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Dental microwear texture analysis shows within-species diet variability in fossil hominins

Robert S. Scott[1]*, Peter S. Ungar[1]*, Torbjorn S. Bergstrom[2], Christopher A. Brown[2], Frederick E. Grine[3], Mark F. Teaford[4] & Alan Walker[5]

Reconstructing the diets of extinct hominins is essential to understanding the paleobiology and evolutionary history of our lineage. Dental microwear, the study of microscopic tooth-wear resulting from use[1–4], provides direct evidence of what an individual ate in the past. Unfortunately, established methods[5–10] of studying microwear are plagued with low repeatability and high observer error[11]. Here we apply an objective, repeatable approach for studying three-dimensional microwear surface texture to extinct South African hominins. Scanning confocal microscopy[12,13] together with scale-sensitive fractal analysis[14–19] are used to characterize the complexity and anisotropy of microwear. Results for living primates show that this approach can distinguish among diets characterized by different fracture properties. When applied to hominins[20], microwear texture analysis indicates that *Australopithecus africanus* microwear is more anisotropic, but also more variable in anisotropy than *Paranthropus robustus*. This latter species has more complex microwear textures, but is also more variable in complexity than *A. africanus*. This suggests that *A. africanus* ate more tough foods and *P. robustus* consumed more hard and brittle items, but that both had variable and overlapping diets.

To understand the relationships between diet and dental microwear, we first examined living animals with different diets. *Cebus apella*, for example, eats more fruit flesh and hard, brittle seeds[2], whereas *Alouatta palliata* consumes more leaves and other tough items[22,23]. We measured microwear complexity by area–scale fractal complexity (Asfc) (Fig. 1). The Asfc is significantly higher ($\chi^2 = 36.97$, $P < 0.0001$; Kruskal-Wallis test) and more variable ($F = 81.65$, $P < 0.0001$; F-test) for *C. apella* (13.99 ± 11.034, all values are mean ± s.d. unless otherwise stated) than for *A. palliata* (0.98 ± 1.221). The anisotropy variable, exact proportion length–scale anisotropy of relief (epLsar) (calculated with a scale observation of 1.8 μm, epLsar$_{1.8}$), quantifies the degree of directionality in surface roughness at a fine scale. The anisotropy is significantly higher ($\chi^2 = 16.32$, $P < 0.0001$; Kruskal-Wallis test) and more variable ($F = 2.38$, $P < 0.05$) for *A. palliata* (epLsar$_{1.8}$ 0.0052 ± 0.00215) than for *C. apella* (0.003 ± 0.0014) (Fig. 2a, b). These results suggest that hard, brittle foods associated with pits in microwear feature analyses[9,10,24] leave a more complex microwear texture (>Asfc), whereas tough foods associated with scratches in microwear feature analyses[9,10,24] produce a more anisotropic microwear texture (>Lsar).

Fossil hominin results indicate that *P. robustus* (Asfc 4.29 ± 2.150) has microwear textures more complex ($\chi^2 = 8.17$, $P < 0.005$; Kruskal-Wallis test) and more variable in complexity ($F = 16.82$, $P < 0.0005$) than *A. africanus* (Asfc 1.686 ± 0.52) (Fig. 2c, d). These results are consistent with the hypothesis that *P. robustus* incorporated more hard and brittle foods in its diet[20,25]. However, some overlap in Asfc for the hominins (Fig. 3b) suggests that *P. robustus* was unlikely to have been a specialized hard-object feeder. It is more

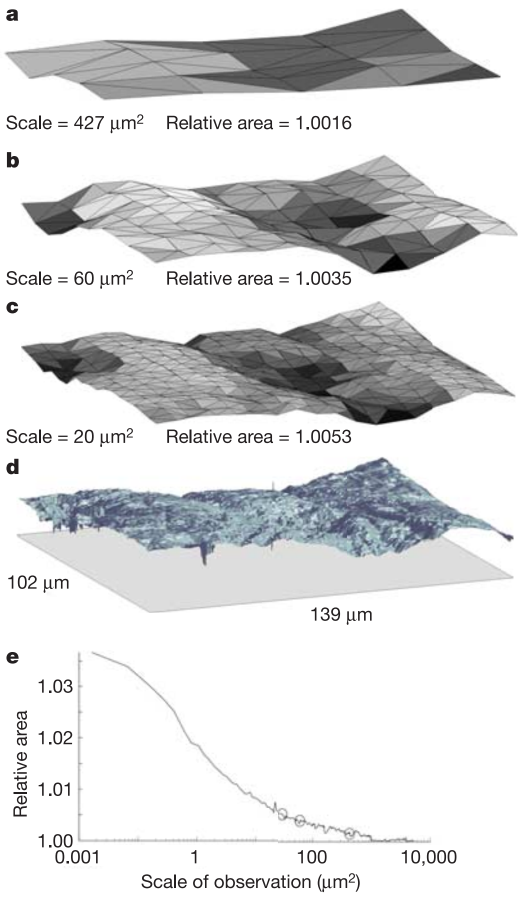

Figure 1 | Scale-sensitive fractal analysis. a–e, Relative area is calculated by dividing the area of a surface, calculated using triangles of a given scale in a virtual tiling algorithm (**a**, **b**, **c**), by the projected area of the surface (**d**). Relative area can then be plotted against scale in a log–log plot (**e**). Asfc[30] is a scale-sensitive measure of roughness and is the slope of the steepest part of the curve fitted to the plot of relative area over scale, multiplied by −1,000.

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[1]Department of Anthropology, University of Arkansas, Fayetteville, Arkansas 72701, USA. [2]Surface Metrology Laboratory, Department of Mechanical Engineering, Worcester Polytechnic Institute, Worcester, Massachusetts 01609, USA. [3]Departments of Anthropology and Anatomical Sciences, Stony Brook University, Stony Brook, New York 11794, USA. [4]Center for Functional Anatomy & Evolution, Johns Hopkins University School of Medicine, Baltimore, Maryland 21205, USA. [5]Departments of Anthropology and Biology, Pennsylvania State University, University Park, Pennsylvania 16802, USA.
*These authors contributed equally to this work.

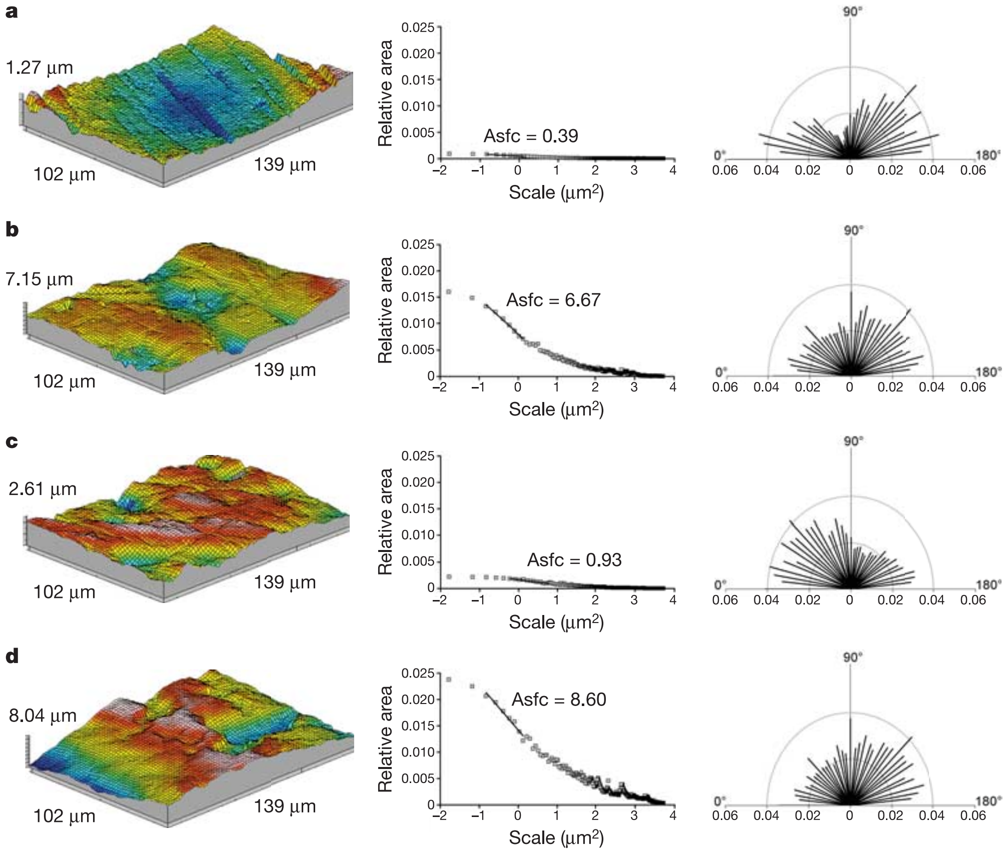

Figure 2 | Microwear texture analyses. a–d, Meshed axonometrics of digital elevation models (left), bivariate plots of relative area versus scale (middle), and rosette plots of normalized relative length at 1.8 μm by orientation (right) for scans on representative specimens of *Alouatta palliata* (NMNH 543117) (**a**), *Cebus apella* (NMNH 518433) (**b**), *Australopithecus africanus* (Sts 61) (**c**), and *Paranthropus robustus* (SK 16) (**d**). Steeper best-fit lines for the steepest order of magnitude on the relative area–scale curves evince higher Asfc values, indicating greater complexity (for example, **b** and **d**). More clumped rosettes (for example, **a** and **c**) have higher values of epLsar, indicating greater anisotropy of the wear fabric.

likely that hard, brittle foods were an occasional but important part of the diet. Previous studies have emphasized average differences between species rather than overlap, because low repeatability[11] associated with observer error made assessments of within-species variability difficult.

In contrast, the microwear textures of *Australopithecus africanus* (epLsar$_{1.8}$ 0.0045 ± 0.00163) show greater anisotropy ($\chi^2 = 3.84$, $P = 0.05$; Kruskal-Wallis test) and epLsar variability ($F = 7.38$, $P < 0.01$) than *P. robustus* (epLsar$_{1.8}$ 0.0028 ± 0.00060) (Fig. 2c, d). These data suggest a tougher diet on average for *A. africanus* compared with *P. robustus*, but one that is also more variable in its toughness.

Microwear texture analysis is a repeatable alternative to methods that rely on subjective feature counts and measurements on two-dimensional photomicrographs generated using a scanning electron microscope (SEM). Variables including Asfc and Lsar, which are based on scale-sensitive fractal analysis, can distinguish microwear found on molars of extant primates with contrasting diets (Fig. 3a). These variables also distinguish the microwear found on molars of extinct South African hominins (Fig. 3b). The reduction in observer error and the possibility of using larger samples dramatically improves estimations of microwear variability, and creates a new opportunity to model diet and subsistence variability in both extinct species and bioarchaeological samples.

The evidence presented here with respect to South African hominin molar microwear affirms some differences between *P. robustus* and *A. africanus*. For instance, wear fabrics of *P. robustus* are more complex and less anisotropic than those of *A. africanus*. These differences suggest a diet composed of more hard and brittle foods for *P. robustus* and more tough foods for *A. africanus*[20,25].

On the other hand, the contrasts in microwear texture variability found here offer new insights. The greater variation in complexity for *P. robustus* and in anisotropy for *A. africanus* suggests that these species altered different components of their diet, but that there was probably substantial overlap in the fracture properties of their preferred foods. Thus, the clear differences between *A. africanus* and *P. robustus* microwear may relate, in part, to differences in critical dietary resources consumed only periodically during the year.

The study of dietary variability in fossil hominins has until now been problematic, given small sample sizes, subjective identification of individual features and observer error[11]. The overlap and variability identified here for *Paranthropus* and *Australopithecus* was not apparent from earlier studies[20,25]. This suggests that early hominin diet differences might relate more to microhabitat, seasonality or fall-back food choice than to oversimplified, dichotomous food preferences[26–28].

METHODS

The samples of the extant primates included high-resolution epoxy replicas of mandibular second molars of the New World monkeys, *Cebus apella* ($n = 35$) and *Alouatta palliata* ($n = 25$). Specimens are accessioned at the US National Museum of Natural History and provenience is known only generally. *C. apella* specimens were collected in central and eastern Brazil and *A. palliata* specimens were collected in Panama (from Darien to Bocas del Toro). The fossil specimens were the same as those considered by Grine[25], including *Paranthropus robustus* from Swartkrans (~1.9–1.5 Myr ago; $n = 9$) and *Australopithecus africanus* from Sterkfontein (~2.8–2.4 Myr ago; $n = 10$).

Specimens were examined using a Sensofar Plμ white-light scanning confocal imaging profiler with a ×100 objective[12,13]. Four adjacent areas on Facet 9 (ref. 29) of the specimens were scanned, sampling a total area of a 276 × 204 μm. These were then levelled using SolarMap Universal, producing digital elevation models with a vertical sampling interval of 0.005 μm and a lateral (*x* and *y*) sampling interval of 0.18 μm.

The resulting data were analysed using scale-sensitive fractal analysis[14–19], an objective and repeatable approach to quantifying the complexity and directionality of surface roughness and their scales. Scale-sensitive fractal analysis is based on the idea that the apparent area of a rough surface, and the length of a profile from a rough surface, change with the scale of observation. Thus, surface textures appear smooth at sufficiently coarse scales, and rough with increasing resolution

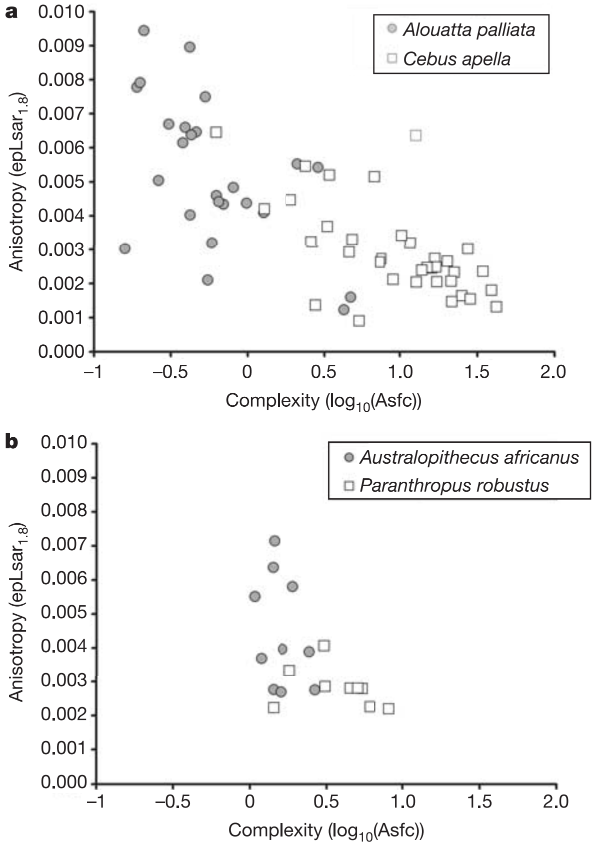

Figure 3 | Anisotropy and complexity. a, b, Bivariate plots of epLsar$_{1.8}$ versus Asfc for *Alouatta palliata* and *Cebus apella* (**a**), and *Australopithecus africanus* and *Paranthropus robustus* (**b**). The values plotted are means based on the four scans with adjoining edges from each specimen.

at sufficiently fine scales. Changes in areas with scale are used to characterize complexity. These are calculated as changes in relative area, defined as the calculated surface area at a particular scale (Fig. 1a–c) divided by planometric area (Fig. 1d). The slope of the steepest part of the curve fitted to a log–log plot of relative area over some scale range (multiplied by $-1{,}000$) (Figs 1e and 2) is termed area–scale fractal complexity (Asfc)[30]. For each scan studied here, 560 relative areas were calculated for scales from $\sim 5{,}300\,\mu\text{m}^2$ to $\sim 0.17\,\mu\text{m}^2$ using Kfrax (http://www.surfract.com). Asfc was calculated for each scan over one order of magnitude, and mean Asfc was calculated for each specimen.

Relative lengths of depth profiles differ with orientation when the roughness of a surface has directionality (that is, when the surface is anisotropic). We define relative lengths at given orientations as vectors. Thirty-six vectors were calculated at 5° intervals for each scale and then normalized. For a given scale, normalized vector lengths or 'exact proportion' relL_a are equal to $(\mathrm{rel}L_a - 1)/\Sigma(\mathrm{rel}L_a - 1)$, where rel$L$ is relative length and a is the orientation of the length scale analysis. This normalization is functionally equivalent to normalizing by the mean of rel$L$ when the number of orientations calculated is constant across the comparison. Longer normalized relative length vectors in the rosette plots generally correspond to more wear features normal to the direction of the vector.

Normalized relative length vectors can be displayed graphically in a rosette diagram (Fig. 2). The length of the mean vector is a new measure of surface anisotropy called exact proportion length–scale anisotropy of relief (epLsar). epLsar was calculated for each scan using Kfrax with a scale of observation of $1.8\,\mu\text{m}$, and mean epLsar was calculated for each specimen.

Descriptive and inferential statistics were computed using SAS 9.1.

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1. Walker, A. C., Hoeck, H. N. & Perez, L. Microwear of mammalian teeth as an indicator of diet. *Science* **201,** 808–810 (1978).
2. Rensberger, J. M. in *Development, Function and Evolution of Teeth* (eds Butler, P. M. & Joysey, K. A.) 415–438 (Academic, New York, 1978).
3. Ryan, A. S. Anterior dental microwear and its relationship to diet and feeding behaviour in three African primates (*Pan troglodytes troglodytes, Gorilla gorilla gorilla*, and *Papio hamadryas*). *Primates* **22,** 533–550 (1981).
4. Gordon, K. D. A study of microwear on chimpanzee molars: implications for dental microwear analysis. *Am. J. Phys. Anthropol.* **59,** 195–215 (1982).
5. Solounias, N., Teaford, M. & Walker, A. Interpreting the diet of extinct ruminants: the case of a non-browsing giraffid. *Paleobiology* **14,** 287–300 (1988).
6. Ungar, P. S., Simons, J.-C. & Cooper, J. W. A semiautomated image analysis procedure for the quantification of dental microwear. *Scanning* **13,** 31–36 (1991).
7. Pastor, R. F. Dietary adaptations and dental microwear in Mesolithic and Chalcolithic South Asia. *J. Hum. Ecol.* (special issue) **2,** 215–228 (1992).
8. Molleson, T., Jones, K. & Jones, S. Dietary change and the effects of food preparation on microwear patterns in the Late Neolithic of abu Hureyra, northern Syria. *J. Hum. Evol.* **24,** 455–468 (1993).
9. Teaford, M. F. A review of dental microwear and diet in modern mammals. *Scanning Microsc.* **2,** 1149–1166 (1988).
10. Strait, S. G. Molar microwear in extant small-bodied faunivorous mammals: an analysis of feature density and pit frequency. *Am. J. Phys. Anthropol.* **92,** 63–79 (1993).
11. Grine, F. E., Ungar, P. S. & Teaford, M. F. Error rates in dental microwear quantification using SEM. *Scanning* **24,** 144–153 (2002).
12. Boyde, A. & Fortelius, M. New confocal LM method for studying local relative microrelief with special references to wear studies. *Scanning* **13,** 429–430 (1991).
13. Ungar, P. S., Brown, C. A., Bergstrom, T. S. & Walker, A. Quantification of dental microwear by tandem scanning confocal microscopy and scale-sensitive fractal analyses. *Scanning* **25,** 189–193 (2003).
14. Brown, C. A. & Savary, G. Describing ground surface texture using contact profilometry and fractal analysis. *Wear* **141,** 211–226 (1991).
15. Brown, C. A., Charles, P. D., Johnsen, W. A. & Chesters, S. Fractal analysis of topographic data by the patchwork method. *Wear* **161,** 61–67 (1993).
16. Brown, C. A., Johnsen, W. A. & Hult, K. M. Scale-sensitivity, fractal analysis and simulations. *Int. J. Mach. Tool. Manu.* **38,** 633–637 (1998).
17. DeChiffre, L. *et al.* Quantitative characterization of surface texture. *Annals CIRP* **49,** 635–652 (2000).
18. Brown, C. A. & Siegmann, S. Fundamental scales of adhesion and area-scale fractal analysis. *Int. J. Mach. Tool. Manu.* **41,** 1927–1933 (2001).
19. Bergstrom, T. S. & Brown, C. A. Interaction between horizontal scanning instruments and surfaces. *Int. J. Mach. Tool. Manu.* **41,** 1995–2000 (2001).
20. Grine, F. E. & Kay, R. F. Early hominid diets from quantitative image analysis of dental microwear. *Nature* **333,** 765–768 (1988).
21. Eisenberg, J. F. *Mammals of the Neotropics* Vol. 1. *The Northern Neotropics: Panama, Colombia, Venezuela, Guyana, Suriname, French Guiana* 233–261 (Univ. Chicago Press, Chicago, 1989).
22. Estrada, A. Resource use by howler monkeys (*Alouatta palliata*). *Int. J. Primatol.* **5,** 105–131 (1984).
23. Neville, M. K., Glander, K. E., Braza, F. & Rylands, A. B. in *Ecology and Behavior of Neotropical Primates* Vol. 2 (eds Mittermeier, R. A., Rylands, A. B., Coimbra-Filho, A. F. & de Fonseca, G. A. B.) 349–453 (World Wildlife Fund, Washington DC, 1988).
24. Crompton, R. H., Savage, R. & Spears, I. H. The mechanics of food reduction in *Tarsius bancanus*: hard-object feeder, soft-object feeder or both? *Folia Primatol.* **69**((suppl. 1)), 41–59 (1998).
25. Grine, F. E. Dental evidence for dietary differences in *Australopithecus* and *Paranthropus*. *J. Hum. Evol.* **15,** 783–822 (1986).
26. Wrangham, R. W., Conklin-Brittain, N. L. & Hunt, K. D. Dietary response of chimpanzees and Cercopithecines to seasonal variation in fruit abundance. I. Antifeedants. *Int. J. Primatol.* **19,** 971–998 (1998).
27. Stanford, C. B. & Nkurunungi, J. B. Behavioral ecology of sympatric chimpanzees and gorillas in Bwindi Impenetrable National Park, Uganda: Diet. *Int. J. Primatol.* **24,** 901–918 (2003).
28. Lambert, J. E., Chapman, C. A., Wrangham, R. W. & Conklin-Brittain, N. L. The hardness of cercopithecine foods: implications for the critical function of enamel thickness in exploiting fallback foods. *Am. J. Phys. Anthropol.* **125,** 363–368 (2004).
29. Kay, R. F. The evolution of molar occlusion in the Cercopithecidae and early Catarrhines. *Am. J. Phys. Anthrop.* **46,** 327–352 (1977).
30. American Society of Mechanical Engineers, *National Standard B46.1: Surface Texture, Surface Roughness, Waviness and Lay* (American Society of Mechanical Engineers, New York, 2002).

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