For the work reported here, the standard is the Pee Dee belemnite (PDB) carbonate.

10. Studies (*2*) in which bones from mice raised on diets of known and constant $\delta^{13}C$ values were analyzed have shown that the $\delta^{13}C$ value of the diet is on average -3.2 per mil relative to the $\delta^{13}C$ value of the collagen fraction. Similarly, the diet has a $\delta^{13}C$ value which is on average -9.6 per mil relative to the $\delta^{13}C$ value of the carbonate fraction. The accuracy of the $\delta^{13}C$ value of a diet estimated from the $\delta^{13}C$ value of either fraction is on the order of ±0.5 per mil.
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15. We thank H. N. Hoeck for providing the bone samples. This work was supported by grant EAR 76-22751 A01 from the National Science Foundation. This is contribution 3047, Division of Geological and Planetary Sciences, California Institute of Technology.

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Microwear of Mammalian Teeth as an Indicator of Diet

Abstract. *Microwear details on teeth of two sympatric species of hyrax are correlated with major dietary differences observed in the wild. Grazing (*Procavia johnstoni*) and browsing (*Heterohyrax brucei*) species can be distinguished. The results show that diets of extinct species may be deduced from tooth microwear.*

Hypotheses concerning the diets of extinct hominoid species have played an important part in discussions of human origins (*1–4*). Direct testing of these hypotheses has proved difficult; most research has involved ambiguous comparisons of early hominoid teeth with those of living mammals and conclusions drawn from either associated archeological finds or inferred local paleoecology. Two of us (A.W. and L.P.) are attempting to test dietary hypotheses directly by finding correlations between known diet and tooth microwear in a variety of living mammals. If the correlations prove to be strong, it will be possible to test dietary hypotheses by examining the microwear on extinct hominoid teeth.

To establish stringent controls, we sought to examine teeth of pairs of extant species that meet the following criteria: (i) the feeding behaviors of the two species are known from careful field observations; (ii) the specimens used are from wild populations; (iii) the two species are of similar size, with similar teeth and masticatory systems; and (iv) the specimens are from the same local area, to avoid variations produced by local soils and climate. Several pairs of such species have been examined, although it has proved difficult to meet the fourth criterion, that of sympatry. Collecting samples of larger, and sometimes rare, mammals is impossible today, which made it necessary to use museum collections, the composition of which has been influenced by many historical factors. Even when two appropriate species are known to be sympatric, museum collections often do not include sympatric samples. However, one pair of closely related species does meet all the criteria for this study and can be used to determine the relative influence of browsing and grazing on tooth microwear.

Hoeck (*5*) has made a detailed study of the feeding behavior of two sympatric species of hyrax, *Procavia johnstoni matschiei* Neuman 1900 and *Heterohyrax brucei dieseneri* Brauer 1917, which live together in the Serengeti National Park, Tanzania. Feeding and reproductive behaviors separate individuals of these two species, which otherwise share living holes, urinate and defecate in the same places, have similar feeding periods, and bask together (Fig. 1). *Procavia johnstoni* is almost exclusively a grazer and *H. brucei* is almost exclusively a browser (*5, 6*). In addition, *P. johnstoni* is larger than *H. brucei*. The mean adult body weight of *P. johnstoni* is 3.14 kg (standard deviation, 0.60 kg; $N = 60$) while that of *H. brucei* is 1.79 kg (standard deviation, 0.26 kg; $N = 121$).

In the field study, the feeding characteristics of three allopatric family groups (two *H. brucei* and one *P. johnstoni*) and four sympatric family groups (two of each species) living on five kopjes (rocky outcrops) were studied. The vegetation of the kopjes was divided into four classes (grass, forb, bush, and tree), the plant species were identified, and indices of diversity and similarity were calculated. Plant biomass was approximated by a foliage density factor and the seasonal variation was recorded. Counts of plant species ranged from 65 to 95. Bushes and trees account for only about a quarter of the species, but they gave the highest foliage density. Seasonal leaf, flower, and fruit cycles were found in the grasses, forbs, and small bushes, but larger bushes and trees never lost leaves completely. There are marked dry and wet seasons. The latter is November to May, with a rainfall peak in March and April.

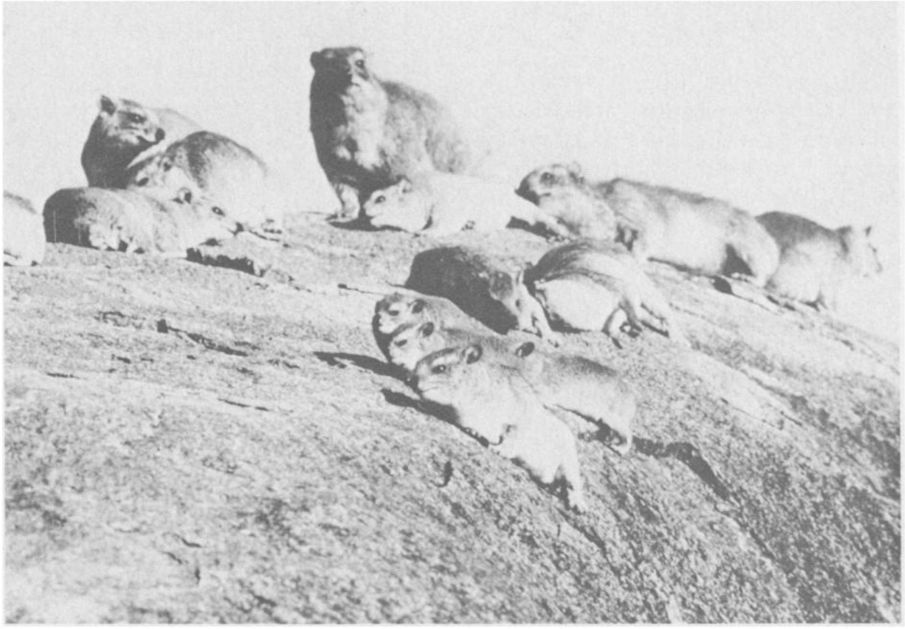

Fig. 1. Basking hyraxes. A group of *H. brucei* is in the foreground and several larger *P. johnstoni* are in the background.

The feeding behavior of the hyrax groups was recorded regularly during both wet and dry seasons. *Heterohyrax brucei* fed on 64 plant species, but between 2 and 11 species made up 90 percent of the diet. There was a high correlation (correlation coefficient $\bar{r} = .90$, $P < .01$) between the comparative abundance of vegetation and the proportion of the vegetation classes eaten by *H. brucei*. While showing preference for certain plants, all four groups fed roughly in proportion to foliage density. *Heterohyrax brucei* browsed on bushes and trees in both wet (81 percent) and dry (92 percent) seasons, but ate some grass in the wet season. *Procavia johnstoni* was seen feeding on 79 plant species. This species showed great seasonal

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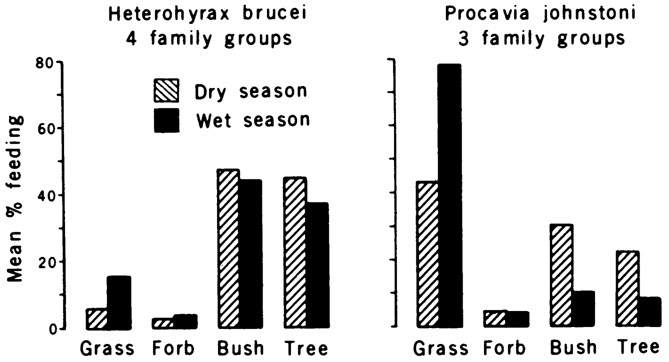
preferences, eating 78 percent grasses in the wet season, but browsing extensively (57 percent) in the dry season. Because of its strong preference for grasses, there is no correlation between the proportions of vegetation classes eaten by *P. johnstoni* and their comparative abundance. Feeding preferences are shown in Fig. 2. *Procavia johnstoni* leaves the kopjes to graze, creating cropped areas, the size of which varies with rainfall. Competition for food seemed especially likely during the dry season, when both species are browsing, but no evidence was found for displacement induced by competition. Virtually no aggressive interactions were observed between the two species.

Hyrax teeth resemble those of rhinoceroses in shape, having large, lophed upper premolars and molars that work against narrower, lophed premolars and molars. The premolars are molariform. Upper molar teeth (mostly M^1 and M^2), were taken from 19 *P. johnstoni* and 23 *H. brucei* skulls collected from the study area. They were cleaned with water and acetone, and then mounted on stubs and coated with 300-Å gold-palladium. Whole tooth surfaces were examined by scanning electron microscopy at low magnifications and selected areas were photographed at higher magnifications. Teeth were rotated in all positions to ensure that all relief was observed, and comparative photographs were taken, as far as differences in size and wear allowed, of the same areas of each tooth. Both species have enamel prisms about 5 μm in diameter and dentinal tubules about 1.5 μm in diameter, spaced about 6 μm apart.

In all specimens of *H. brucei* examined, whether from wet or dry seasons, both enamel and dentin surfaces were extremely smooth. The outlines of the enamel prisms were clearly demarcated by the lesser relief of the interprismatic matrix. On exposed dentin surfaces, the tubular nature is clearly seen, as the tubules are exposed on the summits of low dentin mounds. Microscratches on the occlusal surfaces are infrequent, but traumatic defects involving several prisms or tubules are seen and normally take the form of deep, sharp-edged pits. The overall impression of *H. brucei* teeth is that the occlusal surfaces have been finely polished so that the harder, or more organized, prismatic and tubular sheath material stands in relief (Fig. 3, A and B). In *P. johnstoni* the surfaces differed in samples from the wet and dry seasons. Teeth collected during the wet season showed heavy wear that obscured enamel prism outlines and dentin

Fig. 2. Seasonal feeding preferences in *H. brucei* and *P. johnstoni*. Values are means for family groups. Each group of four columns (one season) equals 100 percent.



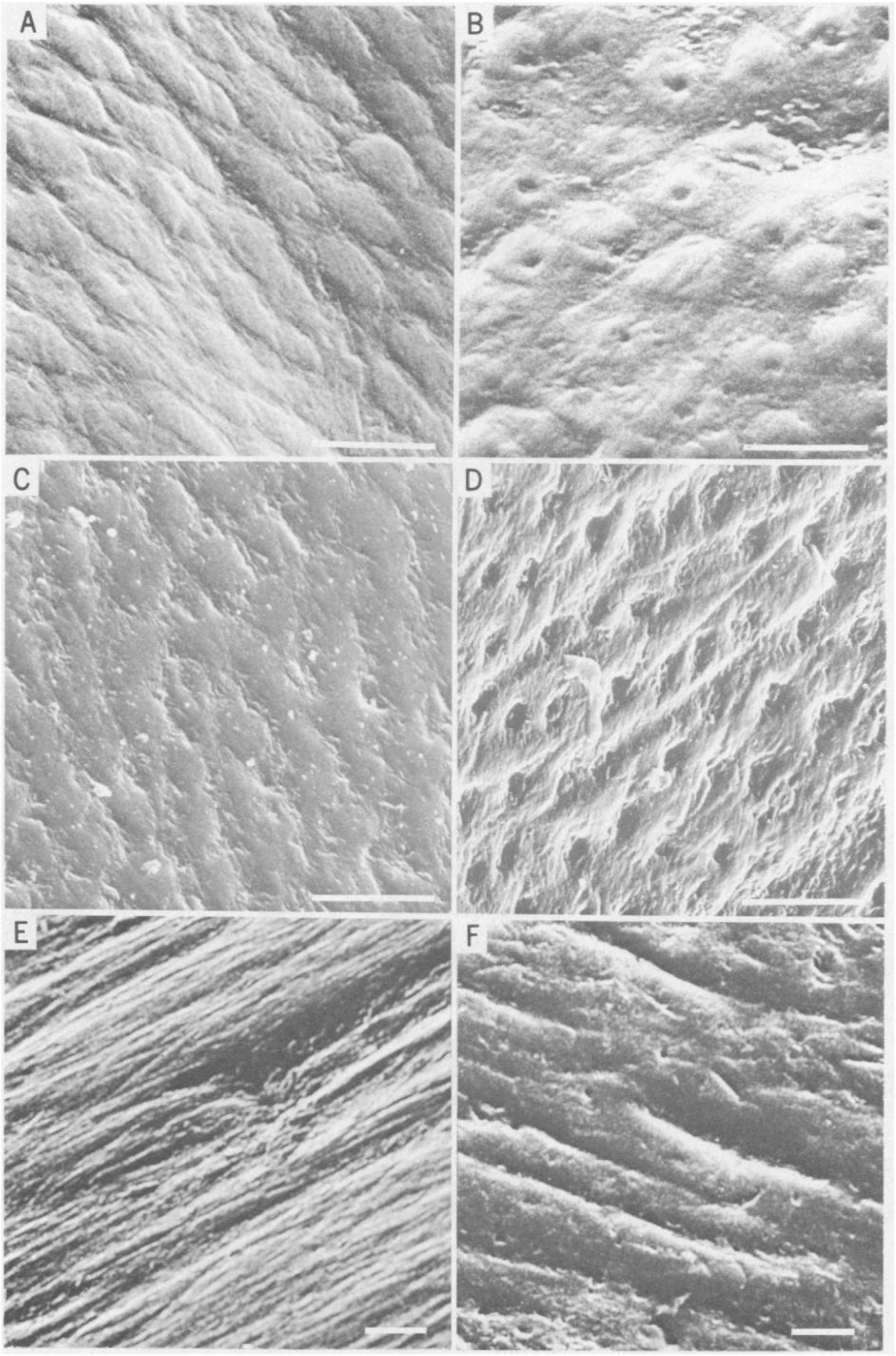


Fig. 3. Scanning electron micrographs of (A) *H. brucei* enamel and (B) *H. brucei* dentin, showing details of enamel prisms and dentinal tubules; (C) *P. johnstoni* enamel and (D) *P. johnstoni* dentin from a dry season specimen, showing persistence of enamel prism outlines and dentinal tubular structures; and (E) *P. johnstoni* enamel and (F) *P. johnstoni* dentin from a wet season specimen, showing obliteration of enamel prisms and dentinal tubular structures by abrasion. Scale bars, 10 μm.

Fig. 4. Phytoliths from fecal pellets of *P. johnstoni*. Scale bar, 100 μm.

tubular structures. The occlusal surfaces were scored by fine, parallel microscratches ranging from 0.2 to 2 μm in width, with the majority below 1 μm in width. Quantification is difficult for such reasons as irregular tooth surfaces, specimen tilt angle, and obliteration of scratches by subsequent ones, but there are commonly as many as 50 parallel scratches along a 100-μm-wide strip. Some larger surface scratches are seen occasionally. Figure 3, E and F, demonstrate enamel and dentin surfaces in a specimen from the middle of the wet season. The surface conditions of the teeth in dry season *P. johnstoni* specimens approach those of *H. brucei* specimens. Figure 3, C and D, show the appearance of the enamel and dentin in a *P. johnstoni* tooth from the beginning of the wet season (end of November). The enamel prism outlines are seen. Dentin tubules are still seen, but are scored by fine scratches that cut into the dentin surface. Coarser scratches about 2 μm across are paralleled by many finer ones.

Thus, the microwear on teeth worn during browsing episodes in *P. johnstoni* resembles that on teeth of browsing *H. brucei*. This wear consists of extremely fine polishing that brings the underlying structures into relief. Grazing during the wet season in *P. johnstoni* is accompanied by a significant change to heavy wear that includes obliteration of surface prismatic and tubular relief by multiple episodes of abrasion by fine particulate material. It is likely that the abrasive material consisted of opaline phytoliths (plant opal), which are known to occur in much larger concentrations in grasses than in many dicotyledonous plants (*7*). Baker *et al.* (*7*) reported that wear on sheep's teeth in New Zealand is probably caused by the abrasive action of opaline phytoliths in the masticated grass, estimating that 10 kg of plant opal passed through individual sheep in 1 year. They also showed that amorphous silica, as found in plant opal, is much harder than the apatite of enamel and dentin (*8*).

Fecal pellets of *P. johnstoni* and *H. brucei* from the Serengeti populations were examined for traces of phytoliths. Six 0.3-g samples of fecal pellets were macerated for 1 week in concentrated nitric acid. After washing in distilled water and alcohol, undigested remnants were floated off the samples by the addition of bromoform, leaving a small residue of dense particles. In the samples of *H. brucei* pellets, hardly any recognizable plant silica was seen. In contrast, samples from *P. johnstoni* pellets were comprised mainly of complete and fractured phytoliths of several types (Fig. 4). The common phytoliths are bulliform and are 50 μm in maximum length. Harpoon-shaped and small dumbbell-shaped ones are encountered, but are less common. There are small rock particles in both species' pellets. These are primarily of quartz, but mica, tourmaline, and augite are also found. The size of these dust particles is 50 to 200 μm. These may have been splashed on leaves during storms, but both species have them in about equal amounts. Since *H. brucei* is almost exclusively a browser, it is more likely that this dust was wind-borne. It is clear that phytoliths are ingested in quantity by *P. johnstoni* and it seems very likely that these silicified plant cells, rather than the dust particles, are the cause of the microscratches, since dust is present in both species' dung. The great majority of the microscratches are not themselves wide enough for a whole phytolith to have been pressed into the surface by occlusal forces. Rather, the scratches must have been caused by protruding edges of phytoliths that appeared when the cells were broken and the grass was sheared between the teeth. Many of the phytoliths in the pellet samples are broken and many more have damaged edges. The agents that fine-polish the tooth surfaces of *H. brucei* and browsing *P. johnstoni* are presumed to be cellulose and lignin.

It is thus possible to distinguish between the patterns of microwear of species that browse and those that graze, even, as in this case, to detect species that graze only during certain seasons. Therefore, examination of microwear on a fossil tooth would give information about the diet of an individual only for the period just before it died—this is another example of the biases that influence paleontological samples. Similar examinations of teeth from browsers and grazers among primates, artiodactyls, and perissodactyls, samples in which the controls are less stringent, also show the differences reported here.

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