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PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B

Phil. Trans. R. Soc. B (2010) **365**, 3345–3354
doi:10.1098/rstb.2010.0033

Molar microwear textures and the diets of *Australopithecus anamensis* and *Australopithecus afarensis*

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Many researchers have suggested that *Australopithecus anamensis* and *Australopithecus afarensis* were among the earliest hominins to have diets that included hard, brittle items. Here we examine dental microwear textures of these hominins for evidence of this. The molars of three *Au. anamensis* and 19 *Au. afarensis* specimens examined preserve unobscured antemortem microwear. Microwear textures of these individuals closely resemble those of *Paranthropus boisei*, having lower complexity values than *Australopithecus africanus* and especially *Paranthropus robustus*. The microwear texture complexity values for *Au. anamensis* and *Au. afarensis* are similar to those of the grass-eating *Theropithecus gelada* and folivorous *Alouatta palliata* and *Trachypithecus cristatus*. This implies that these *Au. anamensis* and *Au. afarensis* individuals did not have diets dominated by hard, brittle foods shortly before their deaths. On the other hand, microwear texture anisotropy values for these taxa are lower on average than those of *Theropithecus*, *Alouatta* or *Trachypithecus*. This suggests that the fossil taxa did not have diets dominated by tough foods either, or if they did that directions of tooth–tooth movement were less constrained than in higher cusped and sharper crested extant primate grass eaters and folivores.

Keywords: *Australopithecus*; molar; diet; microwear textures

1. INTRODUCTION

Researchers have recognized for more than three decades that patterns of microscopic use wear on teeth hold the potential to provide information about the diets of early hominins (e.g. Grine 1977, 1981, 1986; Puech 1979; Ryan 1980; Walker 1981; Ungar *et al.* 2006). Many studies of hominin dental microwear have been published over the past thirty years, including feature-based quantitative analyses of molar occlusal surface microwear in *Australopithecus afarensis*[1] and *Australopithecus anamensis* (Grine *et al.* 2006*a*,*b*). Data presented here extend this work by comparing the microwear textures of these species with those of other early hominins and recent primate taxa with known diets. Results indicate that sampled *Au. anamensis* and *Au. afarensis* individuals tend to have relatively simple microwear surface textures varying in degree of anisotropy. This pattern is comparable to that previously reported for *Paranthropus boisei* (Ungar *et al.* 2008), but differs from that of *Au. africanus*, and especially of *Paranthropus robustus* (Scott *et al.* 2005; see also Grine 1986).

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One contribution of 14 to a Discussion Meeting Issue 'The first four million years of human evolution'.

(a) *Background*

Australopithecus anamensis and *Au. afarensis* have traditionally been argued to be the earliest hominins to show an adaptive shift from diets dominated by soft, sugary forest fruits to hard and brittle or abrasive foods (Ward *et al.* 1999; Teaford & Ungar 2000; White *et al.* 2000; Wood & Richmond 2000; Walker 2002; Macho *et al.* 2005). *Australopithecus afarensis*, for example, has long been noted to have thickly enamelled, large and flat crowned cheek teeth and robustly constructed crania and mandibles, at least when compared with our nearest living relatives, the chimpanzees (e.g. McHenry 1984; Hylander 1988; White *et al.* 2000). This enhanced craniodental toolkit has led workers to suggest that 'nuts, seeds, and hard fruit may have been an important component to the diet of this species' (Wood & Richmond 2000).

These hominins have also been thought to have had dietary adaptations intermediate between those of frugivorous forest apes and later hominins. White *et al.* (2000), for example, considered them to have taken the 'initial functional steps that would eventually culminate in the far more derived, specialized masticatory apparatus of later hominid species' such as *Au. africanus* and especially *Par. boisei* and *Par. robustus*. As White *et al.* (1981) noted, while *Au. africanus* showed several craniodental features foreshadowing the functional specializations seen in

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Paranthropus, *Au. afarensis* retained at least some more primitive traits, such as relatively larger front teeth and less swollen and inflated cusps on their postcanines. Picq (1990) further suggested that the height and thickness of the *Au. afarensis* mandibular corpus, and robusticity of the symphysis, were intermediate between those of chimpanzees on the one hand and those of *Au. africanus* and especially *Paranthropus* species on the other. He argued the same for the height of the ramus and size of the mandibular condyle.

Picq (1990) used these lines of evidence to build a scenario in which *Au. afarensis* was still dependent on the fruits of the forest, but seasonally sought sustenance in more open settings with 'tougher foods containing abrasive structures' and 'nuts protected by skins or a hard shell'. Ungar & Teaford (2001) called this a 'mixed forest–savanna resource adaptation'. Ungar (2004) further noted that the degree of differences in occlusal slope and relief between *Au. afarensis* and chimpanzees are as expected for differences in 'fallback' foods, suggesting that the early hominins may have preferred soft, sugar-rich fruits, but had the ability to make more effective use of hard, brittle resources as seasonal availabilities required.

Following its initial description, *Au. anamensis* quickly took on the role of 'intermediate form' in terms of dietary adaptation between the earlier *Ardipithecus* and *Au. afarensis*. Like *Au. afarensis*, *Au. anamensis* had thicker post-canine tooth enamel and larger average cheek teeth than *Ardipithecus*, again suggesting a dietary shift towards harder foods or more abrasive ones (Ward *et al.* 1999; Teaford & Ungar 2000; Wood & Richmond 2000; Walker 2002; Suwa *et al.* 2009). Still, in comparison with *Au. afarensis*, *Au. anamensis* molars were 'not very high-crowned' (Walker 2002), and the larger values for enamel thickness in *Au. anamensis* when compared with *Ar. ramidus* may reflect, at least in part, increased tooth size in the former (Suwa *et al.* 2009, supporting online material). Further, *Au. anamensis* lacked changes in the geometry of the mandible and maxilla seen in *Au. afarensis*, *Au. africanus* and especially *Paranthropus* (Ward *et al.* 1999), such as greater mandibular corpus robusticity, which might buttress the jaw against higher peak force magnitudes or repetitive loading in mastication (Teaford & Ungar 2000). These differences led Teaford & Ungar (2000) to speculate that hard and perhaps abrasive foods may have become even more important components of the diet of *Au. afarensis*. Walker (2002) suggested that changes from *Au. anamensis* to *Au. afarensis* were carried to extremes in *Au. africanus* and especially *Paranthropus*.

The microwear evidence paints a somewhat more complex picture. One might predict heavy pitting associated with hard-object consumption in *Au. anamensis* and *Au. afarensis* and an increase in pitting from the earlier to the later species. Contrary to expectation though, both show fairly fine features and microwear surfaces dominated by striations rather than pits (Grine *et al.* 2006*a*,*b*; Suwa *et al.* 2009, supporting online material). This pattern is more similar to that seen in the tough food folivore *Gorilla gorilla beringei* than in hard-object feeders, such as the grey-cheeked mangabey *Lophocebus albigena* and the brown capuchin, *Cebus apella*. Further, the microwear pattern for these hominins is remarkably homogeneous between specimens across both time and paleoecological context. Grine *et al.* (2006*a*,*b*) suggest that these results highlight the difference between 'faculty' and 'biological role' (Bock & von Wahlert 1965) or dietary potential and what an animal eats on a day-to-day basis. As a result, Grine *et al.* (2006*a*,*b*) suggested that the shift in diet-related adaptive morphology in *Au. anamensis* and *Au. afarensis* may relate more to occasional but critical fallback food exploitation than to preferred resources.

We might predict, if *Au. africanus* and especially *Par. boisei* and *Par. robustus* show further craniodental specializations for the consumption of hard, brittle foods, that samples of these species should have more individuals showing high levels of microwear pitting or surface complexity with fewer fine, parallel striations and with texture anisotropy, compared with *Au. afarensis* and especially *Au. anamensis*.

Here we present the first microwear texture analysis of *Au. afarensis* and *Au. anamensis* for comparison with *Au. africanus*, *Par. boisei* and *Par. robustus*. Microwear texture analysis has proved to provide a three-dimensional characterization of microwear surfaces free from the need to identify and measure individual features (e.g. Ungar *et al.* 2003, 2007*a*,*b*, 2008; Scott *et al.* 2005, 2006, 2009*a*; El-Zaatari 2008; Krueger *et al.* 2008; Ungar & Scott 2009; Krueger & Ungar in press). While microwear texture analysis and conventional feature-based analyses to date have yielded similar results for other hominins (compare Grine (1986) with Scott *et al.* (2005) and Ungar *et al.* (2006) with Ungar & Scott (2009)), texture analyses are particularly well suited for between-studies comparisons, because data collected are free from observer measurement error. Further, microwear texture results for *Au. africanus*, *Par. robustus* and *Par. boisei* are available in the literature for comparison (Scott *et al.* 2005; Ungar *et al.* 2008). Indeed, only texture data are available for *Par. boisei*.

Microwear texture analysis studies indicate that hard-object feeding extant primates (and other mammals) tend to have higher average levels of texture complexity and lower levels of anisotropy on their molar occlusal surfaces than seen in tough food eaters (see Ungar *et al.* 2007*b* for a review). Here we test the hypothesis that interpretations of craniodental functional morphology described above are reflected in microwear texture patterns. If so, *Au. afarensis* and especially *Au. anamensis* specimens should show less surface complexity and more anisotropy than those of *Au. africanus*, and especially *Par. boisei* and *Par. robustus*.

2. MATERIAL AND METHODS

Dental microwear texture data are presented here for the molar teeth of *Au. anamensis* from Kanapoi and Allia Bay in Kenya and *Au. afarensis* from the Laetolil Beds in Tanzania and the Hadar Formation in Ethiopia. Specimens included in this study are the same as

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Table 1. Microwear texture analysis data for *Au. anamensis* and *Au. afarensis*.

specimen	*Asfc*	$epLsar_{1.8}$	*Smc*	$HAsfc_9$	$HAsfc_{81}$
Au. anamensis					
KNM-ER 35236	0.97466	0.00307	0.15015	0.58516	0.71286
KNM-KP 29287	0.80791	0.00299	0.20908	0.34424	0.58869
KNM-KP 34725	1.30999	0.00244	0.50835	0.38439	0.83670
Au. afarensis					
AL 128-23	0.64728	0.00122	0.70776	0.30052	0.37230
AL 145-35	0.87280	0.00337	0.26841	0.45188	0.56429
AL 188-1	0.53380	0.00390	0.34143	0.29913	0.33684
AL 200-1b	0.70342	0.00572	0.21016	0.40769	0.57363
AL 225-8	1.06196	0.00594	0.26836	0.61132	0.99634
AL 288-1i	0.68804	0.00184	1.20858	0.34728	0.49713
AL 333-74	0.53915	0.00602	0.50798	0.24058	0.33415
AL 333w-12	1.16543	0.00374	0.27184	0.45849	0.50411
AL 333w-1a	0.71150	0.00553	0.59957	0.32997	0.37838
AL 333w-57	0.69913	0.00382	0.34153	0.26405	0.31046
AL 333w-59	0.19077	0.00285	0.94135	0.34335	0.38715
AL 333w-60	0.77945	0.00515	0.41635	0.31759	0.36561
AL 366-1	0.85189	0.00090	0.59981	0.35013	0.42788
AL 400-1a	0.72866	0.00223	0.41634	0.26509	0.38790
AL 486-1	0.97104	0.00139	0.15015	0.38916	0.44262
AL 487-1c	0.46932	0.00236	0.26690	0.36286	0.39707
LH4	0.54767	0.00163	2.40210	0.27204	0.29177
LH 15	1.07480	0.00419	0.20835	0.72182	0.87299
LH 22	0.82274	0.00319	0.59962	0.25273	0.31400

those employed in feature-based SEM microwear analyses reported by Grine *et al.* (2006*a*,*b*).

All permanent molars available to us were first examined to determine the suitability for microwear analysis. Those that preserved wear facets were cleaned with cotton swabs soaked in alcohol or acetone to remove adherent dirt or preservatives. Moulds of occlusal surfaces were then made using President Jet Regular Body vinyl dental impression material (Coltène-Whaledent Corp.), and casts were produced from these molds using Epotek 301 epoxy and hardener (Epoxy Technologies Inc.).

Replicas were examined by light microscopy and SEM as necessary to determine the suitability for microwear analysis following the criteria described by Teaford (1988). Most specimens had occlusal surfaces obscured by taphonomic damage and so had to be excluded from this study. In the end, the molars of only three of the *Au. anamensis* specimens and 19 *Au. afarensis* individuals available to us were found to preserve unobscured antemortem occlusal surface microwear. A list of all specimens considered can be found in Grine *et al.* (2006*a*,*b*) and those included in this study are presented in table 1.

All specimens included in this study were analysed using a Sensofar Plμ white-light confocal profiler (Solarius, Inc.) with an integrated vertical scanning interferometer. Three-dimensional point clouds were collected for 'phase II' facets (the buccal occlusal surfaces of lower molars and the lingual occlusal surface of uppers) using a 100× long working distance objective. The point clouds sampled elevations at intervals of 0.18 μm along the *x*- and *y*-axes, with a vertical resolution of 0.005 μm. Data were obtained for four adjacent fields on facets 9 or 10n, for a combined work envelope of 276 μm × 204 μm. The feature-based study of these specimens reported in Grine *et al.* (2006*a*,*b*) used a pixel resolution of 0.25 μm and combined sample area of 0.04 mm^2.

Resulting point clouds were analysed using ToothFrax and SFrax scale-sensitive fractal analysis (SSFA) software (Surfract Corp.). SSFA as applied to microwear research is described in detail elsewhere (e.g. Scott *et al.* 2006). The basic premise is that surface texture varies with scale of observation, and that this variation can be used to characterize functionally relevant aspects of microwear. SSFA texture variables included in this study are area-scale fractal complexity (*Asfc*), anisotropy (*epLsar*), scale of maximum complexity (*Smc*) and heterogeneity of complexity (*HAsfc*). Values for individual specimens are reported as medians of the four fields sampled for each specimen.

Area-scale fractal complexity is a measure of change in roughness with scale. The faster a measured surface area increases with resolution, the more complex the surface. Anisotropy is characterized as variation in lengths of transect lines measured at a given scale (we use 1.8 μm) with orientations sampled at 5° intervals across a surface. An anisotropic surface will have shorter transects in the direction of the surface pattern than perpendicular to it (e.g. a transect that cross-cuts parallel scratches must trace the peaks and valleys of each individual feature). Thus, a heavily pitted surface typically has high *Asfc* and low *epLsar* values, whereas one dominated by homogeneous, parallel striations has low *Asfc* and high *epLsar* values. Other variables used to characterize microwear surface texture include *Smc*, the scale range over which *Asfc* is calculated, and *HAsfc*, variation of *Asfc* across a surface (in this

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Table 2. Summary statistics for early hominins.

	Au. anamensis	*Au. afarensis*	*Au. africanus*	*Par. boisei*	*Par. robustus*
n	3	19	10	7	9
Asfc					
mean	1.031	0.740	1.522	0.625	3.543
s.d.	0.256	0.236	0.387	0.268	1.449
epLsar					
mean	0.003	0.003	0.004	0.003	0.002
s.d.	0.000	0.002	0.002	0.002	0.001
Smc					
mean	0.289	0.565	1.834	0.516	0.216
s.d.	0.192	0.521	4.256	0.269	0.053
$HAsfc_9$					
mean	0.438	0.368	0.617	0.460	1.054
s.d.	0.129	0.124	0.259	0.136	0.564
$HAsfc_{81}$					
mean	0.713	0.461	1.004	0.621	2.101
s.d.	0.124	0.187	0.367	0.232	1.026

case, each field of view was divided into a 3×3 grid = $HAsfc_9$, and a 9×9 grid = $HAsfc_{81}$). High *Smc* values should correspond to more complex coarse features. High *HAsfc* values are observed for surfaces that vary in complexity across a facet.

Statistical analyses focused on comparisons of microwear textures of *Au. afarensis* with those of *Au. africanus* and *Par. robustus* from South Africa as reported in Scott *et al.* (2005) and with *Par. boisei* from eastern Africa as reported by Ungar *et al.* (2008). *Australopithecus anamensis* data could not be compared statistically with those of the other hominins given an available sample of only three specimens, although newly recovered specimens (e.g. Haile-Selassie, this volume) hold the potential for larger microwear datasets in the future. First, differences in central tendencies between taxa were assessed using a MANOVA performed on ranked data (Conover & Iman 1981) for all variables (*Asfc*, *epLsar*, *Smc*, $HAsfc_9$ and $HAsfc_{81}$). Individual ANOVAs and multiple comparisons tests were used to determine the sources of significant variation. Both Tukey's honestly significant difference (HSD) and Fisher's least significant difference (LSD) tests were used to balance risks of type I and type II errors (Cook & Farewell 1996). Values of $p < 0.05$ for Tukey's HSD tests may be assigned significance with some confidence, whereas values of $p < 0.05$ on Fisher's LSD but not Tukey's LSD tests are considered suggestive but of marginal significance.

Degree of variance in microwear textures within taxa may be as important for distinguishing species as differences in central tendencies, especially given differences in foraging and feeding strategies between primates. With this in mind, raw data for each variable were transformed for Levene's test following the procedure described by Plavcan & Cope (2001) to compare distribution variances between taxa. A MANOVA was used to assess the variation in variance between taxa, and as with the comparisons of central tendencies, ANOVAs and multiple comparisons tests were used to determine the sources of significant variation as needed.

Complexity and anisotropy results for *Au. anamensis* and *Au. afarensis* were also compared with those for a series of extant primates with known differences in feeding behaviors to put the microwear texture analysis results for these hominins in the context of modern primate diets. The baseline series includes: (i) the mantled howler, *Alouatta palliata* and the silvered leaf monkey, *Trachypithecus cristatus*, *C. apella* and *L. albigena* from the dataset reported by Scott *et al.* (2005); (ii) *G. gorilla beringei*, *G. g. gorilla*, *Pan troglodytes* and the orangutan *Pongo pygmaeus* from Ungar *et al.* (2007*b*); and (iii) the yellow baboon *Papio cynocephalus* and the gelada baboon *Theropithecus gelada* from Scott *et al.* (2009*b*). The mantled howler and silvered leaf monkey are typically characterized as folivores, whereas the brown capuchin and grey-cheeked mangabey are considered to be hard-object fallback feeders. Among the great apes, chimpanzees are the most frugivorous, and gorillas, especially the *G. g. beringei* sample considered here (the Fossey collection at the US National Museum of Natural History), are the most folivorous (see references in Ungar *et al.* 2007*b*). Orangutans are intermediate in their diets. Finally, geladas are specialized grass eaters, whereas yellow baboons have a more catholic diet including fruits, leaves and animal prey (see Post 1982; Norton *et al.* 1987; Dunbar 1988; Altmann 1998; Pochron 2000; Bentley-Condit 2009).

3. RESULTS

Results for *Au. anamensis* and *Au. afarensis* are presented in tables 1–4 and are illustrated in figures 1 and 2.

(a) *Comparisons with other fossil hominins*

The early hominins are well-separated from one another by microwear texture complexity. First, the specimens from South Africa have higher *Asfc* values on average than those from eastern Africa, regardless of the species considered. Within the eastern African sample, *Au. anamensis* may have slightly higher complexity on average than *Au. afarensis* or *Par. boisei*, but larger samples of *Au. anamensis* are really needed to evaluate this (only one *Au. anamensis* specimen is outside the range of *Au. afarensis* or *Par. boisei*). No significant variation in

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Table 3. Analyses of hominin microwear texture data (central tendencies). All data rank transformed to mitigate violation of assumptions inherent to parametric statistics (Conover & Iman 1981). $*p < 0.05$ for Fisher's LSD test, $**p < 0.05$ for both Tukey's HSD and Fisher's LSD tests (shown in italic).

	value	*F*	d.f.	*p*-value	
multivariate test results					
Wilks's λ	0.037	205.783	539	0.000	
Pillai trace	0.963	205.783	539	0.000	
Hotelling–Lawley trace	26.382	205.783	539	0.000	
ANOVA test results	*Asfc*	*epLsar*	*Smc*	$HAsfc_9$	$HAsfc_{81}$
F	32.397	2.735	4.056	12.096	23.204
d.f.	443	443	443	443	443
p-value	0.000	0.041	0.007	0.000	0.000
paired comparisons	*Asfc*	*epLsar*	*Smc*	$HAsfc_9$	$HAsfc_{81}$
Au. afarensis × *Au. africanus*	*−19.279***	−6.037	−1.084	*−15.421***	*−19.616***
Au. afarensis × *Au. anamensis*	−9.579*	1.596	12.649	−6.421	−12.982*
Au. afarensis × *Par. boisei*	4.564	2.977	−2.613	−8.421	−8.887*
Au. afarensis × *Par. robustus*	*−27.357***	13.263*	*16.705***	*−27.088***	*−29.982***
Au. africanus × *Au. anamensis*	9.700	7.633	13.733	9.000	6.633
Au. africanus × *Par. boisei*	*23.843***	9.014	−1.529	7.000	10.729*
Au. africanus × *Par. robustus*	−8.078*	*19.300***	*17.789***	−11.667*	−10.367*
Au. anamensis × *Par. boisei*	14.143*	1.381	−15.262	−2.000	4.095
Au. anamensis × *Par. robustus*	*−17.778***	11.667	4.056	*−20.667***	*−17.000***
Par. boisei × *Par. robustus*	*−31.921***	10.286	*19.317***	*−18.667***	*−21.095***

Table 4. Analyses of hominin microwear texture data (variance). Microwear data transformed for Levene's test ($X' = |X—$ mean (X)|) following Plavcan & Cope (2001). $*p < 0.05$ for Fisher's LSD test, $**p < 0.05$ for both Tukey's HSD and Fisher's LSD tests (shown in italic).

	value	*F*	d.f.	*p*-value	
multivariate test results					
Wilks's λ	0.127	5.627	20 130	0.000	
Pillai trace	1.254	3.837	20 168	0.000	
Hotelling–Lawley trace	4.174	7.827	20 150	0.000	
ANOVA test results	*Asfc*	*epLsar*	*Smc*	$HAsfc_9$	$HAsfc_{81}$
F	24.38	3.828	3.822	4.476	10.296
d.f.	443	443	443	443	443
p-value	0.000	0.010	0.010	0.004	0.000
paired comparisons	*Asfc*	*epLsar*	*Smc*	$HAsfc_9$	$HAsfc_{81}$
Au. afarensis × *Au. africanus*	−0.140	0.000	*−2.087***	−0.118	−0.157
Au. afarensis × *Au. anamensis*	−0.009	0.001*	0.181	−0.010	0.048
Au. afarensis × *Par. boisei*	−0.035	0.000	0.090	−0.023	−0.072
Au. afarensis × *Par. robustus*	*−1.078***	*0.001***	0.282	*−0.305***	*−0.68***
Au. africanus × *Au. anamensis*	0.131	0.001	2.268*	0.107	0.205
Au. africanus × *Par. bosei*	0.105	0.000	2.177*	0.095	0.084
Au. africanus × *Par. robustus*	*−0.938***	0.001*	*2.368***	−0.187*	*−0.523***
Au. anamensis × *Par. boisei*	−0.026	−0.001*	−0.091	−0.012	−0.120
Au. anamensis × *Par. robustus*	*−1.069***	0.000	0.101	−0.294*	*−0.728***
Par. boisei × *Par. robustus*	*−1.043***	*0.001***	0.191	*−0.282***	*−0.608***

complexity is noted between *Au. afarensis* and *Par. boisei*. Within the South African sample, *Par. robustus* has more complex microwear surfaces on average than *Au. africanus*. The *Par. robustus* sample also shows significantly greater variation in its complexity values than do any of the other taxa. All other taxa have similar levels of within-species variation in complexity.

The species do not differ as much in anisotropy as they do in complexity, though *Par. robustus* has both a lower average *epLsar* and less variability in this variable than either *Au. africanus* or *Au. afarensis*. The *Par. robustus* sample also has a lower average scale of maximum complexity than *Au. afarensis*, *Au. africanus* or *Par. boisei*, though no other significant differences in *Smc* central tendencies are noted. In addition, *Au. africanus* has significantly greater variation in *Smc* values than *Au. afarensis*, *Par. robustus* and (marginally) both *Au. anamensis* and *Par. boisei*. It should be noted though that the high *Au. africanus* variance is driven by a single outlier with an extremely high *Smc* value. The *Par. robustus* sample also has higher average *HAsfc* values than *Au. anamensis*, *Au. afarensis*, *Par. boisei* or (at least marginally) *Au. africanus*. In addition, *Au. africanus* has higher *HAsfc* values than *Au. afarensis*. Further, *Par. boisei* has marginally lower *HAsfc* values than *Au. africanus*, but marginally higher

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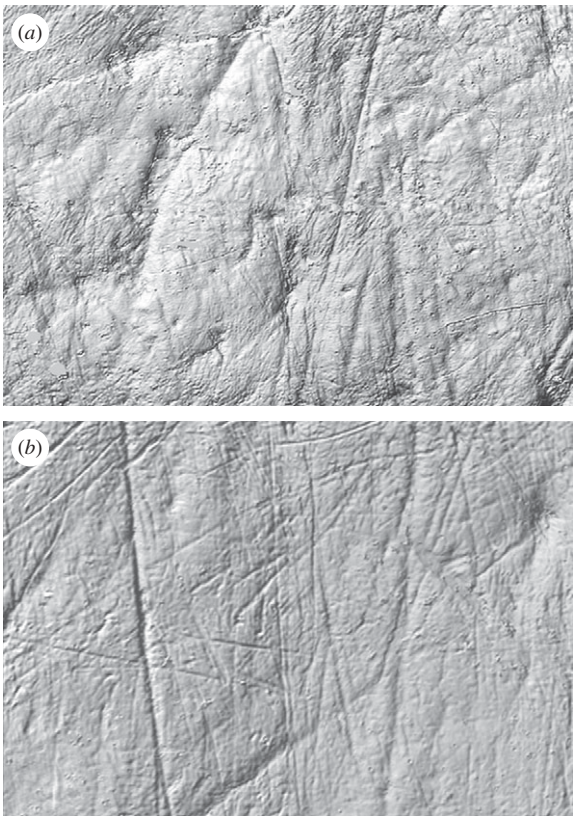

Figure 1. Photosimulations of molar microwear surfaces of (*a*) *Au. anamensis* and (*b*) *Au. afarensis* generated from point cloud data collected using the white-light confocal profiler. Each image represents a surface 208 μm × 280 μm.

heterogeneity (at least for $HAsfc_{81}$) than *Au. afarensis*. Finally, *Par. robustus* has more variation in its *HAsfc* values than *Au. anamensis*, *Au. afarensis*, *Au. africanus* and *Par. boisei*.

In summary, *Au. afarensis* microwear textures are most similar to those of *Par. boisei*, with the only difference being a marginally higher average value for one of the heterogeneity measures. *Australopithecus afarensis* also has lower complexity on average and less heterogeneity than *Au. africanus*, as well as less variation in scale of maximum complexity (though the latter result is driven largely by a single outlier). *Australopithecus afarensis* differs most markedly from *Par. robustus*. *Australopithecus afarensis* has lower complexity and heterogeneity of complexity, higher scale of maximum complexity, and marginally higher anisotropy. The degree of variation in anisotropy values is also greater for *Au. afarensis*, though the variation in complexity and heterogeneity are greater in *Par. robustus*. In fact, *Par. robustus* is very much the 'outlier' compared with the other taxa in most cases. This hominin tends towards a greater spread in and larger average values for complexity, scale of maximum complexity and heterogeneity of complexity, though less spread in, and lower values for anisotropy.

Results for *Au. anamensis* are more difficult to have confidence in, given its sample size, though these do separate clearly from *Par. robustus*. There are some additional 'hints' suggested by the data if the patterns hold with larger samples. *Australopithecus anamensis* has marginally higher average complexity and lower variation in anisotropy than either *Au. afarensis* or *Par. boisei*, as well as marginally higher heterogeneity than *Au. afarensis*. These results will be of limited interpretability until larger samples are available for study.

(b) *Comparisons with extant primates*

Microwear complexity and anisotropy results for *Au. anamensis* and *Au. afarensis* are illustrated alongside data for living primates in figure 3. These hominins are on the low end for both *Asfc* and *epLsar*, both in their means and in their variations, when considered in light of the extant primate baseline. The distributions and central tendencies of complexity values for these hominins are most comparable to those reported for *A. palliata*, *T. gelada* and *T. cristatus*. They lack the degrees of dispersion in *Asfc* seen in the other primates, especially *C. apella*, *P. cynocephalus* and *L. albigena*. In contrast, the anisotropy values for the hominins are most different from those for *A. palliata*, *T. gelada* and *T. cristatus* and are more similar to those of the other primates, especially *P. troglodytes* and *P. cynocephalus*.

4. DISCUSSION

(a) Microwear and the diets of *Au. anamensis* and *Au. afarensis*

Dental microwear texture analysis results suggest that neither the *Au. anamensis* nor the *Au. afarensis* individuals included in this study had diets dominated by hard, brittle foods in the days, weeks or perhaps even months prior to their deaths. While these species have been suggested to show an adaptive shift from diets dominated by soft forest fruits to hard, brittle foods (e.g. Ward *et al.* 1999; Teaford & Ungar 2000; White *et al.* 2000; Wood & Richmond 2000; Walker 2002), none of the specimens examined exhibit the high microwear surface texture complexity expected of a hard-object feeder. The distribution of *Asfc* values more closely resembles those of the grass-eating *T. gelada* and the folivores *A. palliata* and *T. cristatus* than hard-object feeding *L. albigena* or *C. apella*.

The anisotropy results for *Au. anamensis* and *Au. afarensis* are, on the other hand, most different from those of *A. palliata*, *T. cristatus* and *T. gelada* among the baseline series. These three extant primates have higher average anisotropy values than the early hominins. High anisotropy is often taken as a proxy for tough food consumption and repetitive chew cycles with opposing teeth moving past one another along constrained paths. At first glance, this might suggest that *Au. anamensis* and *Au. afarensis* specimens sampled also avoided tough foods in the period prior to death, although the combination of low anisotropy and low complexity averages in *Au. anamensis* and *Au. afarensis* is unusual for primates. Most extant primate samples published to date have either high anisotropy averages combined with low complexity values, associated with the consumption of tough foods, or low anisotropy combined with high complexity averages consistent with a hard-brittle item diet.

We propose that *Au. anamensis* and *Au. afarensis* may have indeed consumed tough foods, but that their

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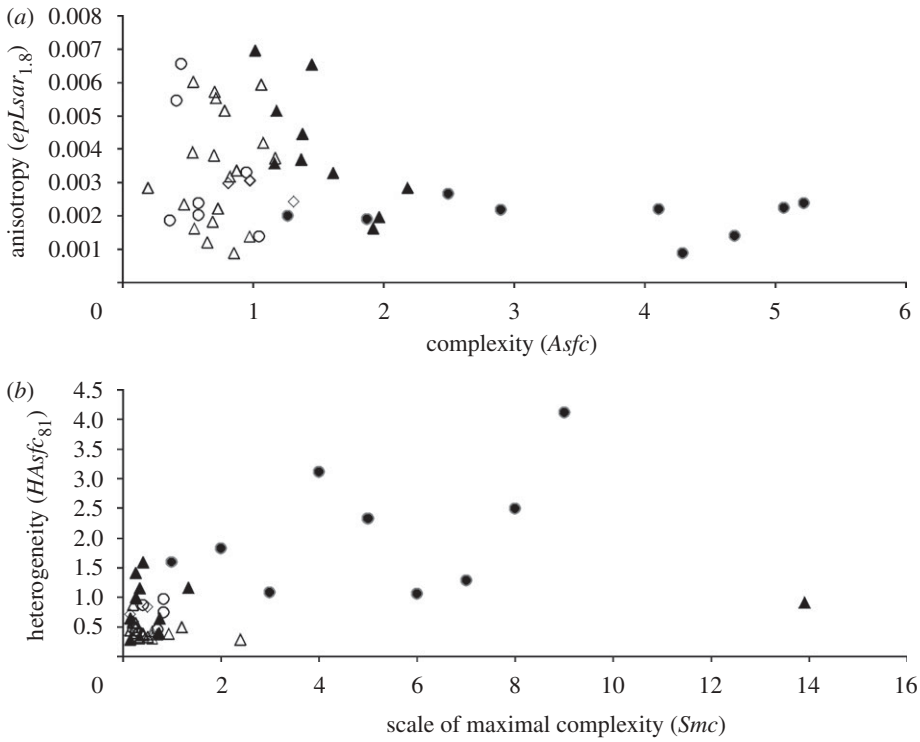

Figure 2. Plots of (*a*) anisotropy versus complexity and (*b*) heterogeneity of complexity versus scale of maximum complexity (below) for early hominin individuals considered by taxon. Open triangle, *Au. afarensis*; filled triangle, *Au. africanus*; open circle, *Par. boisei*; filled circle, *Par. robustus*; diamond, *Au. anamensis*.

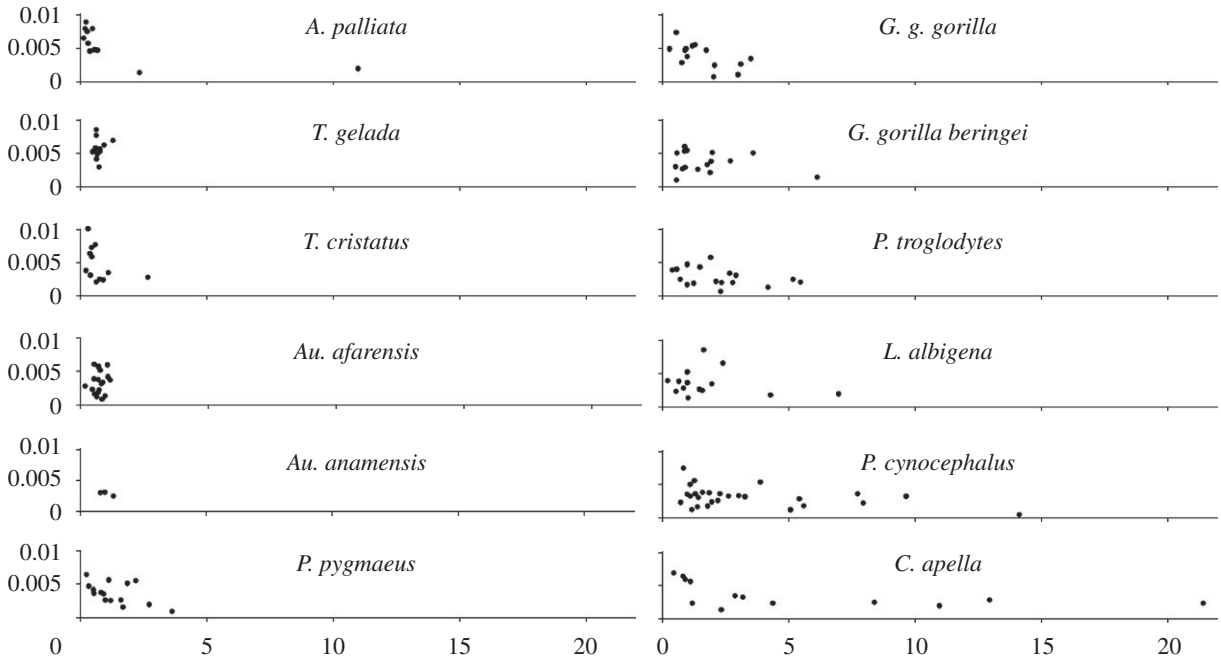

Figure 3. Plots of anisotropy versus complexity for various extant primates, compared with data for *Au. anamensis* and *Au. afarensis*.

anisotropy values are low because their dentognathic morphology did not limit occlusal movements to the degree presumed for primates with steeper occlusal surfaces, such as *A. palliata*, *T. cristatus* and *T. gelada*. The flatter teeth of early hominins offer fewer constraints to masticatory movements during food fracture and may therefore allow 'grinding' action (*sensu* Simpson 1933; Kay & Hiiemae 1974), wherein food items are milled between opposing surfaces. The combination of flat teeth and tough foods would be expected to result in a combination of low complexity and low anisotropy. Still, the relationship between microwear feature anisotropy and occlusal topographic relief remains to be investigated fully.

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(b) *Comparisons with other early hominins*

Studies of craniodental functional morphology have suggested to several researchers a tendency towards increasing specialization for hard objects from *Au. anamensis* to *Au. afarensis*, *Au. africanus* and finally *Par. robustus* and *Par. boisei* (see White *et al.* 1981, 2000; Ward *et al.* 1999; Teaford & Ungar 2000; Wood & Richmond 2000; Walker 2002). *Australopithecus africanus* evinces a higher average *Asfc* than *Au. afarensis*, and *Par. robustus* has an even higher average *Asfc* value. The same is true for heterogeneity and variation in the scale of maximum complexity (though the latter result appears to be driven by a single outlier). These findings are all consistent with an increasing component of hard, brittle items in the diet of *Au. africanus* compared with *Au. afarensis* and *Par. robustus* compared with *Au. africanus*.

On the other hand, the distribution of *Asfc* values for *Par. boisei* is very similar to that of *Au. afarensis*. Further, while the sample for *Au. anamensis* is too small for a reasonable comparison with other taxa, its mean *Asfc* value and heterogeneity are, if anything, slightly higher than that of *Au. afarensis*. Thus, if high texture complexity is considered to be a proxy for the consumption of hard, brittle items, there is no evidence for an increase in the role of such foods in the diet from *Au. anamensis* to *Au. afarensis* to *Par. boisei*.

Ungar *et al.* (2008) remarked on the apparent discordance between microwear in *Par. boisei* and biomechanical models for this species based on craniodental functional morphology. They proposed that *Par. boisei* may represent a hominin example of Liem's Paradox, wherein craniodental specializations developed as an adaptation to processing less preferred, mechanically challenging foods, even though the microwear suggests that these hominins rarely consumed such foods. This does not, however, explain either the microwear differences between *Par. boisei* and *Par. robustus* (given similarities in their gnathodental adaptations) or the similarities between *Par. boisei*, *Au. anamensis* and *Au. afarensis* (given differences in their gnathodental adaptations).

The story becomes even more complicated when we consider these taxa in their presumed phylogenetic contexts, especially the purported anagenetic lineage leading from *Au. anamensis* to *Au. afarensis*, *Par. aethopicus* and finally *Par. boisei* (Kimbel *et al.* 2006; Rak *et al.* 2007). Many workers have suggested an ancestor–descendant relationship between *Au. anamensis* and *Au. afarensis* (Ward *et al.* 1999, 2001; White *et al.* 2000, 2006; Walker 2002). Such relationships are consistent with numerical cladistic studies (Strait *et al.* 1997; Strait & Grine 2004) and with changes in dentognathic characters among temporally successive samples from Kanapoi, Allia Bay, Laetoli and Hadar (Kimbel *et al.* 2006).

Studies of cranial morphology have suggested that the pattern of intracranial venous sinus drainage is shared between *Au. afarensis* and *Paranthropus* species for the exclusion of *Au. africanus* and *Homo* (Falk & Conroy 1983; Kimbel 1984; Falk 1988), and additional fossils have reinforced this similarity (Kimbel *et al.* 2004; de Ruiter *et al.* 2006). Kimbel *et al.* (2004) have, moreover, identified an additional six cranial characters that *Au. afarensis* shares with one or more species of *Paranthropus*, although they regarded them, like the pattern of intracranial venous drainage, as being homoplastic. Most recently, similarities in ramal morphology between *Au. afarensis* and *Par. robustus* mandibles have been observed by Rak *et al.* (2007), who interpreted them as synapomorphies, suggesting that *Au. afarensis* and *Par. robustus* are united in a single clade and that this possibly includes *Par. aethiopicus* and *Par. boisei*, although no fossils attributable to the latter two species preserve the relevant anatomy. The evidence suggesting an ancestor–descendant relationship between *Au. afarensis* and *Paranthropus*, and particularly that for an *Au. afarensis*–*Par. aethiopicus*–*Par. boisei* lineage in eastern Africa, is not wholly inconsistent with their hypothesized cladistic relationships (Strait *et al.* 1997; Kimbel *et al.* 2004; Strait & Grine 2004).

Similarities in microwear texture results for *Au. anamensis*, *Au. afarensis* and *Par. boisei* may make sense if these taxa comprise an anagenetic lineage and all shared food-type preferences. One possible scenario might be increasing craniodental specializations through the lineage for repetitive loading given consumption of tough foods in the face of morphological constraints imposed by relatively flat cheek teeth. This would be consistent with a C_4 isotope signature in *Par. boisei* (van der Merwe *et al.* 2008) and the consumption of tough grasses or sedges, assuming that the specimens examined thus far are representative. Carbon stable isotope studies of *Au. anamensis*, *Au. afarensis* and additional *Par. boisei* specimens would provide a valuable test of this hypothesis.

On the other hand, if *Par. boisei* and *Par. robustus* form a clade excluding *Au. africanus*, the two early hominins from South Africa probably independently increased their consumption of hard, brittle foods as evidenced by increased pit percentages in both hominins. In any case, the microwear texture patterns of the eastern African early hominins are more similar to one another than to those of the South African early hominins, independent of whether one is considering *Australopithecus* or *Paranthropus*.

So in the end, what can be said of the microwear of *Au. anamensis* and *Au. afarensis*? We may reasonably infer that specimens examined for this study did not have a diet dominated by hard and brittle foods, at least shortly before death. Picq (1990) proposed that *Au. afarensis* often consumed soft foods that were not fracture resistant, but had craniomandibular adaptations for seasonal consumption of hard, brittle foods. Grine *et al.* (2006*a*,*b*) further suggested that traditional microwear results for both *Au. anamensis* and *Au. afarensis* are best explained by food preferences for less mechanically challenging foods, though as Ungar (2004) noted, their occlusal morphology would have allowed the consumption of hard, brittle items in times of dietary stress when favored foods were unavailable. The microwear texture analysis data presented here cannot be used to falsify the notion of rare hard-object feeding, but it also provides no evidence for it. Whether or not the craniodental specializations seen in *Au. anamensis* and *Au. afarensis* are adaptations for the occasional consumption of

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hard, brittle foods, however, their microwear texture patterns are consistent with the regular consumption of softer and or tougher items.

We are grateful to curators at the National Museums of Ethiopia, Kenya and Tanzania for permission to examine and make moulds of specimens in their care and thank Alejandro Peréz-Peréz for his assistance with preparing these replicas. Kristin Krueger helped with the preparation of figure 1. This study was funded by the US National Science Foundation.

ENDNOTE

[1]One of us (F.E.G.) prefers the nomen *Praeanthropus afarensis*, as use of the generic name *Australopithecus* for *Au. anamensis* and *Au. afarensis* probably violates the criterion of monophyly (Grine & Strait 2000). Because of the lack of consensus among the authors on the taxonomy of these hominins, we employ here the more commonly used nomenclature.

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