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Dietary proclivities of *Paranthropus robustus* from Swartkrans, South Africa

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Abstract: Pleistocene *Paranthropus robustus* fossils from Swartkrans have yielded stable isotope values suggesting some foraging on C_4 plants possibly including underground storage organs. Dental microwear texture analysis on *P. robustus* (SK 6, SK 34 and SK 47) from Swartkrans Member 1 is performed to examine whether tooth surface damage from mastication agrees with prior dietary inferences from carbon isotopes. There is considerable variation in textural characteristics among the *P. robustus* specimens. Specifically, adult SK 34 stands apart from the two subadult specimens, SK 6 and SK 47, suggesting life history could be reflected in patterns of dental microwear texture characteristics, although seasonality and availability of fallback foods may also explain the variation observed in *P. robustus*. The fossils all exhibit elevated surface texture complexity, resembling the values for *Lophocebus albigena* and *Cebus apella*, and to a lesser extent, *Pan troglodytes*. *Paranthropus robustus* is dissimilar to primary folivores, such as *Trachypithecus cristatus* or folivore-frugivores such as *Alouatta palliata* suggesting leaves comprised very little of its diet. The textural fill volume of *P. robustus* differs from that observed in extant primates from tropical forests indicating extreme durophagy, perhaps a function of differences in habitat. Ingestion of extraneous grit on the underground parts of plants and from terrestrial resources, perhaps as fallback foods or as dietary staples, may account for these enamel textural properties and may help explain the mixed C_3/C_4 isotopic signal in *P. robustus*.

Key words: *Australopithecus*, underground storage organs, dental microwear, grit, Pleistocene

Introduction

Paranthropus (or *Australopithecus*) *robustus* was endemic to southern Africa and existed between circa 1.9 million years ago (Ma) to approximately 0.7 Ma (Vrba 1995; Wood and Strait 2004). The Hanging Remnant of Swartkrans Member 1 has yielded by far the greatest number of specimens attributed to *P. robustus* (Brain 1981; de Ruiter et al. 2008). *Paranthropus robustus* was reconstructed as a dedicated biped and exhibits flat bulbous cusps on relatively large molars, molariform premolars, small incisors and short blunt canines (Robinson 1954). This suite of

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dental features has been attributed to the excessive grinding of hard objects (Robinson 1954). The purpose of this study is to investigate three specimens of *P. robustus* (SK 6, SK 34 and SK 47) which have not been previously examined (Scott et al. 2005). The fossils are compared to extant primate taxa using dental microwear texture analysis to address how this suite of enamel characteristics evolved in southern Africa during the early Pleistocene.

Paleoecological setting

It has long been assumed that *P. robustus* lived in an open grassland environment given the larger number of grazers compared to browsing ungulates preserved at Swartkrans (Vrba 1985), along with grazing primates such as *Theropithecus oswaldi* (Elton 2007). The paleoecology of Swartkrans has been reconstructed as a relatively open habitat with some edaphic grasslands and a permanent water source in the region (Brain 1981; 2004; Delson 1984; Vrba 1985; 1995; Reed 1997; Avery 2001; Reed and Rector 2006). However, as the number of bovid grazers increased, the number of *P. robustus* in the fossil assemblages decreased. This inverse relationship suggested *P. robustus* may have preferred riverine woodlands compared to open areas (de Ruiter et al. 2008). The micromammalian community recovered from Swartkrans Member 1 indicated both moist and arid grassland taxa were present (Avery 2001). Swartkrans deposits may have been interred during interglacial intervals (Brain 1981), and may have exhibited lower annual rainfall and higher mean temperatures compared to the current climatic conditions (Avery 2001).

Prior dietary reconstructions

In his dietary hypothesis, Robinson (1954) posited *P. robustus* as a consumer of tough vegetation as opposed to *A. africanus* which was described as more omnivorous. Robinson (1954) arrived at this conclusion by observing the extensive wear on *P. robustus* molars and premolars, enamel chipping of the posterior teeth, buccolingual scratches on the postcanine dentition, the massive bone accumulation around the roots of the molars and premolars, and extreme craniofacial superstructures. He attributed the enamel chipping to the ingestion of the gritty underground parts of plants as observed in chacma baboons (*Papio ursinus*) which consume rhizomes, bulbs, corms and roots, particularly in the austral winter. These could have been fallback foods for *P. robustus* in these seasonal environments.

Jolly (1970) suggested *P. robustus*, like earlier *Australopithecus* was a seed predator capable of utilizing a side-to-side grinding action of the teeth. The relatively small anterior dentition, similar to gramnivores such as *Theropithecus*, seemed to corroborate seed predation in *P. robustus*. Further dietary implications arose from investigation of incisor microwear in *P. robustus* which exhibits a smaller density of features compared to *A. africanus*, suggesting less food preparation occurred with the anterior dentition (Ungar and Grine 1991), perhaps replaced with the use of stone and bone tools (Wood and Strait 2004). The mesiodistally narrow incisors of *P. robustus*, intermediate between *Homo erectus* and modern *H. sapiens*, also signaled a limited degree of food processing and paramastication using the anterior teeth (Ungar and Grine 1991). These dimensions differed from those characterizing Pliocene australopiths which had much wider incisors, although not as wide relative to reconstructed body size as those of the great apes (Teaford and Ungar 2000). The small incisors of *P. robustus* suggested large food items were avoided unless they were prepared using technology (Wood and Strait 2004). Its flattened molars and lack of shearing crests indicated a lack of folivory (Teaford and Ungar 2000).

Paranthropus robustus also exhibited a greater incidence of pitting than did *A. africanus* suggesting greater hard-object feeding in the former (Grine 1986). The massive mandibular corpus of *P. robustus* signaled an adaptation to durophagy with jaws capable of withstanding significant functional demands related to wish-boning or torsion when hard-objects were consumed (Teaford and Ungar 2000). Furthermore, *P. robustus* may have consumed grit laden foods or masticated opal phytoliths in plants (Grine 1981). *Paranthropus robustus* was found to exhibit greater enamel surface complexity and less patterning of dental microwear textures than *Australopithecus africanus* (Scott et al. 2005), and to exhibit greater textural complexity than early *Homo* (Ungar and Scott 2009; Ungar et al. 2010).

Australopiths from the South Africa caves were associated with a diet distinct from that sampled from the great apes (Sponheimer and Lee-Thorp 2003; Sponheimer et al. 2006b). The isotopic signal of *P. robustus* samples showed a mixed C_3/C_4 signal, suggesting the consumption of forest resources was substantial (Lee-Thorp et al. 1994; 2007; Sponheimer et al. 2006a,b). In fact most living primates heavily utilize forest foods even in dry areas where these resources are limited (Sponheimer et al. 2006a; Elton 2008). Nevertheless, *P. robustus* must have consumed a considerable amount of C_4 resources which comprised 25–30% of its diet (Lee-Thorp et al. 1994). Such isotopic variation may be indicative of a habitat generalist and could have resulted from the consumption of sedges, termites, grasses, the underground storage organs (USOs) of C_4 plants (de Ruiter et al. 2008), and/or animal protein from grazers (Lee-Thorp et al. 1994). Seasonality probably affected the diet of *P. robustus* as preferred foods may have been available only during part of the year. Furthermore, Swartkrans bordered moist and arid biomes, presenting a wide array of habitats potentially exploitable by *P. robustus* (Avery 2001).

Ratios of Sr/Ca for *P. robustus* suggested omnivory, perhaps with some animal protein in the diet like fossil carnivores preserved at Swartkrans Member 1 (Sillen 1992; Sillen et al. 1995). Inter-seasonal and inter-annual isotopic variation in the diet of *P. robustus* was identified using perykymata (Sponheimer et al. 2006b). The buttressed face, postcanine megadonty and thick enamel cap of *P. robustus* may also be indicative of a broad dietary niche that included fallback foods (Wood and Strait 2004).

Inferring diet and paleoecology

The aim of this study is to infer the diet of *P. robustus* and to substantiate (or not) prior dietary reconstructions. It is expected that if bipedal *P. robustus* were consuming terrestrial foods, it should be similar to semi-terrestrial African apes. Given its lack of shearing crests and broad, flat molars, it is predicted that *P. robustus* will differ from folivorous and folivorous-frugivorous monkeys. Since the grit load of foods in savannas would be expected to exceed that found in tropical forests (Galbany et al. 2009), *P. robustus* is predicted to differ considerably from primates from closed habitats.

Materials and methods

The *P. robustus* sample from Swartkrans included SK 6, SK 34 and SK 47 (Tobias et al. 1977) (Fig. 1). The fossils all derived from the Hanging Remnant of Swartkrans Member 1 (Brain 1981; 1985), dated to circa 1.8 Ma (Brain 2004) or 1.6 Ma using biostratigraphy (de Ruiter 2003), corroborated by a date of 1.63 Ma using ESR on one *P. robustus* specimen, SKW 11 (Curnoe et al. 2001). Herries et al. (2009) suggested the Swartkrans Member 1 deposits are older – 2.1 to 1.9 Ma.

The three fossils which preserve dental microwear include SK 6, a left hemi-mandible with a partial ascending ramus from a young subadult. The left M_2 is recently erupted along with P_3 and P_4, and all three lack substantial attrition, although microwear is noticeably present. The first mandibular molar also shows attrition. Within the internal ramus surface, a developing unerupted and complete M_3 crown can be observed (Fig. 1). SK 6 is the holotype of *Paranthropus crassidens* (Brain 1981).

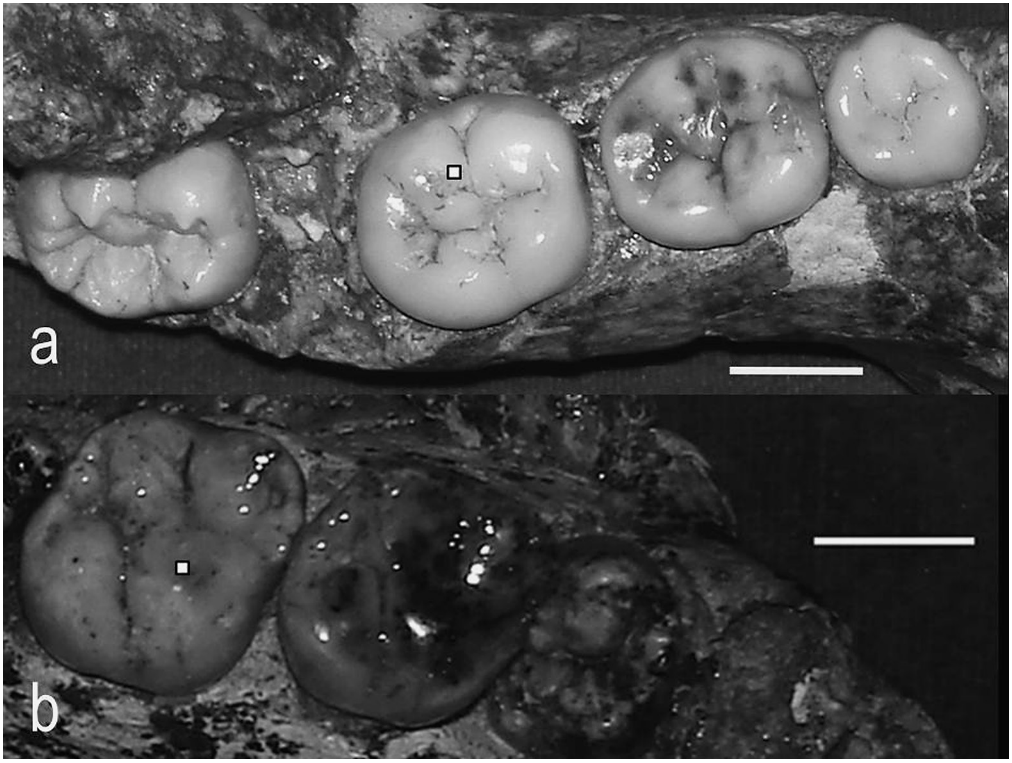

Fig. 1. Occlusal views of (a) SK 6 – a left partial mandible from a subadult showing P_4 to unerupted M_3, and (b) SK 47 – a nearly intact subadult basicranium, showing right P^4 to M^2. The approximate areas scanned on mandibular (SK 6) and maxillary (SK 47) specimens are marked by a white square with a black outline on M_2 of (a) and M^2 of (b)

Also included is SK 34, which contains (a) right and (b) left parts, consisting of unequal hemi-mandibles of a young adult. The cusp morphology of the molars and premolars exhibits substantial attrition but the dentine is not exposed, although the incisal edges and canine tips do show exposures of dentine. The dentition is not extensively worn although all teeth reach the same occlusal plane. The mandibular third molar still preserves some of its original occlusal morphology. The left, SK 34b, is better preserved and subsequently molded.

SK47 is a well preserved juvenile/subadult basicranium including the palate and maxillary alveolus. Both right and left M^2 are *in situ* and were only recently erupted at time of death as evidenced by the lack of heavy attrition on the occlusal facets, although microwear is clearly evident. A late juvenile/early subadult age is further corroborated by the right P^4 which is only one-third erupted, an unossified premaxillary suture, and an unfused spheno-occipital synchondrosis. As in SK 6, the $M^1$of SK 47 is well worn, although SK 6 is suggested to be slightly older in age at death than SK 47 (Brain 1981). Like other *P. robustus* maxillae, SK 47 exhibits a Carabelli "furrow" on the lingual wall of the protocone of RM^1 and RM^2 (Schwartz et al. 1998).

From an examination of hundreds of Plio-Pleistocene hominin fossil molars, Grine (1986) found only nine *P. robustus* appropriate for analysis, suggesting the vast majority exhibited postmortem or preparation artifacts (Grine 1986). There may be other specimens with well-preserved dental microwear that were previously overlooked or rejected by Grine (1986). The new material recovered more recently (e.g., Grine 1989) was not available.

The parameters that justified the inclusion of SK 6, SK 34 and SK 47 in this study were (1) presence of scratches consistent with extant primate analogues with known diets; (2) absence of extreme differences in surface relief; (3) lack of preparation or casting defects; and (4) absence of a pockmarked surface. All specimens were first examined under 40× and 100× to accept or reject the surface before scanning.

Dental microwear analysis

Three *P. robustus* specimens (SK 6, SK 34 and SK 47) were molded at the Transvaal Museum (currently the Ditsong National Museum of Natural History), Pretoria, South Africa using Regular Body President Jet Plus 4605 (polyvinylsiloxine) from Coltène-Whaledent. Regular body was chosen because of its high reproducibility of the original enamel surface (Galbany et al. 2004; 2006). The fossil teeth were first cleaned with shellac remover and isopropyl alcohol prior to the application of molding material. Positive replicas (dental casts) from the negative impressions (dental molds) were prepared using a 1:5 mix of hardener and epoxy resin (Buehler). The hardener was poured first, followed by epoxy resin into a graduated cylinder and agitated by vigorous stirring before being emptied into plastic tubes and centrifuged for one minute. The resulting casting mixture was then poured into the dental molds which were *a priori* nestled into putty cradles affixed beforehand with putty hardener (Buehler). The dental casts were allowed to dry for 24 hours at room temperature before they were extracted from the molds.

Textural properties of the comparative taxa were obtained from Ungar et al. (2008) and have been featured elsewhere (Scott et al. 2005; 2006; 2012). The same instruments and procedures utilized to collect data for the comparative sample were also utilized for the *P. robustus* sample. The comparative taxa included mantled howler monkeys, *Alouatta palliata* (n =11), tufted capuchin monkeys, *Cebus apella* (n = 13), western lowland gorillas, *Gorilla gorilla gorilla* (n = 9), grey-cheeked mangabeys, *Lophocebus albigena* (n = 15), common chimpanzees, *Pan troglodytes troglodytes* (n = 17) and silvered langurs, *Trachypithecus cristatus* (n = 12).

The diets of the comparative taxa differ considerably. Whereas *A. palliata* is often described as a folivore, its diet comprises substantial amounts of fruit (Estrada 1984; Chamberlain et al. 1993). *Cebus apella* also consumes notable quantities of fruit as well as bromeliads, insects, and often engages in extractive foraging (Jack 2011). Fruit pursuers include *G. gorilla* which additionally eats leaves, herbs, bark, pith and insects (Doran-Sheehy et al. 2009), as well as *L. albigena* which consumes ripe, unripe and rotten fruit, insects, bark and hard seeds (Lambert et al. 2004), and *P. troglodytes* which, in addition to fruit, has been observed eating leaves, insects and pith (Head et al. 2011). In contrast, *T. cristatus* consumes primarily leaves, but occasionally eats fruit, and at times, soil and sand (Brotoisworo and Dirgayusa 1991).

Scanning was performed using a white-light confocal microscope (Sensofar Plμ) at 100× magnification coupled with an optical imaging system (Solarius Development Inc.). Scanning occurred on the enamel surface on facet 9 of the protocone of the second maxillary molar for SK 47 and on the hypoconid of the second mandibular molars for SK 6 and SK 34 (Fig. 1). Facet 9 is a "Phase II" facet which functions as a grinding surface (Kay and Hiiemae 1977; Gordon 1982; Krueger et al. 2008). Four adjoining scans for the three specimens (Fig. 2) were captured from a 138 × 102 μm viewing field derived from a total sampled area comprising 276 × 204 μm (Scott et al. 2006). Digital elevation maps were created to depict textural complexity and distinctions in enamel surface elevation (Fig. 3). After the scans were leveled in the program SolarMap Universal, scale-sensitive fractal analysis was performed to extract data from the point cloud using Toothfrax to calculate complexity (*Asfc*), scale of maximum complexity (*Smc*) and anisotropy (*epLsar*), and SFrax (Surfract.com) to estimate textural fill volume (*Tfv*) (Scott et al. 2006).

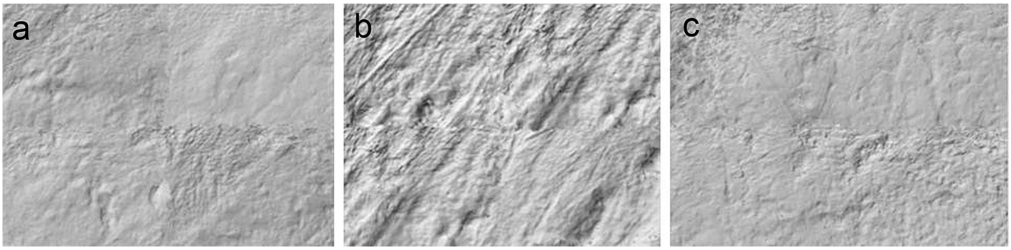

Fig. 2. Reconstructed enamel surface scans for *P. robustus* showing (a) SK 6, (b) SK 34 and (c) SK 47

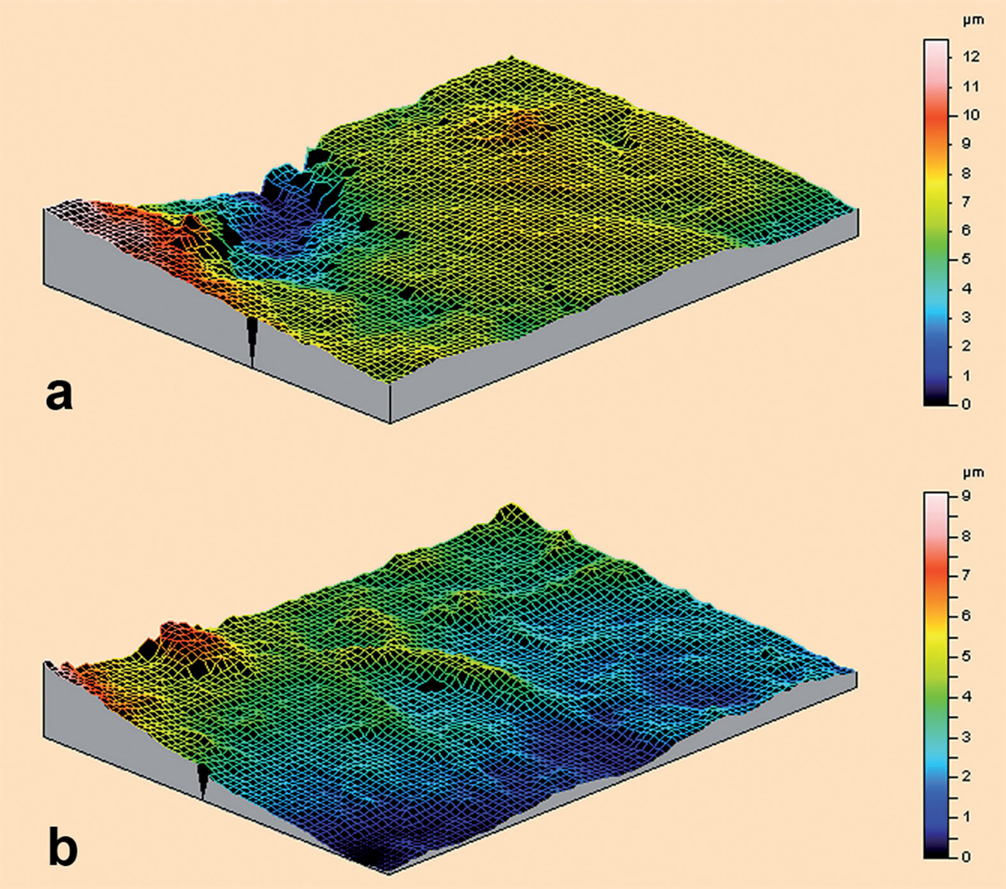

Fig. 3. Surface relief reconstructions for SK 47 provide examples of textural complexity characterizing *P. robustus*, cf. (a) and (b)

Microwear texture characteristics

Surface roughness is contingent on the scale of observation such that a surface may appear smooth at a lower magnification but uneven at a higher resolution. Area-scale fractal complexity (*Asfc*) compares differences in the textural complexity of a surface from 7200 μm^2 to 0.02 μm^2. Complexity (*Asfc*) is estimated as the steepest point slope of a log-log comparison of relative length area compared to scale of observation. An additional indicator of enamel surface roughness, scale of maximum complexity (*Smc*), derives from the range of slope values from which *Asfc* is obtained (Scott et al. 2006; 2012; Ungar et al. 2010). These two measures, scale of maximum complexity (*Smc*) and complexity (*Asfc*), demonstrate the degree to which hard and brittle food items are masticated. For example, hard-object consumers such as *L. albigena* exhibits elevated *Smc* and *Asfc*, whereas *C. apella* shows high values only for *Asfc* (Scott et al. 2006; 2012).

Anisotropy (*epLsar*) describes the patterning of enamel surface relief such that a distinct orientation of microwear texture can be observed. Anisotropy (*epLsar*), or the "exact proportion of Length-scale anisotropy of relief" (Scott et al. 2006) is a proxy for the amount of tough foods, such as leaves and stems, are consumed (Scott et al. 2009).

Textural fill volume (*Tfv*) is calculated from an algorithm which compares the volume of the scanned surface using square cuboids with different facet lengths (10 μm and 2 μm) to estimate the degree of surface dental microwear compared to facet curvature (Scott et al. 2006), and serves to separate hard-object consumers and extractive foragers such as *C. apella* with high values from folivorous *A. palliata* with much lower values (Scott et al. 2009; 2012).

Statistical methods

Median values were utilized to limit a positive skewing of the central tendency (Scott et al. 2006) and were rank-transformed so that parametric statistics could be applied (Conover and Inman 1981). An F test was conducted to test the null hypothesis of equality of variance between *P. troglodytes* (n = 17) and *P. robustus* (n = 3). Since the critical f-value was larger than the observed f values, standard between-group tests of significance could not be conducted. Linear regression between all possible pair-wise comparisons of dental microwear texture characteristics was performed, and significantly related textures ($P < 0.05$) were plotted as bivariate graphs shown with 95% confidence ellipses around group centroids for the extant species. Discriminant Function Analysis provided canonical scores axes which were plotted with 95% confidence ellipses around group centroids; confirmatory jack-knifed classification rates were also examined. Mahalanobis distances (D^2) and *post-hoc* probabilities of group membership were included to address how well the *P. robustus* specimens corresponded to the centroid of each taxon and the degree to which the fossils conformed to the *P. robustus* grouping. A cluster analysis was incorporated, using the means of the dental microwear textures for the extant taxa and including all three *P. robustus* specimens separately, to provide a multivariate proxy of diet.

Results

The taxa exhibit profound differences (Table 1), including *P. robustus*, which shows moderate values for complexity (*Asfc*) and the highest value for scale of maximum complexity (*Smc*); SK 34 shows an extremely elevated value compared to SK 6 and SK 47. For anisotropy (*epLsar*) SK 47 exhibits a much lower value than do SK 6 and SK 34. For textural fill volume (*Tfv*) SK 6 and SK 47 show the highest value; SK 34 stands apart from the other fossils with a lower value.

Bivariate analyses

Several pairwise comparisons of dental microwear texture characteristics are significant. The relationship between scale of maximum complexity (*Smc*) and complexity (*Asfc*) shown in Figure 4a is significant ($P = 0.001$; $r = 0.359$). Similarly, a linear regression of textural fill volume (*Tfv*) and complexity (*Asfc*) shown in Figure 4b, exhibits a highly significant P value ($P < 0.001$; $r = 0.373$). Anisotropy (*epLsar*) is significantly related ($P < 0.001$) to both scale of maximum complexity (*Smc*) and complexity (*Asfc*).

Table 1. Descriptive statistics for complexity (*Asfc*), scale of maximum complexity (*Smc*), anisotropy (*epLsar*) and textural fill volume (*Tfv*)

Genus/Specimen	N		*Asfc*	*Smc*	*epLsar*	*Tfv*
A. palliata	11	Mean	0.360	–0.188	6.0×10^{-3}	2610.909
		SD	0.183	1.050	2.1×10^{-3}	3225.700
C. apella	13	Mean	5.466	–0.178	4.0×10^{-3}	9674.846
		SD	6.304	1.101	1.9×10^{-3}	4931.705
G. gorilla	9	Mean	1.597	–0.384	4.0×10^{-3}	8099.714
		SD	1.012	0.567	1.8×10^{-3}	5702.802
L. albigena	15	Mean	1.769	0.623	4.0×10^{-3}	11388.333
		SD	1.740	1.064	2.0×10^{-3}	3389.758
P. troglodytes	17	Mean	2.246	–0.497	3.0×10^{-3}	9344.529
		SD	1.523	0.520	1.0×10^{-3}	5476.855
T. cristatus	12	Mean	0.734	–0.365	5.0×10^{-3}	9532.250
		SD	0.660	0.547	2.6×10^{-3}	5687.205
P. robustus	3	Mean	2.167	1.320	3.0×10^{-3}	15776.443
		SD	0.958	1.744	1.0×10^{-3}	12656.741
SK 6	1		1.430	0.420	3.1×10^{-3}	25865.010
SK 34	1		1.820	3.330	3.2×10^{-3}	1574.720
SK 47	1		3.250	0.210	1.7×10^{-3}	19889.600

Note. N = number of individuals, SD = standard deviation.

Figure 4a shows fundamental distinctions exist between *A. palliata*, and to a lesser extent *T. cristatus*, with relatively low values contrasting with those of *C. apella* and *P. troglodytes* with relatively high values for complexity (*Asfc*). *Lophocebus albigena* and *G. gorilla* exhibit moderately elevated values for complexity.

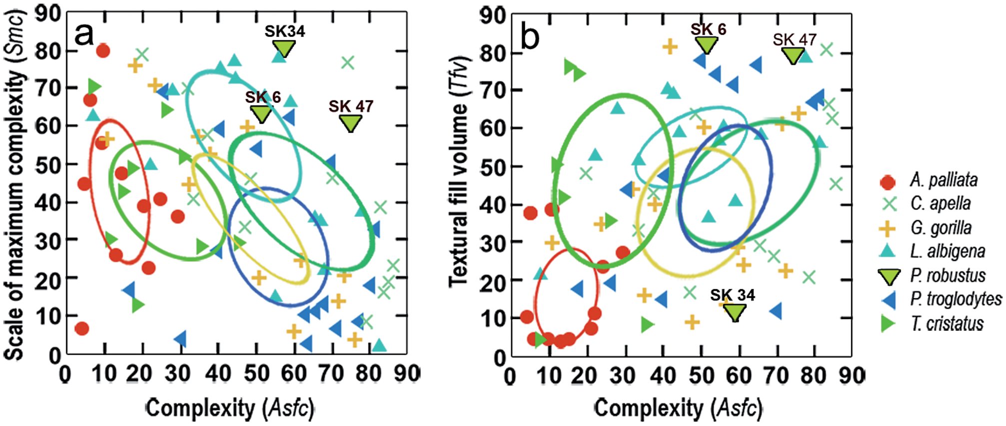

Fig. 4. Bivariate comparison of (a) scale of maximum complexity (*Smc*) and complexity (*Asfc*) and (b) textural fill volume (*Tfv*) and complexity (*Asfc*) are shown with 95% confidence ellipses around group centroids

All three *P. robustus* specimens show high values for complexity (*Asfc*) and scale of maximum complexity (*Smc*). However, SK 34 shows the highest value for scale of maximum complexity (*Smc*) and SK 47 exhibits the highest value for complexity (*Asfc*). Meanwhile, SK 6 falls within the 95% confidence ellipse for the group centroid of *L. albigena*, and is approximated by outliers from *L. albigena* and one *P. troglodytes* (Fig. 4a).

Figure 4b shows differences exist in textural fill volume (*Tfv*) between SK 6 and SK 47 with high values, and *A. palliata* and SK 34 with low values. Four *P. troglodytes* individuals and *G. gorilla*, *C. apella*, *L. albigena* and *T. cristatus* outliers approximate *P. robustus* by exhibiting both high textural fill volume (*Tfv*) and high complexity (*Asfc*) values. The 95% confidence ellipses for the extant taxa do not overlap with the fossils. Specimen SK 34 overlaps the value for one *G. gorilla* and secondarily resembles *P. troglodytes*, *C. apella* and *G. gorilla* outliers (Fig. 4b).

Canonical scores axes

Discriminant function analysis was utilized to ascertain the degree to which individuals correspond to their group, the distribution of groups and which dental microwear textures separated individuals across canonical scores axes. On Canonical Scores Axis 1, representing 71.5% of the variance, *A. palliata* and *T. cristatus* are separated from *P. robustus*, *L. albigena* and *C. apella* (Fig. 5). Specimens SK 34 and SK 6 resemble each other in positive values for Canonical Scores Axis 1, although SK 34 falls on the margin of the 95% confidence ellipse around the group centroid for *C. apella*, whereas SK 6 falls close to the 95% confidence ellipse around the group centroid for *L. albigena*. *Paranthropus robustus* specimen SK 47 is strongly positive on Canonical Scores Axis 1 and is most closely approximated by one *C. apella* outlier. One *P. troglodytes* falls close to SK 6 and two *P. troglodytes* individuals approximate SK 34. Canonical discriminant functions standardized by within variances show that anisotropy (*epLsar*) loads negatively on Canonical Scores Axis 1 whereas complexity (*Asfc*) loads highly positively, indicating *P. robustus* exhibits a combination of low anisotropy (*epLsar*) and high complexity (*Asfc*) values (Table 2).

The second canonical scores axis, accounting for 18.3% of the variance, serves to contrast *T. cristatus*, *L. albigena* and *P. robustus* with negative values from *P. troglodytes*, *G. gorilla* and *C. apella* with positive ones (Fig. 5). On the second axis, SK 6, followed by SK 47, shows greater negative scores whereas SK 34 is much less negative and consequently more difficult to classify. The elevated loadings for scale of maximum complexity (*Smc*) and textural fill value (*Tfv*) on canonical discriminant functions, standardized by within variances, explain the negative projection of *T. cristatus*, *L. al-*

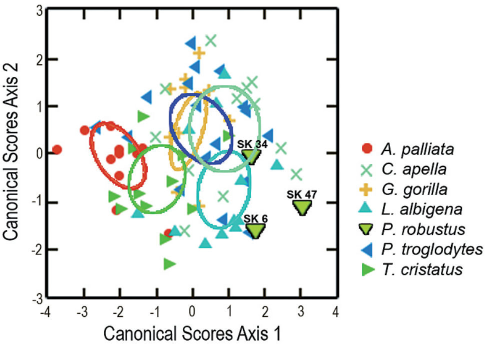

Fig. 5. Canonical Scores Axis 1 (71.5%) and Axis 2 (18.3%) are shown with 95% confidence ellipses around group centroids

Table 2. Canonical discriminant functions standardized by within-variances for Canonical Scores axes

Textural property	CS Axis 1	CS Axis 2
Complexity (*Asfc*)	0.928	0.633
Scale of maximum complexity (*Smc*)	0.758	–0.643
Anisotropy (*epLsar*)	–0.248	0.359
Textural fill volume (*Tfv*)	0.273	–0.555

Note. CS = canonical scores.

bigena and *P. robustus* on Canonical Scores Axis 2 (Table 2).

Jack-knifed classification rates

Jack-knifed classification rates are highest for *A. palliata* (71%) and lowest for *G. gorilla* (21%) whereas the classification rate for *P. robustus* is 67%. One *P. robustus* specimen, SK 6, is misclassified as *L. albigena*. One *L. albigena* and one *C. apella* are misclassified as *P. robustus*.

Mahalanobis distances

The Mahalanobis distances (D^2) for *P. robustus* individuals to the group centroid are relatively small (Table 3). However, SK 6 is slightly more similar to the group centroid for *L. albigena* (2.1) than the corresponding value for the *P. robustus* group centroid (2.4). The D^2 value for SK 34 to the *P. robustus* category is much higher (5.3) than those characterizing the other fossil specimens. However, the posterior probability of SK 34 is elevated in comparison to that for SK 6. *Paranthropus robustus* specimen SK 47 exhibits the lowest D^2 value (1.8) and the highest posterior probability of group membership (0.84) (Table 3).

Cluster analysis

A cluster analysis shows that SK 34 is distinct from the other taxa, followed by SK 47 and *A. palliata* (Fig. 6). The remaining extant taxa, particularly *L. albigena*, cluster with SK 6 but by a relatively long branch length. Taxa deriving from tropical forests, with the exception of *A. palliata*, exhibit relatively short branch lengths, particularly those separating *C. apella*, *P. troglodytes* and *G. gorilla* (Fig. 6).

Discussion and conclusion

Scott et al. (2005) suggest that *A. africanus* and *P. robustus* differ from *A. palliata* which has a diet primarily of leaves,

Table 3. Mahalanobis distances of *P. robustus* to the group centroids of the comparative taxa (with *post-hoc* probabilities of group membership)

Taxon	SK 6	SK 34	SK 47	Average D^2
A. palliata	18 (0.00)	18.5 (0.00)	28.4 (0.00)	21.633
C. apella	5.8 (0.07)	7.1 (0.22)	8.4 (0.03)	7.1
G. gorilla	8.0 (0.02)	10.1 (0.05)	13.2 (0.00)	10.433
L. albigena	2.1 (0.46)	7.9 (0.15)	5.7 (0.12)	5.233
P. robustus	2.4 (0.39)	5.3 (0.54)	1.8 (0.84)	3.166
P. troglodytes	6.9 (0.04)	11.2 (0.03)	10.5 (0.01)	9.533
T. cristatus	8.4 (0.02)	17.6 (0.00)	17.2 (0.00)	14.4

Note. D^2= Mahalanobis distance.

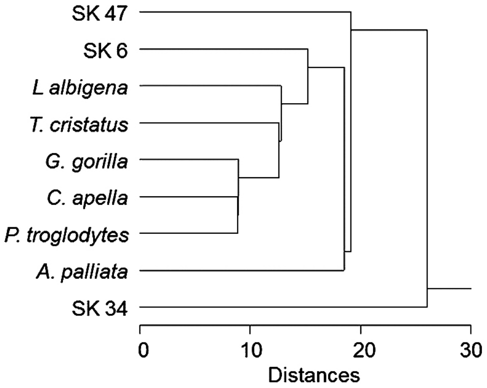

Fig. 6. A cluster analysis shows SK 34 is distinct, followed by SK 47 and *A. palliata*, while SK 6 groups with the remaining extant taxa albeit with a relatively long branch length

stems and fruit, and *Cebus* which consumes greater amounts of fruit and exhibits considerable durophagy and extractive foraging. Higher values for anisotropy (*epLsar*) in *A. africanus* and complexity (*Asfc*) in *P. robustus* are interpreted as evidence of different fallback foods. Scott et al. (2005) examine nine specimens attributed to *P. robustus* including eight from Swartkrans. The means and standard deviations from Scott et al. (2005) are reported in Ungar et al. (2012), and these are compared to the results obtained here (Fig. 7). Specimen SK 47 is similar to the textural properties recorded in Ungar et al. (2012) with the exception of textural fill volume (*Tfv*) (Fig. 7). The values for SK 6 resemble those from Ungar et al. (2012) for scale of maximum complexity (*Smc*) and anisotropy (*epLsar*). However, SK 34 falls outside the range of values reported by Ungar et al. (2012), increasing the variation in textural properties associated with *P. robustus* (Fig. 7).

Some of the variation observed could be attributable to life history differences, and may explain why *P. robustus* subadults, SK 6 and SK 47, differ from adult specimen SK 34 in scale of maximum complexity (*Smc*) and textural fill volume (*Tfv*) (Table 1; Fig. 7). The Sr/Ca ratio of juvenile SK 54 was substantially higher than adults from Swartkrans Member 1 and more like that of *Papio robinsoni* than the fossil carnivore taxa. These differences may suggest *P. robustus* juveniles consumed USOs which exhibit elevated Sr/Ca ratios (Sillen 1992). Corroborating these observations, juvenile *P. robustus* exhibits substantial dentine exposure suggesting an abrasive diet in nonadults, early weaning, or both (Aiello et al. 1991). The scratch marks on the Swartkrans bone tools from the Lower Bank of Member 1, which is believed to be contemporaneous with the Hanging Remnant remains, may have resulted from digging USOs (Brain 1985; 2004). Perhaps subadults were less able to effectively utilize the tools or techniques to remove the extraneous grit on terrestrial resources or USOs in contrast to adults, accounting for the elevated textural fill volume (*Tfv*) in SK 6 and SK 47. Juvenile and subadult chimpanzees are not as well versed in utilizing termite sticks and in nut-cracking activities as adults (McGrew 1992). A subadult sample of *Papio* exhibits a significantly greater degree of pitting than do adults, perhaps also reflecting differences in diet or food preparation (Nystrom et al. 2004). Furthermore, Neandertal subadults are noted to have a significantly greater density of striations compared to adults (Pinilla Pérez et al. 2011), although young and older adult Amerindians were not significantly different in patterns of dental microwear suggesting a leveling of age differences in diet after maturation (Schmidt 2010). However,

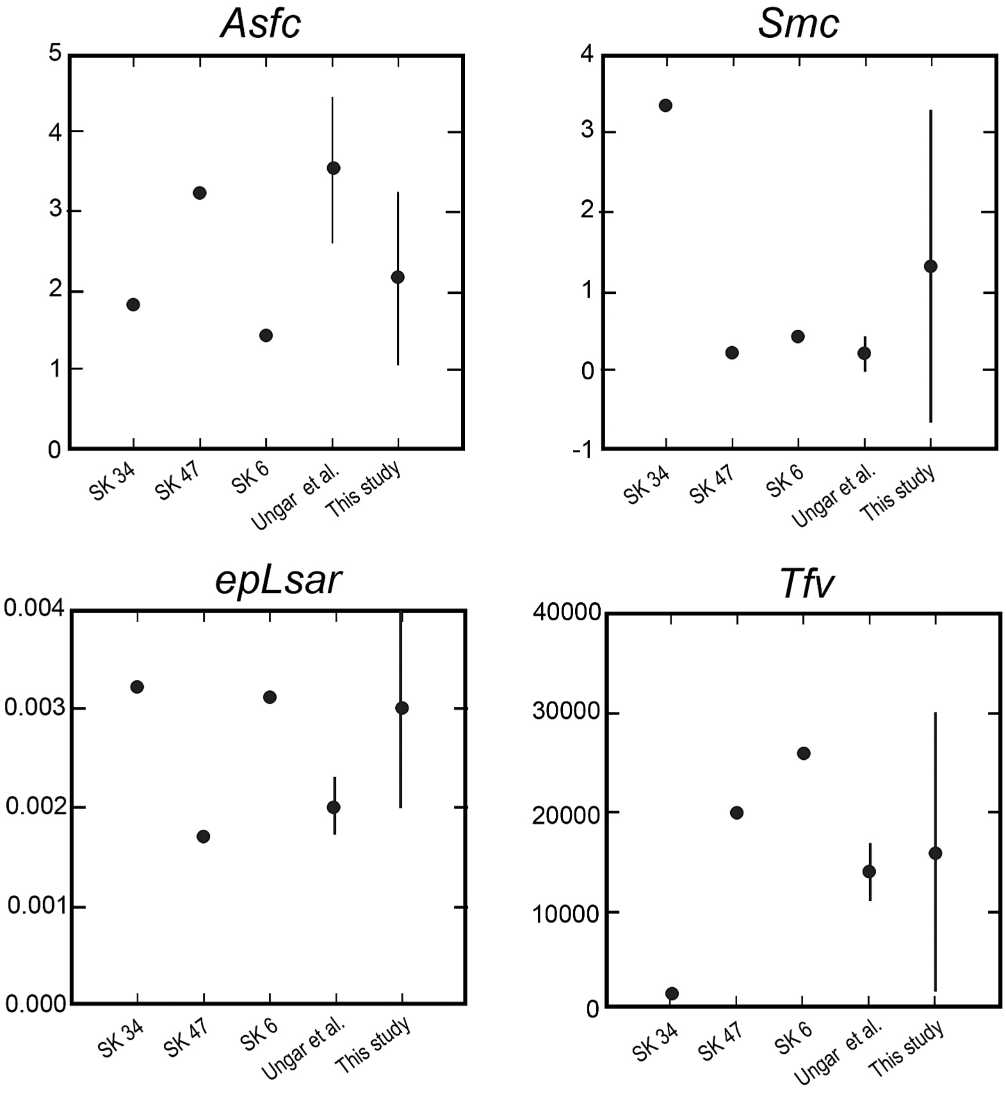

Fig. 7. A comparison of the 95% confidence intervals for the nine *P. robustus* specimens reported in Ungar et al. (2012) and the three *P. robustus* fossils examined in this study

given the variation in *P. robustus* (Fig. 7), idiosyncratic factors related to seasonal diets typical of temperate latitude fauna, and the availability of fallback foods may also account for the differences within these specimens.

Dietary reconstruction of *P. robustus*

Direct evidence of dietary consumption in *Paranthropus* has been explored by a number of researchers (Robinson

1954; Kay 1985; Grine 1986; Scott et al. 2005; Constantino et al. 2010). Kay (1985) suggests that the exceptionally thick enamel of *P. robustus* (and *A. africanus*) could have been an adaptation to the consumption of at least three possible foods, such as seeds, metapodials of ungulates and the underground parts of plants. However, thick enamel cannot be used as evidence for terrestrial foraging since it has also evolved in arboreal primates that specialize on hard foods such as *Cebus* and *Lophocebus*. Rather, it appears to be a consequence of consuming a great variety of different foods, some of which are hard and brittle (Kay 1985).

Paranthropus robustus has been described as exhibiting low anisotropy with respect to *A. africanus* (Scott et al. 2005; Ungar et al. 2010) and early *Homo* (Ungar and Scott 2009). Highly folivorous primates such as *A. palliata* and *T. cristatus* exhibited elevated anisotropy (*epLsar*) (Scott et al. 2006). This may indicate a lack of leaves in the diet of *P. robustus* or suggest that leaves were not a primary food source. The low crests on the molars also point to a diet low in fibrous leaves (Kay 1985).

Similar to *L. albigena*, *P. robustus* exhibits elevated values for scale of maximum complexity (*Smc*) suggesting hard and brittle foods may have been consumed. The consumption of hard and brittle foods including seeds and bark necessitates thick enamel to prevent enamel chipping, such as is found in *L. albigena* (Lambert et al. 2004) and *C. apella* (Jack 2011). Enamel chipping must have been generated by an extreme bite force in *P. robustus* (Constantino et al. 2010), also noted for its thick enamel (Robinson 1954; Wallace 1973; Grine 1981; Schwartz et al. 1998). *Paranthropus robustus* resembles *C. apella* and *L. albigena* in its elevated textural fill volume (*Tfv*). Elevated textural fill volume (*Tfv*) may derive from consuming hard and brittle foods (Merceron et al. 2009) or is possibly the result of the consumption of soil and sand such as in *T. cristatus* (Brotoisworo and Dirgayusa 1991), or when grit inadvertently adheres to meat (Romero et al. 2012). Grit may be the primary factor in the production of dental microwear (Sanson et al. 2007; Lucas et al. 2013). Experimental studies have shown that microwear forms when siliceous grit comes into contact with the teeth (Romero et al., 2012). In addition, Galbany et al. (2014) and Romero et al. (2012) proposed that the production of enamel microwear is dependent on particle size. For example, large particles are more likely to fracture the enamel surface, whereas small particles produce indentations. The terrestrial foraging of *P. robustus* in mixed C_4 habitats would likely deliver a heavier grit load than observed in tropical forests. This would be particularly evident in relatively arid habitats where a layer of grit covers food items (Sanson et al. 2007; Galbany et al. 2009; Dumont et al. 2011). Grit adheres to hypogeous organs (Daegling and Grine 1999) and can be inadvertently ingested when bulbs or corms have outer skins that are not easily removed or cleaned with the mouth or hands.

Underground storage organs could have been a reliable source of energy-rich carbohydrates for *Australopithecus* and early *Homo* (Hatley and Kappelman 1980; Wrangham et al. 1999; Conklin-Brittain et al. 2002; Laden and Wrangham 2005). Some have suggested the possibility that USOs were preferred foods rather than fallback resources explaining the similarity in the postcanine dentition of pigs, bears, and australopiths (Hatley and Kappelman 1980). Savanna environments yield a more abundant and diverse USO distribution than is found in rain forests. Furthermore, 65% of USOs in savannas can be eaten raw compared to only 9.1% from rain forests (Laden and Wrangham 2005). Judging from the relatively large palate in *P. robustus* compared to the great apes, there was a capacious cavity to allow a thorough processing of starchy foods with salivary amylase which enhances digestion (Conklin-Brittain et al. 2002). These resources could have been heavily utilized during seasonal dietary deficits or during drying episodes typical of early Pleistocene southern Africa.

It is worth noting that *P. troglodytes*, *C. apella* and *L. albigena* all consume substantial quantities of insects and all exhibit elevated complexity (*Asfc*) values. The consumption of insect cuticle may explain evidence of hard-object foraging in the Muridae, small primates and some bats (Strait 1993; Rodrigues et al. 2009). Although the external shell of insects lack mineral supports, the cuticle can be extremely stiff (Dirks and Taylor 2012; Vincent and Wegst 2004). The somewhat elevated value for complexity (*Asfc*) in *P. robustus* could originate from terrestrial grit from USOs and meat as well as from hard seeds and/or insects, or a mix of these resources (Backwell and d'Errico 2001; Peters and Vogel 2005).

The isotopic values of *P. robustus* suggest the consumption of some C_4 grassland resources, either in the form of meat from C_4 grazers or C_4 plant roots (Lee-Thorp et al. 1994); C_4 grass blades would have resulted in elevated values of anisotropy (*epLsar*) which is not the case. Ingestion of terrestrial foods should result in greater textural complexity (*Asfc*), scale of maximum complexity (*Smc*) and textural fill volume (*Tfv*) like that seen on *L. albigena* which feeds on seeds with extremely hard and brittle shells, insects and fruit found on ground-level (Lambert et al. 2004). *Paranthropus robustus* shows a pattern of textural characteristics that resembles in part that of *L. albigena* and to a lesser extent, *C. apella*. In this way, the thick enamel and enamel textural properties of *P. robustus* could be reflecting an adaptation to the mechanical properties of foods, as in *L. albigena* and *C. apella*. *Paranthropus robustus* is distinct from arboreal primates that consume substantial quantities of leaves such as *T. cristatus* and *A. palliata* corroborating the lack of folivory inferred from the broad flat molars. The elevated values for complexity (*Asfc*) and textural fill volume (*Tfv*) in *P. robustus* may derive from the consumption of hard seeds and/or insects; however, given its isotopic signal, grit particles associated with terrestrial foraging and the exploitation of USOs derived from C_4 plants may better account for these dental microwear texture properties.

Disclosure statement

The *Paranthropus robustus* fossils utilized in this study have not been reported upon by the author previously and there are no conflicts of interest to declare.

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