal cusp of the P$_3$, the protoconid, reduced in height and the mesial protoconid crest reduced in length and became more rounded (Ward et al., 2001; Kimbel et al., 2006; Delezene and Kimbel, 2011). In extant apes, the maxillary canine is honed along the P$_3$'s mesial protoconid crest; however, in *Australopithecus*, the maxillary canine is not honed along the mesiobuccal face of the P$_3$ but instead is dulled by contact with it (for example, see the wear facet on the A.L. 128-23 P$_3$) (Greenfield, 1990; Kimbel and Delezene, 2009). While hypotheses regarding hominin canine reduction have focused on potential changes in social behavior associated with a reduced emphasis on competition involving the maxillary canine as a weapon, it is also possible that the reduced *Australopithecus* canine became co-opted to function in food acquisition or processing (Ward et al., 2010; Plavcan, 2012). Therefore, it is possible that changes in P$_3$ morphology are not only driven by changes in postcanine food processing that occurred in the talonid, but also by changes associated with food acquisition and processing that would have occurred between the P$_3$ and maxillary canine.

For this study, temporal trends in P$_3$ microwear were considered by examining wear textures across the 700,000 years represented by the *A. afarensis* hypodigm to determine if there was a change in the use of P$_3$ that mirrors temporal changes in crown form (Lockwood et al., 2000; Delezene and Kimbel, 2011). Specifically,

the hypothesis that changes in *A. afarensis* P_3 crown form reflect an increasing reliance on hard objects over time is tested. In addition, the functional differentiation of premolars and molars is evaluated by comparing microwear textures of *A. afarensis* molars and premolars with one another. While it is evident that *A. afarensis* lacked honing wear along the mesial portion of the P_3, microwear is evaluated along the mesial protoconid crest of *A. afarensis* and compared with that of *Pan troglodytes*, which possesses a functional honing complex, to determine the utility of microwear texture analysis to reveal the changing function of the P_3 in early hominins.

Materials

All available P_3s of *A. afarensis* that preserve antemortem microwear were included in this analysis ($n = 19$; see Table 1). These teeth derive from the Laetoli, Maka, and Hadar sites, and span most of the known geographic and temporal range of the species (ca. 3.7–3.0 Ma). The sample includes two specimens (A.L. 440-1 and A.L. 438-3) from the youngest australopith-bearing sediments at Hadar, the KH-2 submember of the Hadar Formation, and three from Laetoli, which represent the oldest P_3s attributed to the *A. afarensis* hypodigm (Kimbel and Delezene, 2009; Harrison, 2011). The sample also spans a range of phenotypes and sizes. Specimens include unicuspid teeth with open anterior foveae, which anchor the plesiomorphic end of the *A. afarensis* P_3 morphocline (A.L. 128-23 and A.L. 288-1), and fully bicuspid ones with completely enclosed anterior foveae. The latter grouping, which includes both small (A.L. 315-22) and large (A.L. 333w-1) teeth, presents numerous apomorphic character states in combination (Delezene and Kimbel, 2011). Phase II microwear data for the P_3 sample were compared with those for *A. afarensis* molars ($n = 19$) published in Ungar et al. (2010), which includes the same specimens described in Grine et al. (2006a), and comprises both maxillary and mandibular molars.

The *A. afarensis* data were compared with molar and premolar microwear textures of the extant hard-object feeding *Cercocebus atys* and of *A. africanus*. It is well documented that *C. atys* feeds on large hard objects (e.g., McGraw et al., 2011), and this taxon has been used as an analog for the hypothesized use of hominin premolars to process hard objects (Strait et al., 2009; Daegling et al., 2011). The *C. atys* data used in this study came from Daegling et al. (2011),
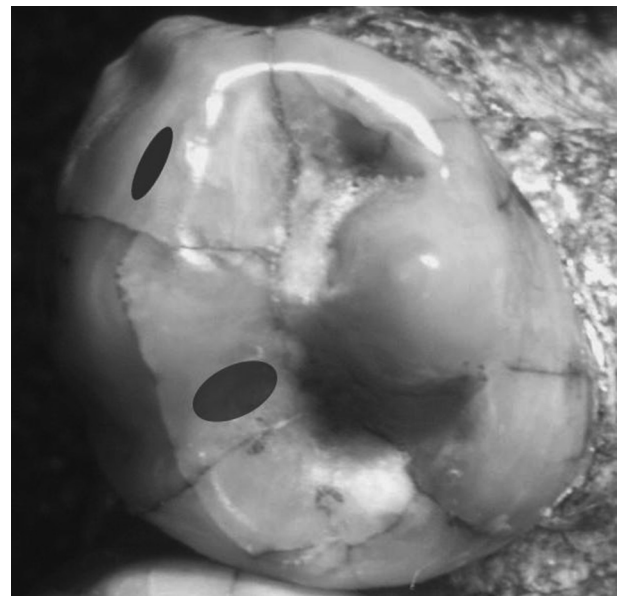
except for the *HAsfc* results, which have not been presented elsewhere, and include analyses of P^4s and M^1s. The *A. africanus* data were taken from Grine et al. (2010), who sampled P3s, P4s, M1s, and M2s. While these published studies did not exclusively sample P_3s, they do allow comparisons of results along the tooth row, and so can offer insights into the question of whether microwear reflects functional differentiation of premolars versus molars.

Finally, microwear textures were also examined along the mesial protoconid crest in *A. afarensis* and a sample of wild-caught *Pan troglodytes troglodytes* ($n = 10$ males and 10 females) in the Hamann–Todd Collection at the Cleveland Museum of Natural History. The chimpanzee sample was included to contrast the microwear signal associated with canine honing with that seen in nonhoning *Australopithecus*.

Methods

High-resolution casts of original specimens were prepared following procedures described in detail elsewhere (e.g., Teaford and Oyen, 1989; Grine et al., 2006b). Occlusal surfaces were cleaned with acetone or alcohol soaked cotton swabs prior to molding, and then impressions were taken using polysiloxane vinyl (President's Jet Regular Body; Coltene–Whaledent Corp., Mawah, New Jersey). High-resolution epoxy polymer casts (Epotek 301; Epoxy Technologies, Inc., Billerica, Massachusetts) were then prepared using these molds.

Microwear texture data were generated from two wear surfaces on the P_3: a Phase II wear facet in the talonid and a wear facet along the buccal side of the mesial protoconid crest (Fig. 1). All specimens were analyzed using a Sensofar Plμ white-light scanning confocal profiler (Solarius, Inc.). Following procedures outlined in Scott et al. (2006, 2012) and Grine et al. (2010), microwear texture data were generated from three-dimensional point clouds sampled using a $100\times$ objective, yielding a lateral (x, y) sampling interval of 0.18 μm and a vertical resolution (z) of 0.005 μm. Four adjacent fields, each 138 μm $\times$ 102 μm in area were considered, which yielded a total

Table 1
Australopithecus afarensis P_3s included in this study. The geological age for the Ethiopian specimens follows Lockwood et al. (2000) and the geological ages for the Laetoli specimens follow from recent redating of the Laetoli volcanic tuffs and relocation of original hominin findspots (Deino, 2011; Harrison, 2011).

Specimen	Geological age (Ma)	Temporal rank
LH-14	3.70	1
LH-24	3.67	2
LH-4	3.67	2
MAK-VP 1/12	3.40	3
A.L. 198-1	3.37	4
A.L. 128-23	3.35	5
A.L. 400-1	3.30	6
A.L. 266-1	3.25	7
A.L. 311-1	3.25	7
A.L. 417-1a	3.25	7
A.L. 315-22	3.22	8
A.L. 655-1	3.22	8
A.L. 333-10	3.20	9
A.L. 333w-1a	3.20	9
A.L. 333w-46	3.20	9
A.L. 333w-60	3.20	9
A.L. 288-1i	3.18	10
A.L. 438-3	3.00	11
A.L. 440-1	3.00	11

Figure 1. Left P_3 of A.L. 333w-1. The large grey shaded area, which is distolingual to the apex of the protoconid, indicates the location of the Phase II facet analyzed on *A. afarensis* P_3s. The narrow ellipse is located along the buccal side of the mesial protoconid crest. The mesial protoconid crest is the site of canine honing in *Pan troglodytes*; however, in the hominins the role of canine honing has been lost.

work envelop of 276 μm × 204 μm. Scale-sensitive fractal analysis software programs (ToothFrax and SFrax, Surfract Corp.) were then used to derive data for six microwear texture variables: area scale fractal complexity ($Asfc$), anisotropy ($epLsar_{1.8}$), scale of maximal complexity (Smc), textural fill volume (Tfv), and two measures of heterogeneity ($HAsfc_9$ and $HAsfc_{81}$) (see Scott et al. (2006) and Ungar et al. (2008) for details). Values for all six microwear texture variables were calculated for each of the four adjacent fields. From these data, the median of the four sampled fields was computed and recorded for each individual. Data analyses were conducted on these median values.

As microwear textures are usually not normally distributed, statistical analyses were performed on rank-transformed data. To determine if *A. afarensis* P_3 talonid expansion is associated with hard object processing and also to test for functional differentiation along the tooth row, Phase II microwear data were compared among *A. afarensis*, *A. africanus*, and *C. atys*. For the Phase II surfaces, a two-way MANOVA with tooth (premolar, molar), taxon (*A. afarensis*, *A. africanus*, *C. atys*), and the interaction between the two factors was run to determine whether there was significant variation in the model. Then, pairwise comparisons were carried out for each tooth type among species and between tooth types within species to determine the sources of that variation. All pairwise comparisons between species were conducted using a Mann–Whitney *U* test. Comparisons of *A. afarensis* P_3 and molar textures to one another were also conducted using Mann–Whitney *U* tests because the data for each tooth type were collected largely from different individuals. For both *A. africanus* and *C. atys*, comparisons between tooth types within species were conducted using Wilcoxon signed-rank tests because textures for premolars and molars were collected from the same individuals. Comparisons of molar and premolar textures for *A. africanus* and *C. atys* (except for $HAsfc_9$ and $HAsfc_{81}$) were previously presented in Grine et al. (2010) and Daegling et al. (2011), respectively. In addition to comparisons of central tendency, variances were compared between species and between teeth within species using Levene's test.

Further, multivariate principal components analysis (PCA) was performed on the total sample of premolars and molars from all species to illustrate sources of interspecific and intraspecific variation for the Phase II microwear data. Because the microwear texture attributes have different scales of measurement, the covariance matrix is unsuitable for computing principal components (Johnson and Wichern, 2007). Therefore, the correlation matrix for the six variables was used to compute the principal components.

To determine whether canine honing leaves a distinctive signature that contrasts with the hominin pattern, microwear textures were gathered along the P_3 mesial protoconid crest of *P. troglodytes* and *A. afarensis*. Using Mann–Whitney *U* tests, pairwise comparisons were made between male and female chimpanzees to test for differences between sexes. Then, male and female chimpanzees were pooled and compared with *A. afarensis*.

Finally, to determine if observed temporal changes in *A. afarensis* P_3 crown morphology (Lockwood et al., 2000; Delezene and Kimbel, 2011) are associated with changes in P_3 function, temporal trends in *A. afarensis* P_3 microwear textures were assessed using the Γ statistic. The two-tailed significance of Γ was determined from 1000 bootstrapped randomizations (see Lockwood et al., 2000).

Results

Comparison of premolar and molar Phase II microwear textures between species

Summary statistics for premolar and molar Phase II facets in the *A. afarensis*, *A. africanus*, and *C. atys* samples are presented in Table 2

Table 2
Summary statistics for premolar and molar Phase II microwear textures.

Variable	Taxon	N	Tooth	Mean	Median	Std. dev.
$Asfc$	*A. afarensis*	19	P_3	0.669	0.670	0.212
			Molars	0.740	0.712	0.236
	A. africanus	13	Premolars	1.107	0.993	0.426
			Molars	1.207	1.178	0.522
	C. atys	14	P^4	4.435	4.055	2.323
			M^1	4.076	4.260	1.726
$epLsar_{1.8}$	*A. afarensis*	19	P_3	0.002	0.002	0.001
			Molars	0.003	0.003	0.002
	A. africanus	13	Premolars	0.003	0.003	0.001
			Molars	0.004	0.004	0.002
	C. atys	14	P^4	0.003	0.002	0.001
			M^1	0.004	0.003	0.001
Smc	*A. afarensis*	19	P_3	0.925	0.419	1.123
			Molars	0.565	0.416	0.521
	A. africanus	13	Premolars	1.072	0.708	1.389
			Molars	0.877	0.822	0.639
	C. atys	14	P^4	27.267	0.238	53.139
			M^1	10.261	0.152	20.382
Tfv	*A. afarensis*	19	P_3	7689.6	8548.7	4429.2
			Molars	3389.6	2805.1	3244.8
	A. africanus	13	Premolars	6173.2	6554.1	4498.8
			Molars	7316.7	4243.8	6404.9
	C. atys	14	P^4	15,678.8	15,690.9	1743.0
			M^1	15,028.6	14,739.4	2108.7
$HAsfc_9$	*A. afarensis*	19	P_3	0.446	0.418	0.114
			Molars	0.364	0.324	0.158
	A. africanus	13	Premolars	0.419	0.415	0.120
			Molars	0.536	0.512	0.179
	C. atys	14	P^4	0.383	0.359	0.128
			M^1	0.366	0.343	0.084
$HAsfc_{81}$	*A. afarensis*	19	P_3	0.625	0.622	0.094
			Molars	0.368	0.343	0.124
	A. africanus	13	Premolars	0.687	0.670	0.165
			Molars	0.813	0.692	0.309
	C. atys	14	P^4	0.708	0.716	0.233
			M^1	0.626	0.627	0.160

and illustrated in Figs. 2–8. For the MANOVA, both tooth type and taxon significantly affect microwear textures, as does the interaction effect (tooth × taxon) (Table 3). As all model parameters showed significant variation, post-hoc pairwise comparisons were conducted for premolars between taxa, molars between taxa, and between premolars and molars within taxa to determine sources of significance.
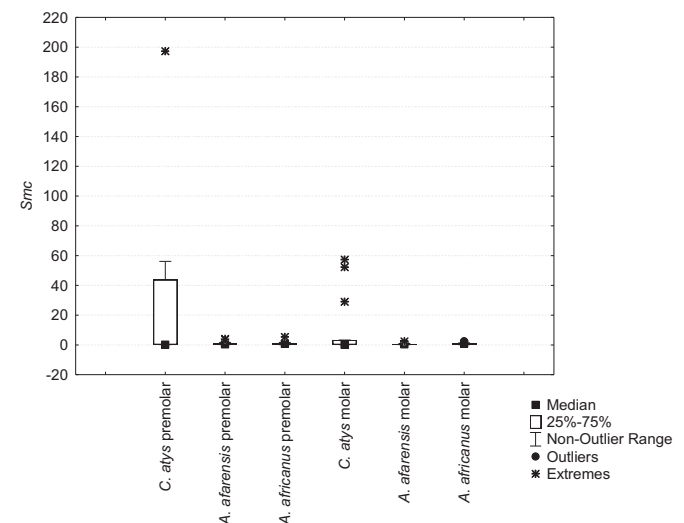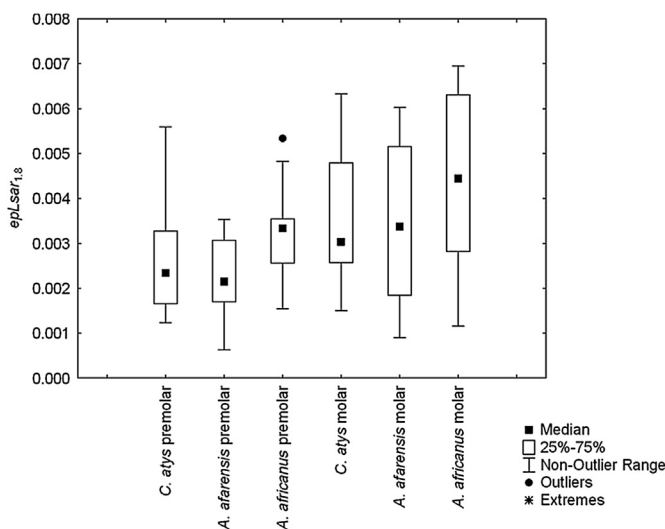

Figure 2. Box and whisker plots for molar and premolar *Smc*. Though no significant differences are observed between taxa, the *C. atys* sample is noted for its broad range and extreme outliers.
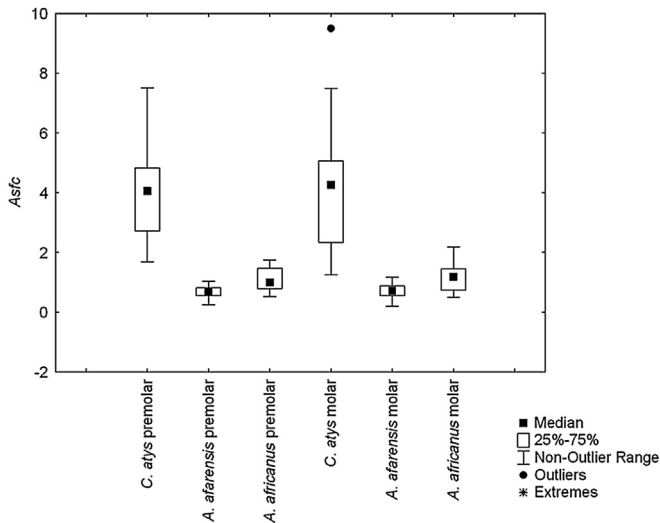
Figure 3. Box and whisker plots for molar and premolar *Asfc*. The postcanine teeth of *C. atys* have significantly more complex microwear textures than the hominins. Additionally, the *C. atys* teeth have an exceptionally broad range compared with either hominin.

For the pairwise comparisons between taxa, only one texture attribute, *Smc*, does not differ significantly between species for either the premolars or the molars (Table 4). Still, with its broad range, the *C. atys* premolar *Smc* distribution is distinct from the hominin distributions (Fig. 2). Indeed, the Levene's tests indicate a significantly larger variance for the *C. atys* premolars than for *A. afarensis* ($F = 13.2$; $p = 0.0001$) and for *A. africanus* ($F = 8.86$; $p = 0.006$). No significant differences are observed between species for molar *Smc* variance.

All pairwise comparisons of premolar *Asfc* between species differ significantly, as do all comparisons of molar *Asfc* (Table 4). The hard-object feeding *C. atys* has the most complex textures and the range of *Asfc* values observed for *C. atys* does not overlap the range for *A. afarensis*. There is only minimal overlap between the ranges of *Asfc* for *C. atys* and *A. africanus* (Fig. 3). The hominin ranges overlap substantially for both molar and premolar *Asfc*; however, the *A. afarensis Asfc* is significantly lower than that for *A. africanus* for both tooth types. The *C. atys* molars are also notable for a wider

Figure 4. Box and whisker plots for molar and premolar *epLsar*$_{1.8}$. Premolars tend to be less anisotropic for all taxa, though the difference only reaches statistical significance for *A. afarensis*.

range of *Asfc* and greater variance than either hominin taxon (Fig. 3). In fact, *C. atys* has a significantly higher variance than *A. afarensis* ($F = 18.79$; $p = 0.0001$) and *A. africanus* ($F = 8.57$; $p = 0.007$). Again, for the premolars *C. atys* also has a significantly higher variance than *A. afarensis* ($F = 28.26$; $p < 0.0001$) and *A. africanus* ($F = 13.51$; $p = 0.0001$). For both the premolars ($F = 11.27$; $p = 0.002$) and molars ($F = 11.13$; $p = 0.002$), *A. afarensis* has a significantly lower variance than *A. africanus*. Thus, both *A. afarensis* molars and premolars are characterized by a narrow range of low *Asfc*.

For *epLsar*$_{1.8}$, the only observed significant difference between species is for the comparison of premolars between the two hominins, for which *A. afarensis* has a significantly lower median than *A. africanus*. Molar *epLsar*$_{1.8}$ does not differ significantly between taxa (Table 4; Fig. 4). No significant differences are observed between taxa for molar *epLsar*$_{1.8}$ variance and for the premolars the only significant difference is between *C. atys* and *A. afarensis* ($F = 4.29$; $p = 0.047$), where *C. atys* has a higher variance. As noted for the molars of *A. afarensis* (Ungar et al., 2010), the P$_3$s combine low complexity and low anisotropy on their wear surfaces, an unusual combination for primates (Fig. 5).

For *Tfv*, the *C. atys* sample differs significantly from both hominins, with larger average *Tfv* values for both premolars and molars (Tables 2 and 4). In fact, the *C. atys* premolars and molars only minimally overlap the range of values for the hominins (Fig. 6); *Tfv* values do not differ between the hominins for either the premolars or molars (Table 4). These results suggest that *C. atys* microwear surfaces have fewer small features than do those of the hominins. In addition, *C. atys* premolars have a significantly lower variance than in both *A. afarensis* ($F = 10.48$; $p = 0.003$) and *A. africanus* ($F = 20.29$; $p = 0.0001$). For the molars, *A. africanus* has a significantly higher variance than *C. atys* ($F = 21.97$; $p < 0.0001$) and *A. afarensis* ($F = 12.78$; $p = 0.0001$). In sum, the premolars and molars of *C. atys* show a narrow range of high *Tfv*; as a higher *Tfv* is associated with hard-object feeding, the low *Tfv* for *A. afarensis* premolars is not consistent with the expected microwear signature of a hard-object feeder.

The two measures of heterogeneity (*HAsfc*$_9$ and *HAsfc*$_{81}$) differ from one another in their variation among species for the premolars and molars. For *HAsfc*$_9$, the *A. afarensis* premolar sample has a significantly larger median than either *C. atys* or *A. africanus* (Tables 2 and 4; Fig. 7). For the molars, the order of the medians is different, with the *A. africanus* sample having a significantly higher median than either *A. afarensis* or *C. atys* (Table 2; Fig. 7). For this measure, *A. afarensis* and *C. atys* are not significantly different (Table 4). For premolar *HAsfc*$_{81}$, no comparisons are significant (Table 4). For molar *HAsfc*$_{81}$, *A. afarensis* has a significantly smaller median than either *A. africanus* or *C. atys*; *C. atys* and *A. africanus* do not differ for this measure (Tables 2 and 4; Fig. 8). In sum, *A. afarensis* molars tend to have the lowest heterogeneity among the three species considered (though not significantly different in all cases) (Tables 2 and 4; Figs. 7 and 8). The opposite is true for premolar *HAsfc*$_{81}$, where the *A. afarensis* median is the highest. As regards variance, no significant differences are observed between samples for either premolar *HAsfc*$_9$ or *HAsfc*$_{81}$. For the molars, *A. africanus* has a significantly higher variance than *C. atys* for *HAsfc*$_9$ ($F = 5.39$; $p = 0.029$) and has a significantly higher variance than both *C. atys* ($F = 7.05$; $p = 0.014$) and *A. afarensis* for *HAsfc*$_{81}$ ($F = 16.17$; $p < 0.0001$).

Comparison of premolar and molar Phase II microwear textures within species

Comparisons of central tendencies for premolar and molar microwear textures for *C. atys* and *A. africanus* are already published. To summarize, Grine et al. (2010) found no significant
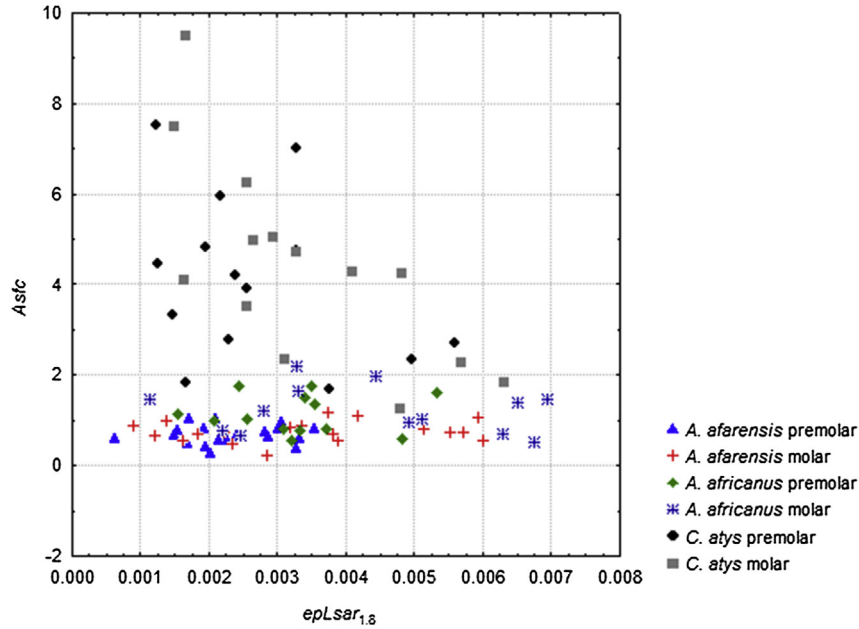
Figure 5. Complexity (*Asfc*) versus Anisotropy (*epLsar*$_{1.8}$) in *A. afarensis* P$_3$s (black triangles) and molars (grey squares). *Australopithecus afarensis* P$_3$s and molars are similarly complex, but the premolars lack the highest levels of anisotropy observed for the molars.

differences between these teeth in *A. africanus*. For *C. atys*, Daegling et al. (2011) analyzed four variables (*Asfc*, *epLsar*$_{1.8}$, *Smc*, and *Tfv*) and found no significant differences between the premolars and molars. When *HAsfc*$_9$ and *HAsfc*$_{81}$ are added to the analysis, there are still no significant differences between the premolars and molars of *C. atys* (Table 5; Figs. 2–4 and Figs. 6–8). Premolar and molar microwear textures are indistinguishable from one another for both *A. africanus* and *C. atys*. The situation is, however, more complex for *A. afarensis*. While no significant differences are observed for *Asfc*, *epLsar*$_{1.8}$, and *Smc*, significant differences were found for *Tfv* (the P$_3$ has the higher median), *HAsfc*$_9$, and *HAsfc*$_{81}$ (the P$_3$ sample is more heterogenous than the molars for both measures) (Tables 2 and 5). Though the *A. afarensis* P$_3$ *Tfv* is significantly higher than for the molars, the observed P$_3$ values are quite distinct and lower than observed for the premolars of the

hard-object-feeding *C. atys*, which was highlighted above. Among the three taxa examined in this study, *A. afarensis* is the only one that shows significant differences between the microwear textures of the premolars and molars, but there is no indication of the large *Tfv* values expected for a hard-object feeder. The data suggest that *A. afarensis* P$_3$s have more small microwear features, while *C. atys* is dominated by large pits.

When Levene's tests are applied to variance between the molars and premolars within taxa, no significant differences are observed for *C. atys*; however, significant differences are observed for each hominin taxon. Both *A. afarensis* ($F = 11.96$; $p = 0.001$) and *A. africanus* ($F = 8.66$; $p = 0.007$) evince higher variance for *epLsar*$_{1.8}$ on molars than premolars. For *Smc*, *A. afarensis* premolars have a higher variance than the molars ($F = 4.67$; $p = 0.037$). Finally, for *A. africanus* the molars vary more for *HAsfc*$_{81}$ than do the premolars ($F = 6.65$; $p = 0.016$).
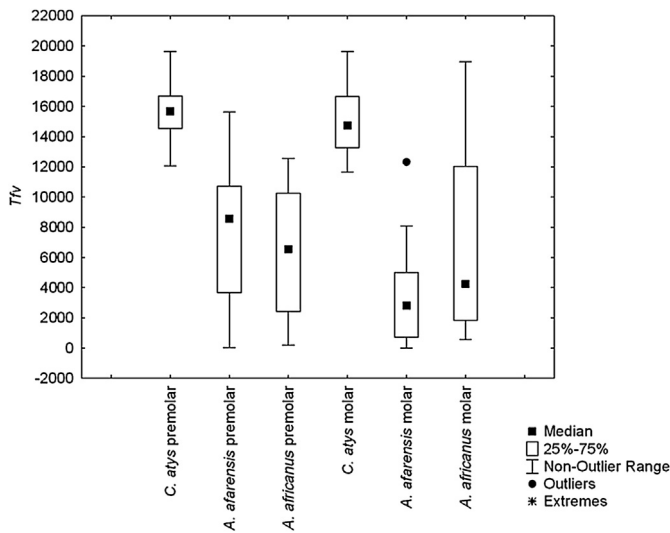
Figure 6. Box and whisker plots for molar and premolar *Tfv*. *C. atys* has the highest median. All taxa have higher *Tfv* for their premolars than their molars, but the comparison is only significant for *A. afarensis*.
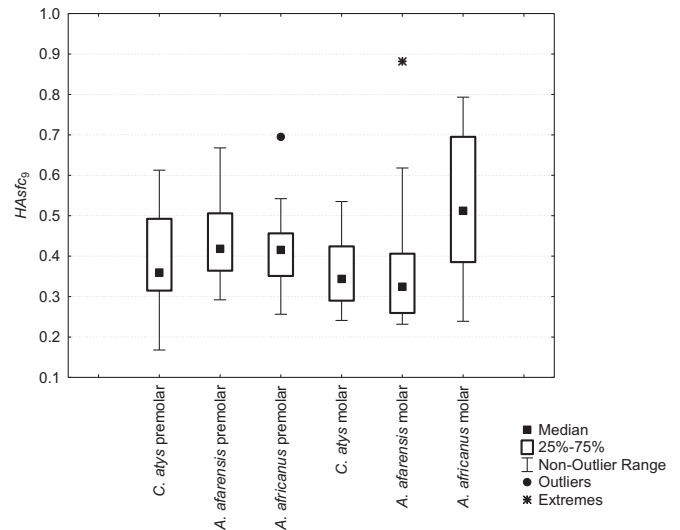
Figure 7. Box and whisker plots for molar and premolar *HAsfc*$_9$ for all taxa.
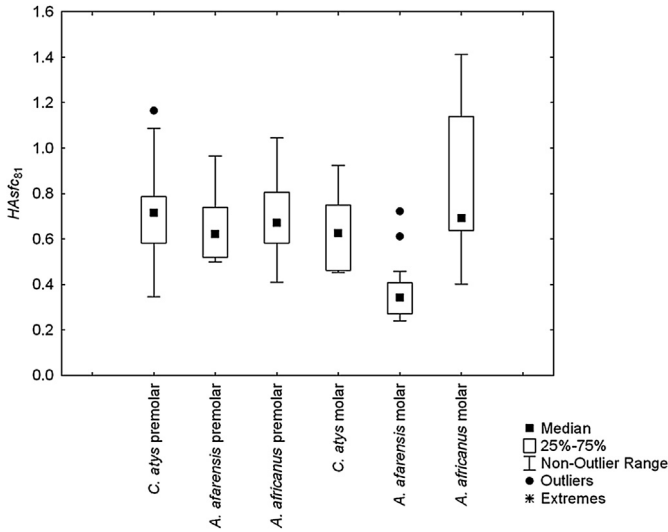
Figure 8. Box and whisker plots for molar and premolar $HAsfc_{81}$ for all taxa.

Principal components analyses of premolar and molar Phase II microwear

The PCA includes all premolars and molars from all three taxa. When the scores for PC 1 and PC 2 are graphed, the *C. atys* premolars and molars largely overlap but plot in a distinct space relative to both hominins (Fig. 9). The *C. atys* teeth are separated from the hominins on PC 2, which contains high loadings for *Asfc* and $HAsfc_{81}$ (Table 6). As expected for a hard-object feeder, *C. atys* premolars and molars have greater complexity than the hominin teeth, which explains their large positive values on PC 2. The premolars and molars of *A. africanus* also largely overlap in this PCA. The converse is true for *A. afarensis*, in which the molars and premolars form distinct clusters when the first two PCs are graphed (Fig. 9). What drives the distinctiveness of the *A. afarensis* P$_3$s relative to the molars is their combination of higher $HAsfc_9$ and $HAsfc_{81}$ and larger *Tfv*, which each load heavily on PC 1 (Table 6). This result is expected given differences between the P$_3$s and the molars for *A. afarensis* in $HAsfc_9$, $HAsfc_{81}$, and *Tfv* (Table 5). Though distinctions in microwear textures are evident for *A. afarensis* premolars and molars, it is important to remember that high *Asfc* and low $epLsar_{1.8}$ are expected for both the premolars and molars of hard-object feeders. This is not seen in the postcanine sample of *A. afarensis*, which are clearly separated from *C. atys* by the PCA (Fig. 10).

Comparison of mesial microwear textures between taxa

Summary statistics for microwear textures along the mesial protoconid crest of the P$_3$ in *A. afarensis* and *P. troglodytes* are presented in Table 7. No significant differences are observed for any microwear texture variables between male and female chimpanzees (Table 8). Between *A. afarensis* and *P. troglodytes*, two variables differ significantly: both *Tfv* and *Smc* have higher medians in

Table 3
Summary of MANOVA of rank-transformed Phase II microwear textures for three taxa (*C. atys*, *A. afarensis*, and *A. africanus*) and tooth type (premolar and molar).

Variable	Wilk's λ	F	Effect df	Error df	p-value
Intercept	0.035606	365.6	6	81	$p < 0.0001$
Tooth	0.814423	3.1	6	81	$p = 0.0092$
Taxon	0.129853	24.0	12	162	$p < 0.0001$
Tooth*Taxon	0.659262	3.1	12	162	$p = 0.0005$

Table 4
Results of Mann–Whitney U tests for Phase II microwear between taxa.

Premolars			Molars		
Variable	Pairwise Comparison	Result	Variable	Pairwise Comparison	Result
Asfc	*C. atys* – *A. afarensis*	Z = 4.84 $p < 0.0001$	*Asfc*	*C. atys* – *A. afarensis*	Z = 4.84 $p < 0.0001$
	C. atys – *A. africanus*	Z = 4.32 $p < 0.0001$		*C. atys* – *A. africanus*	Z = 4.03 $p < 0.0001$
	A. afarensis – *A. africanus*	Z = 2.74 $p = 0.006$		*A. afarensis* – *A. africanus*	Z = 2.51 $p = 0.012$
$epLsar_{1.8}$	*C. atys* – *A. afarensis*	Z = 0.15 $p = 0.884$	$epLsar_{1.8}$	*C. atys* – *A. afarensis*	Z = 0.182 $p = 0.855$
	C. atys – *A. africanus*	Z = 1.80 $p = 0.073$		*C. atys* – *A. africanus*	Z = 1.21 $p = 0.225$
	A. afarensis – *A. africanus*	Z = 2.51 $p = 0.012$		*A. afarensis* – *A. africanus*	Z = 1.25 $p = 0.212$
Smc	*C. atys* – *A. afarensis*	Z = 0.69 $p = 0.489$	*Smc*	*C. atys* – *A. afarensis*	Z = 1.71 $p = 0.087$
	C. atys – *A. africanus*	Z = 0.05 $p = 0.961$		*C. atys* – *A. africanus*	Z = 1.50 $p = 0.133$
	A. afarensis – *A. africanus*	Z = 0.59 $p = 0.552$		*A. afarensis* – *A. africanus*	Z = 1.63 $p = 0.103$
Tfv	*C. atys* – *A. afarensis*	Z = 4.55 $p < 0.0001$	*Tfv*	*C. atys* – *A. afarensis*	Z = 4.81 $p < 0.0001$
	C. atys – *A. africanus*	Z = 4.37 $p < 0.0001$		*C. atys* – *A. africanus*	Z = 2.96 $p = 0.003$
	A. afarensis – *A. africanus*	Z = 0.633 $p = 0.527$		*A. afarensis* – *A. africanus*	Z = 1.63 $p = 0.103$
$HAsfc_9$	*C. atys* – *A. afarensis*	Z = 4.33 $p < 0.0001$	$HAsfc_9$	*C. atys* – *A. afarensis*	Z = 0.44 $p = 0.66$
	C. atys – *A. africanus*	Z = 0.68 $p = 0.497$		*C. atys* – *A. africanus*	Z = 2.38 $p = 0.017$
	A. afarensis – *A. africanus*	Z = 3.89 $p < 0.0001$		*A. afarensis* – *A. africanus*	Z = 2.78 $p = 0.005$
$HAsfc_{81}$	*C. atys* – *A. afarensis*	Z = 0.80 $p = 0.423$	$HAsfc_{81}$	*C. atys* – *A. afarensis*	Z = 4.12 $p < 0.0001$
	C. atys – *A. africanus*	Z = 0.39 $p = 0.699$		*C. atys* – *A. africanus*	Z = 1.41 $p = 0.159$
	A. afarensis – *A. africanus*	Z = 0.25 $p = 0.803$		*A. afarensis* – *A. africanus*	Z = 4.24 $p < 0.0001$

A. afarensis than in *P. troglodytes*. The direction of difference corresponds to fewer small, shallow microwear features on *A. afarensis* P$_3$s, likely reflecting the fact that the honing facet on *P. troglodytes* is polished and lacks deep microwear features. This microwear signature clearly distinguishes the chimpanzee from *A. afarensis* and provides corroborative support for Greenfield's (1990) macrowear evidence that *A. afarensis* did not hone the maxillary canine.

Table 5
Results of pairwise comparisons between Phase II facets of molars and premolars for *A. afarensis*, *A. africanus*, and *C. atys*. For *A. afarensis*, pairwise comparisons were conducted with a Mann–Whitney U-test. For both *A. africanus* and *C. atys*, pairwise comparisons were determined from a Wilcoxon signed-rank test, see text for details.

Variable	*A. afarensis*	*A. africanus*	*C. atys*
Asfc	Z = 0.95 $p = 0.343$	Z = 1.15 $p = 0.249$	Z = 0.09 $p = 0.925$
$epLsar_{1.8}$	Z = 1.91 $p = 0.056$	Z = 1.43 $p = 0.116$	Z = 1.60 $p = 0.109$
Smc	Z = 0.98 $p = 0.328$	Z = 0.25 $p = 0.807$	Z = 0.41 $p = 0.683$
Tfv	Z = 2.82 $p = 0.005$	Z = 0.04 $p = 0.972$	Z = 1.41 $p = 0.158$
$HAsfc_9$	Z = 4.40 $p < 0.0001$	Z = 1.36 $p = 0.173$	Z = 0.22 $p = 0.826$
$HAsfc_{81}$	Z = 4.71 $p < 0.0001$	Z = 0.87 $p = 0.382$	Z = 0.85 $p = 0.397$

Temporal trends in *A. afarensis* P₃ microwear

For both the mesial protoconid crest and the Phase II surface of the *A. afarensis* P₃, none of the six microwear variables exhibits a statistically significant temporal trend (Table 9). For the Phase II facet, $epLsar_{1.8}$ does not show a significant trend towards increased anisotropy but has the lowest p-value of any texture; however, this is driven largely by the contrast between the Laetoli premolars, which are the oldest and among the least anisotropic, and the Ethiopian specimens (Fig. 10). There is no evidence from microwear for a change in the material properties of the foods processed either mesially or distally by the *A. afarensis* P₃.

Discussion

Evidence for hard object processing by *A. afarensis* premolars

Previous analyses have shown that *A. anamensis*, *A. afarensis*, *A. africanus* and *P. boisei* have low molar microwear texture complexity values, suggesting that individuals examined to date did not often use these teeth to process hard objects in the days or weeks before death (Ungar et al., 2008, 2010; Ungar and Spoonheimer, 2011; Henry et al., 2012). A notable exception is *P. robustus*, for which it has been suggested that hard objects were an important fall back resource (Scott et al., 2005). Given constraints imposed by limited gape and facial buttressing above the premolars, Strait et al. (2009, 2010) suggested that the molar microwear analyses in *A. africanus* are misleading, as premolars would have more likely processed hard objects than would have the molars. Strait et al. hypothesized that hard-object processing was a two-step process in this taxon, with the premolars initially breaking through the exteriors of hard objects and the molars processing the softer interiors. If these authors are correct, then premolars and molars should show differences in microwear textures that reflect their functional differentiation. Since extant hard-object-feeding primates tend to have more complex molar Phase II microwear surfaces (here measured as *Asfc*) than soft-object-feeding primates, if the Strait et al. model is correct, then *A. africanus* premolars should exhibit higher *Asfc* than their molars.

Table 6
Factor Loadings for microwear textures for *A. afarensis*, *A. africanus*, and *C. atys* molars and premolars. Those loadings that are ≥ absolute value 0.7 are bolded.

|	PC 1	PC 2	PC 3	PC 4	PC 5	PC 6
Asfc	−0.540	**0.710**	0.083	−0.245	−0.367	0.055
$epLsar_{1.8}$	0.059	−0.374	**0.919**	−0.102	−0.044	0.005
Smc	−0.493	0.266	0.179	0.808	0.012	0.013
Tfv	**−0.799**	0.349	0.119	−0.291	0.370	0.065
$HAsfc_9$	−0.517	**−0.778**	−0.178	0.013	−0.092	0.296
$HAsfc_{81}$	**−0.771**	−0.536	−0.106	−0.060	−0.075	−0.12
% Variance explained	34.0	28.8	15.7	13.5	4.8	3.2
% Cumulative variance explained	34.0	62.8	78.5	92.0	96.8	100

Grine et al. (2010) tested this hypothesis in *A. africanus* and did not find high complexity textures for either the premolars or molars, and no evidence for differences between the teeth (Tables 2 and 5; Fig. 3). In an extant primate hard-object feeder *C. atys*, by contrast, Daegling et al. (2011) found complex microwear textures on *both* the premolars and molars, but again, no differences between the two tooth types (Tables 2 and 5; Fig. 3). The results of these two studies taken together show that microwear provides no evidence that *A. africanus* used its molars and premolars differently.

Because *A. afarensis* P₃ microwear textures are no more complex than the molars and are significantly less complex than the textures observed in *C. atys* premolars (Table 4; Fig. 3), the present study adds to the growing body of evidence indicating that australopiths did not habitually use their premolars to process hard objects. Scott et al. (2012) found that across a broad sample of extant primates, hard-object feeders have median molar *Asfc* values greater than 2.0, which is also true for the premolars of *C. atys* (Table 2; Fig. 3) (Daegling et al., 2011). The median *Asfc* values for *A. afarensis* P₃s and molars are well below 2.0 and are remarkably similar to one another (Table 2; Fig. 3). A total of 32 *A. afarensis* individuals were analyzed in this study, and not one approaches the level of complexity observed in *C. atys* or the 2.0 value (Fig. 3). This includes the youngest *A. afarensis* specimens from Hadar, from the KH-2 submember of the Hadar Formation, which samples a relatively
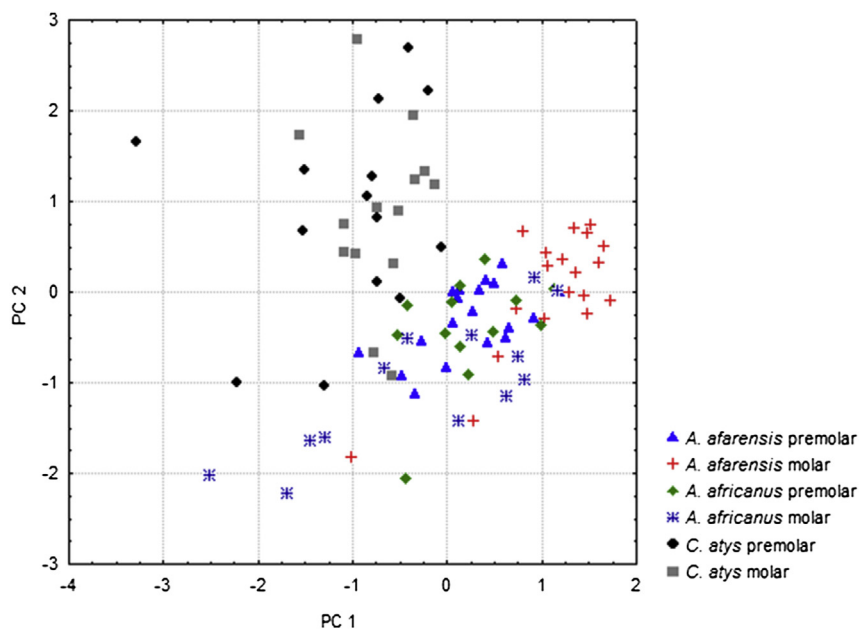
Figure 9. For the PCA, the *C. atys* postcanine teeth are easily distinguished from the hominins. *A. afarensis* is unique as a sample for the lack of overlap for its P₃s and molars.
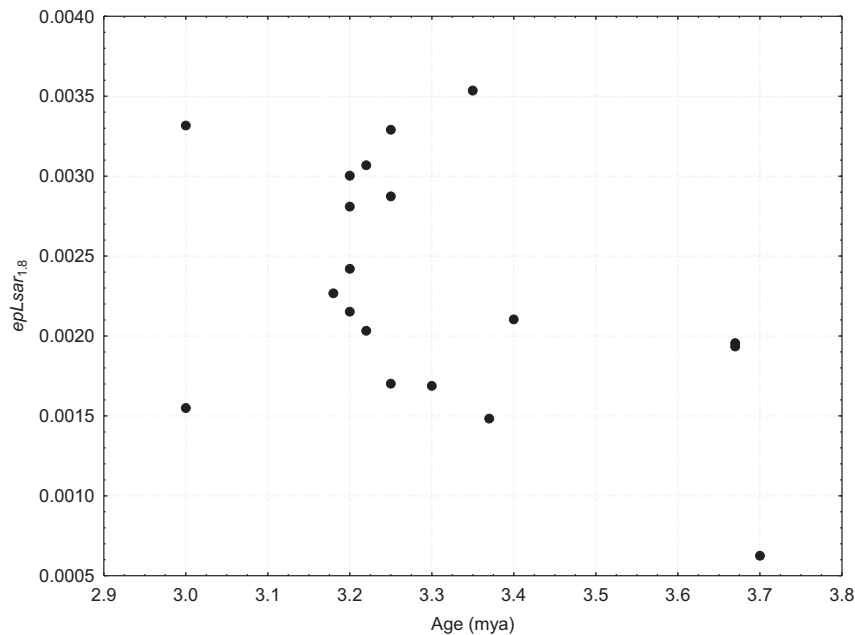
Figure 10. Temporal trend for $epLsar_{1.8}$. The Laetoli sample is the oldest and contains the most anisotropic P_3 texture, which lowers the overall *p*-value for this trend, though it still does not reach the level of statistical significance.

arid, open habitat (Reed, 2008). The KH-2 sample is noted for having large mandibles (Lockwood et al., 2000; Kimbel et al., 2004; Delezene and Kimbel, 2011); yet, even with these, the P_3s (A.L. 438-3, A.L. 440-1) do not have the complex microwear textures expected for a hard-object feeder. Therefore, premolar and molar microwear evidence is not consistent with hard objects being a common target for *A. afarensis*, regardless of habitat type (Grine et al., 2006a, b; Ungar et al., 2010). Results suggest that observed temporal trends for P_3 mesiodistal length reduction, P_3 shape change (Lockwood et al., 2000; Delezene and Kimbel, 2011), and an increase in mandibular size (Lockwood et al., 2000) are related to something other than consistently increasing tooth use for crushing hard objects.

Molar and premolar microwear have to date been compared directly in few primate species, but the pattern for *A. africanus* (Grine et al., 2010), *C. atys* (Daegling et al., 2011), and three platyrrhine species (McKusick and Teaford, 2007) is one of consistent microwear on Phase II wear surfaces along the postcanine row, suggesting no detectable functional differentiation by food-fracture properties. In this study, *A. afarensis* P_3s and molars are not distinguishable for *Smc*, *Asfc*, and $epLsar_{1.8}$, but are significantly different for *Tfv* (higher in P_3s than molars) and both $HAsfc_9$ and $HAsfc_{81}$ (the P_3s are more heterogenous) (Table 5). While small

sample sizes for the oldest *A. afarensis* P_3 sample from Laetoli prohibit robust statistical comparison between tooth types, the direction of median difference between molar and premolar textures is consistent across sites and time (Table 10), suggesting that higher P_3 *Tfv*, $HAsfc_9$, and $HAsfc_{81}$ are a stable feature of *A. afarensis* postcanine microwear. Scott et al. (2005) argued that *Tfv* reflects the size of microwear features. Compared with the molars, *A. afarensis* P_3s have higher *Tfv*, which suggests that there are fewer small microwear features on the premolars than the molars. While high *Tfv* values are associated with hard-object feeding, the values for premolar *Tfv* observed for *A. afarensis* only minimally overlap those of *C. atys* (Fig. 6). Thus, there is no evidence from *Tfv* for hard-object processing by *A. afarensis* premolars. While the possibility remains that *A. afarensis* premolars and molars differ subtly in their roles in food processing, the microwear signature from both sets of teeth clearly do not match those expected for a hard-object feeder. In fact, the unusual combination of low *Asfc* and low $epLsar_{1.8}$ observed for the *A. afarensis* molars (Ungar et al., 2010) is repeated for the Phase II facets of the P_3.

Table 7
Summary statistics for P_3 mesial protoconid crest microwear.

Variable	Taxon	*n*	Mean	Median	Std. dev.
Asfc	*A. afarensis*	16	1.57	1.28	1.086
	P. troglodytes	20	1.36	0.81	2.053
$epLsar_{1.8}$	*A. afarensis*	16	0.000	0.000	0.001
	P. troglodytes	20	0.003	0.003	0.002
Smc	*A. afarensis*	16	6.21	0.51	22.866
	P. troglodytes	20	28.32	0.15	79.854
Tfv	*A. afarensis*	16	10,767.11	10,563.78	2801.255
	P. troglodytes	20	7532.59	6839.16	4837.228
$HAsfc_9$	*A. afarensis*	16	0.45	0.43	0.154
	P. troglodytes	20	0.45	0.40	0.183
$HAsfc_{81}$	*A. afarensis*	16	0.94	0.61	0.849
	P. troglodytes	20	0.89	0.73	0.554

Table 8
Results of pairwise comparisons between mesial protoconid crest microwear of P_3s for male and female *P. troglodytes*. Pairwise comparisons were conducted with a Mann–Whitney *U*-test.

Variable	*P. troglodytes* ♂ versus *P. troglodytes* ♀	*A. afarensis* versus *P. troglodytes*
Asfc	Z = 0.00	Z = 1.88
	p = 1.00	p = 0.06
$epLsar_{1.8}$	Z = −0.53	Z = −0.10
	p = 0.60	p = 0.92
Smc	Z = −0.94	Z = 2.83
	p = 0.34	p = 0.01
Tfv	Z = −0.98	Z = 2.20
	p = 0.33	p = 0.03
$HAsfc_9$	Z = −0.15	Z = 0.16
	p = 0.88	p = 0.87
$HAsfc_{81}$	Z = 0.23	Z = −0.57
	p = 0.82	p = 0.57

Table 9
Temporal trends in *A. afarensis* P_3 phase II microwear. None of the six variables exhibits a significant temporal trend.

Phase II microwear	Γ	Spearman's rank	Mesial microwear	Γ	Spearman's rank
Asfc	$\Gamma = 86.1$	$r_s = 0.004$	*Asfc*	$\Gamma = 173.8$	$r_s = 0.071$
	$p = 0.881$	$p = 0.989$		$p = 0.586$	$p = 0.774$
epLsar$_{1.8}$	$\Gamma = 0.314$	$r_s = 0.441$	*epLsar*$_{1.8}$	$\Gamma = 0.347$	$r_s = -0.044$
	$p = 0.195$	$p = 0.059$		$p = 0.601$	$p = 0.857$
Smc	$\Gamma = 111.1$	$r_s = -0.293$	*Smc*	$\Gamma = 338.9$	$r_s = 0.561$
	$p = 0.699$	$p = 0.223$		$p = 0.678$	$p = 0.012$
Tfv	$\Gamma = 940,274.3$	$r_s = -0.115$	*Tfv*	$\Gamma = 1263081.4$	$r_s = -0.077$
	$p = 0.730$	$p = 0.640$		$p = 0.552$	$p = 0.754$
HAsfc$_9$	$\Gamma = 78.3$	$r_s = -0.250$	*HAsfc*$_9$	$\Gamma = 52.3$	$r_s = -0.017$
	$p = 0.340$	$p = 0.302$		$p = 0.526$	$p = 0.946$
HAsfc$_{81}$	$\Gamma = 84.3$	$r_s = -0.003$	*HAsfc*$_{81}$	$\Gamma = 95.0$	$r_s = 0.009$
	$p = 0.311$	$p = 0.991$		$p = 0.758$	$p = 0.971$

Australopithecus afarensis yields the only sample studied to date to show significant differences in central tendency between premolar and molar microwear textures. Such differences might reflect functional differentiation of premolar and molar teeth in this hominin but not in *A. africanus* or *C. atys*. It must be kept in mind, however, that the tooth types in the *A. afarensis* sample are not precisely the same as for *A. africanus* or *C. atys*, which complicates interpretation. For *C. atys*, P^4s were compared with M^1s and the *A. africanus* sample includes a mixture of premolar (P3s and P4s) and molar (M1s and M2) positions. Gordon (1982) found, in an early study of chimpanzee microwear, an association between feature density and molar position. She hypothesized that these differences resulted from gradients in bite force, which decreases mesially along the tooth row, and the arc length that each tooth traces during the chewing cycle, which increases mesially along the tooth row (e.g., Gordon, 1982, 1984a, 1984b, 1984c; Mahoney, 2006). Because adjacent postcanine teeth were compared in *C. atys*, such biomechanical effects would be least pronounced in this taxon among the three samples considered in this study. Still, the significant differences in *A. afarensis* premolar and microwear textures highlight the need for further studies including all premolars and molars that are grounded in specific hypotheses derived from the biomechanics of the masticatory system. For example, low anisotropy observed on *A. afarensis* postcanine teeth is intriguing and suggests variable tooth-food-tooth contact. When viewed from

Table 10
Summary statistics for geographically-divided samples of *A. afarensis*.

Variable	Taxon	N	Tooth	Mean	Median
Asfc	Laetoli	3	P_3	0.609	0.589
			Molars	0.815	0.823
	Ethiopia	16	P_3	0.688	0.676
			Molars	0.726	0.707
epLsar$_{1.8}$	Laetoli	3	P_3	0.002	0.002
			Molars	0.003	0.003
	Ethiopia	16	P_3	0.003	0.003
			Molars	0.003	0.004
Smc	Laetoli	3	P_3	1.156	1.353
			Molars	1.070	0.600
	Ethiopia	16	P_3	0.877	0.417
			Molars	0.470	0.379
Tfv	Laetoli	3	P_3	6305.1	5764.8
			Molars	5720.7	4163.8
	Ethiopia	16	P_3	7735.4	8694.3
			Molars	2952.5	2786.3
HAsfc$_9$	Laetoli	3	P_3	0.692	0.691
			Molars	0.461	0.259
	Ethiopia	16	P_3	0.606	0.605
			Molars	0.346	0.325
HAsfc$_{81}$	Laetoli	3	P_3	0.742	0.751
			Molars	0.416	0.272
	Ethiopia	16	P_3	0.652	0.643
			Molars	0.359	0.345

a nano-perspective (i.e., the impacts of microscopic points of contact), then low anisotropy suggests variable jaw/tooth movements, whereas higher heterogeneity suggests more variable microscopic point contacts. Evaluation of such hypotheses will require the development of a larger extant comparative baseline of microwear of living primates with varying degrees of premolar molarization, laboratory studies of animals fed known food items, and relevant biomechanical models to explain differences in tooth-food-tooth interaction, macroscopically and microscopically, along the dental rows.

Microwear along the A. afarensis mesial protoconid crest

Studies of microwear associated with canine honing have been limited (e.g., Ryan, 1979, 1981; Walker, 1984) and this study is the first to apply microtexture analysis to this dental function. Microwear along the mesial protoconid crest captures distinctions in the use of the P_3 as a honing device for the maxillary canine. In both male and female chimpanzees, the mesial protoconid crest functions as a hone for the maxillary canine. In the australopiths, in contrast, the short maxillary canine is not honed and apical canine wear is substantial. In line with their shared function as a honing device, the male and female chimpanzee P_3 microwear signatures do not differ (Table 9) and the microwear textures of the combined chimpanzee sample are distinct from that of *A. afarensis* (Table 10). The direction of differences suggests that there are fewer small microwear features on the *A. afarensis* mesial protoconid crest, which is consistent with canine honing polishing the chimpanzee mesial protoconid crest and creating few deep microwear features. Larger features are evident along the crest in *A. afarensis* and these features resulted from more direct contact between the apex of the maxillary canine and P_3 mesial protoconid crest. The transition from a honing to a nonhoning P_3 is already evident prior to the origin of *Australopithecus* (Suwa et al., 2009) and the current analysis indicates that there is no evidence from microwear for a change in the use of the canine in food acquisition and processing behaviors over time within the *A. afarensis* lineage.

Conclusion

Despite possessing a dental morphology "admirably equipped to process hard brittle objects" (Teaford and Ungar, 2000:13508), neither premolar nor molar microwear provides unambiguous evidence that dedicated hard-object feeding is the likeliest explanation of increasing megadonty and premolar molarization in australopith evolution — at least when extant primate hard-object feeders are the guide (Ungar and Spoonheimer, 2011). As expected for a taxon that lacks a functional canine honing complex, the microwear signature along the *A. afarensis* P_3 mesial protoconid crest is clearly distinct from that of the honing *P. troglodytes*.

Additionally, there is no evidence from neither the Phase II facet nor from the mesial protoconid crest of the P$_3$ for a temporal change in the mechanical properties of the foods consumed by *A. afarensis*. Thus, microwear provides no evidence that a change in the mechanical properties of the foods consumed is responsible for directional changes observed in early *Australopithecus* P$_3$ crown form. The finding of significant differences in *A. afarensis* for *Tfv*, *HAsfc$_9$*, and *HAsfc$_{81}$* between the P$_3$ and the molars is unique among the limited sample of catarrhines examined to date and highlights the need for more specific hypotheses that tie masticatory biomechanics and tooth form to functional differences along the postcanine tooth row.

Acknowledgments

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