Dental microwear and diets of African early \textit{Homo}

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Abstract

Conventional wisdom ties the origin and early evolution of the genus \textit{Homo} to environmental changes that occurred near the end of the Pliocene. The basic idea is that changing habitats led to new diets emphasizing savanna resources, such as herd mammals or underground storage organs. Fossil teeth provide the most direct evidence available for evaluating this theory. In this paper, we present a comprehensive study of dental microwear in Plio-Pleistocene \textit{Homo} from Africa. We examined all available cheek teeth from Ethiopia, Kenya, Tanzania, Malawi, and South Africa and found 18 that preserved antemortem microwear. Microwear features were measured and compared for these specimens and a baseline series of five extant primate species (\textit{Cebus apella}, \textit{Gorilla gorilla}, \textit{Lophocebus albigena}, \textit{Pan troglodytes}, and \textit{Papio ursinus}) and two protohistoric human foraging groups (Aleut and Arikara) with documented differences in diet and subsistence strategies. Results confirmed that dental microwear reflects diet, such that hard-object specialists tend to have more large microwear pits, whereas tough food eaters usually have more striations and smaller microwear features. Early \textit{Homo} specimens clustered with baseline groups that do not prefer fracture resistant foods. Still, \textit{Homo erectus} and individuals from Swartkrans Member 1 had more small pits than \textit{Homo habilis} and specimens from Sterkfontein Member 5C. These results suggest that none of the early \textit{Homo} groups specialized on very hard or tough foods, but that \textit{H. erectus} and Swartkrans Member 1 individuals ate, at least occasionally, more brittle or tough items than other fossil hominins studied.

Keywords: Hominin; Feeding adaptations; \textit{Homo habilis}; \textit{Homo rudolfensis}; \textit{Homo erectus}

Introduction

Diet underlies many of the behavioral and ecological differences that separate primate species (and foraging peoples) from one another, and should therefore be a key to understanding the paleobiology and ecology of early hominins. It follows, then, that changes in feeding adaptations should have also played an important role in the origin and early evolution of the genus \textit{Homo}. While there is considerable interest in the evolution of human diet, the dental evidence for feeding behaviors among the earliest representatives of our genus has received little attention compared with analyses of their australopith predecessors. In this paper, we present the first comprehensive molar microwear analysis of \textit{Homo} specimens from the Plio-Pleistocene of Africa.

Models for the diets of early \textit{Homo}

Researchers have created elaborate scenarios for the origin and early evolution of our genus. Most of these depend on the apparent contemporaneity of early \textit{Homo} species, Oldowan technology, and the spread of \textit{C}_4 grasslands across eastern and southern Africa. According to these models, environmental change provided the motive, and technology offered the opportunity for the origin and adaptive radiation of our genus.
The three commonly recognized species of African early *Homo* have overlapping geochronological ranges, perhaps indicating coexistence over two hundred millennia or more. Most *Homo habilis* specimens come from Olduvai Gorge and Koobi Fora, and date to between ca. 1.87 Ma and 1.65 Ma, although A.L. 666-1 from Hadar possibly extends the range of this species back to 2.33 Ma (Kimbel et al., 1996). Specimens attributed to *H. habilis* at Sterkfontein fall within this time frame (Tobias, 1991). *Homo rudolfensis* has a similar temporal range, with most fossils dating between 1.90 Ma and 1.85 Ma at Koobi Fora. Other specimens from Koobi Fora, the Omo, Chemeron, and Malawi might extend this range to between 2.4 Ma and 1.55 Ma (Wood, 1991a; Bromage et al., 1995; Suwa et al., 1996; Sherwood et al., 2002). East African *Homo erectus* had an even greater temporal span, from 1.89 Ma (or perhaps even 1.95 Ma) at Koobi Fora to less than 660 ka at Baringo (Susman et al., 1983; Wood and Vannoten, 1986; Feibel et al., 1989). *Homo erectus* specimens from Swartkrans also fall within this temporal range (Vrba, 1985; Rightmire, 1990b; Tobias, 1991; Wood, 1991a; McKee et al., 1995).

Most researchers relate the first appearances of these species during the late Pliocene to major episodes of global cooling and drying (Vrba et al., 1995). C₄ grasslands evidently spread across eastern Africa after about 2.5 Ma, concomitant with periodic fluctuations in climate (Cerling, 1992). This change corresponds roughly to the postulated times of the emergence of *H. habilis* and *H. rudolfensis*. Climate may have played a role in the origin of *H. erectus*, too, as this species appeared during a period of significant faunal turnover (Behrensmeyer et al., 1997). Although researchers debate the tempo of this turnover (Potts, 1998), most agree that changes to cooler, more variable climates had a substantial effect on mammalian diversity, including early *Homo*.

The earliest archaeological remains date to about 2.5 Ma, and include both stone tools and cut-marked faunal remains from Ethiopia (de Heinzelin et al., 1999; Semaw et al., 2003). This material demonstrates that Pliocene hominins were making and using stone tools to process animal remains, almost certainly for consumption. While other hominins were present at the time (Walker et al., 1986; Asfaw et al., 1999), most would agree that one or more species of early *Homo* most likely made and used Oldowan technology. The appearance of stone tools suggests an expanded toolkit beyond the perishable items used by living great apes for the procurement or preparation of food (Panger et al., 2002). It is also noteworthy that the earliest large concentrations of stone tools and modified bones at sites such as DK and FLK 22 at Olduvai Gorge and FxJj 1 at Koobi Fora are approximately coincident with the earliest known *H. erectus* (Blumenschine and Masao, 1991).

In sum, there is near synchrony of three events in East Africa approximately 2.5 Ma: 1) the emergence of *Homo habilis* and *H. rudolfensis*; 2) the beginning of the spread of grasslands and increasing climatic variation; and 3) the appearance of the earliest modified stone tools and cut-marked bones. Furthermore, *H. erectus* appears at about the same time as large archaeological concentrations and significant faunal turnover. These concurrent events may or may not be related, but they have served as the basis for scenarios used to explain the origin and early radiation of our genus. Changing environments and an expanded tool kit have been linked with a changing resource base and changing dietary adaptations. These scenarios come in “meat-eating” and “plant-eating” varieties.

**Meat-eating scenarios**

Darwin (1871) considered hunting and meat consumption to have played important roles in human evolution, and many have developed this notion since. The idea is that, as grasslands began to spread and forest resources became scarce, hominins relied more and more on savanna adapted ungulates as a food source. This change in ecology started a feedback loop wherein improved hunting abilities followed an expanded toolkit, increased sociality, and larger brains, which were made possible by increased protein consumption (Washburn, 1963; Lee and DeVore, 1968; Isaac, 1971; Dart and Wolberg, 1971; Daegling and Hylander, 2000; Stanford and Bunn, 2004). These scenarios have become increasingly sophisticated with improved understanding of nutrition and digestive physiology. Some recent models consider possible relationships between meat consumption and brain size in light of tissue energy requirements (Milton, 1987; Leonard and Robertson, 1994; Aiello and Wheeler, 1995). Others stress the role of animal fat as a possible source of long-chain polyunsaturated fatty acids to help form brain tissue (Speth, 1989; Eaton et al., 2002).

**Plant-eating scenarios**

Other researchers have argued that hominins began to focus on xeric plants rather than animals as the savanna spread across eastern and southern Africa during the Plio-Pleistocene (Linton, 1971; Wolpoff, 1973; Coursey, 1973). Indeed, most documented human foragers eat more plant foods than meat (Zihlman and Tanner, 1978). Recent models that emphasize xeric plant consumption by early hominins have focused on underground storage organs, or USOs. The two most common scenarios, the “Grandmother hypothesis” (O’Connell et al., 1999) and the “Cooking hypothesis” (Wrangham et al., 1999), share much in common. Both include a transition from “apelike” to “humanlike” subsistence in *H. erectus*, as evidenced by larger female body mass and a reduction in tooth size.

These models are often sophisticated and elegant, but they do not tell us what early *Homo* ate. We prefer to view them as hypotheses, some of which may be tested with data derived from the hominin fossils themselves. While researchers have considered the dietary implications of tooth size, shape, and mineralized tissue chemistry of early *Homo* (for a review, see Ungar et al., in press), very limited work has been published for these species on one of the most effective and
broadly applied methods for inferring diets of past peoples and fossil species—dental microwear.

Dental microwear of early Homo

Dental microwear research has now been carried out for more than half a century, and numerous studies have documented relationships between the densities, sizes, and shapes of microscopic wear features in teeth and the fracture properties of foods eaten by living primates and other mammals (for reviews, see Teaford, 1991; Rose and Ungar, 1998; Ungar, 2002b). Primates that eat mostly hard, brittle nuts and seeds, for example, have more microwear pitting, whereas those that eat tough leaves often have relatively more microwear striations. Species that consume soft fruits tend to be intermediate in their ratios of pits to scratches (Teaford and Walker, 1984; Teaford, 1988a). Studies of wild populations of primates have shown that microwear can, in fact, reflect rather subtle differences in diet between populations (Teaford, 1985; Teaford and Robinson, 1989; Teaford and Glander, 1991).

There have been few studies of the dental microwear of early Homo, but the limited work that has been done hints at some interesting possibilities. Puech and colleagues (Puech et al., 1983a; Puech, 1984) noted, for example, evidence of enamel and dentine erosion on some molar teeth of *H. habilis* from Olduvai Gorge. This implied to them the consumption of unripe, acidic fruits by these hominins. In another study, Waddle (1988) found high incidences of small microwear pits in the occlusal surfaces of some early Homo molars from Swartkrans (Members 1 and 2). While she considered this study preliminary, its results might be consistent with Walker and Shipman’s (1997) observations of “extreme gouging and battering” in eastern African *H. erectus* cheek teeth. Finally, Martínez et al. (2004) examined buccal surface microwear in *H. habilis* specimens from eastern Africa. Their study focused not on diet reconstruction per se, but rather on the relationship (or lack thereof) between microwear density and inferred age of death. These studies make it clear that much work remains to be done on the dietary implications of dental microwear in early Homo.

Materials and methods

This study presents dental microwear data for all available early Homo molar specimens from eastern and southern Africa. These data are compared with those used in this study (Table 1). The usable fraction of the total sample (ca. 23%) is similar to that found for Plio-Pleistocene monkeys from some of these same sites (Leakey et al., 2003; El Zaataari et al., 2005).

The fossil sample

We examined all available molar teeth of *Homo* specimens from the Plio-Pleistocene of Africa at the National Museum of Ethiopia, the National Museums of Kenya, the National Museum of Tanzania, the Transvaal Museum, and the University of the Witwatersrand. A few specimens were excluded from this study following initial inspection because of obvious postmortem damage to entire occlusal surfaces or because we deemed them too fragile to mold. All other specimens were replicated following standard procedures (see below). Casts of cheek teeth were produced for 83 specimens. These fossils were recovered from 1) Sterkfontein, Swartkrans, and Drimolen in South Africa; 2) Olduvai Gorge in Tanzania; 3) Koobi Fora, West Turkana, Baringo, and Lainyamok in Kenya; and 4) the Omo and Hadar in Ethiopia. Casts of the UR 501 molar teeth from Uraha, Malawi were also prepared (molds courtesy of Tim Bromage).

Tooth replicas were first examined by binocular light microscopy at 50× and, if necessary, at 500× by scanning electron microscopy to determine suitability for microwear analysis. The vast majority of specimens were deemed unsuitable because of taphonomic damage (e.g., etching, erosion) that obscured or obliterated antemortem microwear. This circumstance was most often the case for surface finds and specimens that had been subjected to fluvial transport. Specific criteria used to evaluate occlusal surfaces are presented in detail elsewhere (Teaford, 1988b; King et al., 1999). A few other specimens had to be excluded because they are unworn. Ultimately, we could include with confidence only 18 specimens (*n* = 5 for *Homo erectus*; *n* = 6 for *Homo habilis*; *n* = 3 for early *Homo* from Sterkfontein Member 5C, and *n* = 4 for early *Homo* from Swartkrans Member 1) in this microwear analysis. Those specimens that did not preserve antemortem microwear can be identified by comparing the list of all specimens examined (Appendix I) with those used in this study (Table 1). The usable fraction of the total sample (ca. 23%) is similar to that found for Plio-Pleistocene monkeys from some of these same sites (Leakey et al., 2003; El Zaataari et al., 2005).

Table 1

<table>
<thead>
<tr>
<th>Specimen</th>
<th>Tooth</th>
<th>Formation</th>
<th>Member</th>
<th>Taxonomic attribution</th>
</tr>
</thead>
<tbody>
<tr>
<td>OH 4</td>
<td>LM₁</td>
<td>Olduvai Gorge</td>
<td>Bed I</td>
<td>Homo habilis</td>
</tr>
<tr>
<td>OH 7</td>
<td>LM₁</td>
<td>Olduvai Gorge</td>
<td>Bed I</td>
<td>Homo habilis</td>
</tr>
<tr>
<td>OH 15</td>
<td>RM₁</td>
<td>Olduvai Gorge</td>
<td>Bed II</td>
<td>Homo habilis</td>
</tr>
<tr>
<td>OH 16</td>
<td>LM₁</td>
<td>Lemuta Mb.</td>
<td>Homo</td>
<td>Homo habilis</td>
</tr>
<tr>
<td>OH 41</td>
<td>LM₁</td>
<td>Olduvai Gorge</td>
<td>Bed II</td>
<td>Homo habilis</td>
</tr>
<tr>
<td>Stw 19b</td>
<td>RM₂</td>
<td>Sterkfontein</td>
<td>Dump D-3</td>
<td>Homo habilis</td>
</tr>
<tr>
<td>KMN-ER 807</td>
<td>RM₁</td>
<td>Koobi Fora Fm.</td>
<td>KBS Mb.</td>
<td>Homo erectus</td>
</tr>
<tr>
<td>KMN-ER 820</td>
<td>RM₁</td>
<td>Koobi Fora Fm.</td>
<td>Okote Mb.</td>
<td>Homo erectus</td>
</tr>
<tr>
<td>KMN-WGT 15000</td>
<td>LM₁</td>
<td>Nachukui Fm.</td>
<td>Natoo Mb.</td>
<td>Homo erectus</td>
</tr>
<tr>
<td>OH 60</td>
<td>RM₁</td>
<td>Olduvai Gorge</td>
<td>Bed I</td>
<td>Homo erectus</td>
</tr>
<tr>
<td>SK 15</td>
<td>LM₁</td>
<td>Swartkrans</td>
<td>Mb. 2</td>
<td>Homo erectus</td>
</tr>
<tr>
<td>SE 1508</td>
<td>LM₁</td>
<td>Sterkfontein</td>
<td>Mb. 5C</td>
<td>Homo sp. indet. A</td>
</tr>
<tr>
<td>SE 1579</td>
<td>LM₁</td>
<td>Sterkfontein</td>
<td>Mb. 5C</td>
<td>Homo sp. indet. A</td>
</tr>
<tr>
<td>Stw 80</td>
<td>LP₁</td>
<td>Sterkfontein</td>
<td>Mb. 5C</td>
<td>Homo sp. indet. A</td>
</tr>
<tr>
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<td>LM₁</td>
<td>Swartkrans</td>
<td>Mb. 1</td>
<td>Homo sp. indet. B</td>
</tr>
<tr>
<td>SK 45</td>
<td>RM₁</td>
<td>Swartkrans</td>
<td>Mb. 1</td>
<td>Homo sp. indet. B</td>
</tr>
<tr>
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<td>LM₁</td>
<td>Swartkrans</td>
<td>Mb. 1</td>
<td>Homo sp. indet. B</td>
</tr>
<tr>
<td>SK 2635</td>
<td>LM₁</td>
<td>Swartkrans</td>
<td>Mb. 1</td>
<td>Homo sp. indet. B</td>
</tr>
</tbody>
</table>

* Stw 19b was recovered from Dump D-3, while associated specimens Stw 33 (LP₁) and Stw 34 (LM₁) are recorded as having been recovered from Dump D-18, which Kuman and Clarke (2000) believe must be an error. Dump D-3 breccia is consistent with its derivation from Member 5A.
Specimen attributions

There is currently no consensus among paleoanthropologists concerning either the number of Pliocene—early Pleistocene species attributable to Homo or the hypodigms of these taxa (Stringer, 1986; Lieberman et al., 1988; Chamberlain, 1989; Groves, 1989; Rightmire, 1990a; Miller, 1991; Wood, 1991a,b, 1992; Rightmire, 1993; Grine et al., 1993, 1996; Blumenschine et al., 2003). While a comprehensive review of the arguments is beyond the scope of this paper, the taxonomic attribution of the specimens needs to be discussed because it can have marked effects on the interpretation of microwear data.

We recognize at least three species of early Homo in the Plio-Pleistocene deposits of eastern and southern Africa, including H. habilis, H. rudolfensis, and H. erectus (=Homo ergaster). We concur with Wood (1991a, 1992, 1993) and others in distinguishing two species among the craniodental specimens traditionally regarded (Howell, 1978; Tobias, 1991) as Homo habilis, namely H. habilis sensu stricto and H. rudolfensis. On the other hand, we do not distinguish H. ergaster as a separate species from H. erectus; rather, we agree with those that observe continuous variation among these fossils, and regard them as constituting a single species lineage (e.g., Rightmire, 1990b; Bräuer and Mbua, 1992; Bräuer, 1994).

While some have suggested that there is more than one species in the traditional H. habilis hypodigm from Olduvai Gorge (Leakey, 1976; Rightmire, 1993; Blumenschine et al., 2003), we accept the attributions of Wood (1991a, 1992, 1993) and Tobias (1991), who have undertaken the most exhaustive studies of these fossils to date. Thus, OH 4, OH 7, OH 15, OH 16, and OH 41 are considered to represent H. habilis for the purposes of the analyses presented here. None of the specimens from the Shungura Formation, Koobi Fora Formation, and Chiwondo Beds that have been attributed or likened to H. rudolfensis by Wood (1991a, 1992, 1993), Bromage et al. (1995), and Suwa et al. (1996) preserve molars that are useful for the study of microwear. The usable dental sample for H. erectus molars from eastern Africa includes two specimens from Koobi Fora (KNM-ER 807, KNM-ER 820) and the Nariokotome boy (KNM-WT 15000). One additional specimen from Olduvai Gorge, OH 60, has been attributed to H. erectus on the basis of very small size (Ungar et al., 2001).

Most workers that have studied the hominin remains from Sterkfontein have attributed or likened the Stw 53 cranium from Member 5A (Partridge, 2000) to H. habilis (Howell, 1978; Tobias, 1991). The Stw 19b molar was recovered from a breccia dump, the composition of which suggests that it is likely to have come from Member 5A, which is referred to by Kuman and Clarke (2000) as the “Stw 53 infill.”

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1 Homo habilis and H. rudolfensis may not display “adaptive coherence” with Homo sapiens (Wood and Collard, 1999). However, there is strong evidence that they share a closer evolutionary relationship with later species of Homo than with any currently recognized species of Australopithecus (Strait and Grine, 2001). As such, the generic assignment of H. habilis and H. rudolfensis is largely a matter of personal preference and does not affect the question of whether or not they are distinct species.

We follow the attribution of specimens from this particular sedimentary unit to H. habilis (Howell, 1978; Tobias, 1991; Kimbel et al., 1997).

The taxonomy of other Homo specimens from Sterkfontein is less certain. Tobias (1965) likened specimens from Robinson’s excavations of the “Extension Site” [Member 5C of Partridge (2000)] to H. habilis. Kuman and Clarke (2000), on the other hand, suggested that the Stw 80 mandible, excavated from this deposit by Hughes, is similar to the Swartkrans Member 1 jaw, SK 15, which has been attributed to H. erectus (or H. ergaster) by most workers (Howell, 1978; Rightmire, 1990a; Kuman and Clarke, 2000). In addition to Stw 80, a number of isolated teeth have been recovered from Sterkfontein Member 5C (Stw 82, SE 1508, and SE 1579). Because there is a lack of consensus or empirical evidence pertaining to the specific attribution of these Member 5C specimens, we treat them as a separate group.

The taxonomy of Swartkrans specimens that belong to the genus Homo has been reviewed recently by Grine (2005). Most workers accept that the Member 2 fossils, including SK 15, are attributable to H. erectus (Robinson, 1961; Howell, 1978; Rightmire, 1990a; Tobias, 1991; Wood, 1991a). We follow these researchers, and include SK 15 in that species. On the other hand, there is a notable lack of consensus regarding the specific attribution(s) of the Swartkrans Member 1 specimens. They have recently been referred to H. erectus, H. habilis, or possibly a novel species that is not currently recognized in the Plio-Pleistocene deposits of eastern Africa (Howell, 1978; Walker, 1981; Clarke, 1985; Bilsborough and Wood, 1988; Tobias, 1991; Grine et al., 1993, 1996; Kimbel et al., 1997; Grine, 2001). Because of this debate, we treat the Swartkrans Member 1 specimens (SK 27, SK 45, SK 847, SK 2635) as a separate group. The descriptive statistics calculated for microwear variables for each of these specimens are presented in Appendix II to allow others to group specimens and perform analyses according to their own preferred taxonomies.

The baseline sample

The baseline sample used in this analysis was divided into four groups: extant African apes, “hard-object” feeding monkeys, USO-eating chacma baboons, and archaeological samples of protohistoric peoples (see Appendix II for a list of specimens).

All of the extant primate species studied here have been analyzed for dental microwear patterns previously (Teaford and Walker, 1984; Teaford, 1988a; Daegling and Grine, 1999). These taxa were studied by different observers using different analytical techniques. Direct comparison of published results with one another, or with results for fossils presented here would, however, be problematic. Overall, interobserver error rates are about 9% using a given technique, and results obtained through different quantification protocols vary by about 17% (Grine et al., 2002). This should serve as a cautionary tale for those who assemble and compare microwear data from different research projects, especially those that employ different
techniques of microwear analysis. In order to ensure the legitimacy of our baseline series for interpreting the early Homo results, we analyzed both the fossils and all extant taxa (including those for which data are already available in the literature) using the same observers and the same analytical protocol (see below).

The African apes were included in the comparison because they have been suggested to be reasonable models for early hominin behavior, especially given phyletic affinities (see Rodman, 2002, and references therein). We analyzed the subspecies Pan troglodytes troglodytes and Gorilla gorilla beringei because of their contrasting diets (see below). Cebus apella and Lophocebus albigena were included because of suggestions that early hominins may have evolved as hard-object feeders (Kay, 1981). Papio ursinus was included because of recent emphasis on USOs as an important or keystone resource for early Homo (see above). Finally, two human groups were included because of plausible similarities in subsistence practices between recent foraging peoples and early Homo. The Arikara and Aleut were selected because their diets are well documented and differ in the degree of animal tissue consumption. This difference is important, given hypotheses concerning the role of meat in the diets of early Homo.

The diets of these peoples and nonhuman primates are recorded with varying degrees of detail in the literature. Furthermore, interpretations of microwear results for museum specimens based on naturalistic studies of other individuals in the wild should not be pushed too far. Primate diets can be affected by idiosyncratic food preferences and differences in microhabitat, study site, observation technique, season, and even year of observation (Olupot, 1998; Doran et al., 2002; Chapman et al., 2002). Because we do not have specific feeding information for the individuals considered in this analysis, summaries presented here should only be taken as rough guides when interpreting microwear.

Gorilla gorilla beringei is the most folivorous of the gorilla subspecies. Specimens included in this study come from a very well-documented sample housed at the U.S. National Museum of Natural History. These individuals were exhumed and collected in the Virunga Mountains in 1979 and identified by Dian Fossey and Jay Matternes. Many were studied in the wild, with individual names recorded for specimens (Fossey, 1983). Virunga mountain gorilla diets are dominated by leaves and stems, which often make up more than 90% of foods eaten (Fossey and Harcourt, 1977; Vedder, 1984; Watts, 1984, 1990). Mountain gorillas living at lower elevations, such as at Bwindi, take more fruits as availability permits (Robbins and McNeillage, 2003; Stanford and Nkurunungi, 2003), but even these populations eat mostly leaves.

Pan troglodytes troglodytes, in contrast, consumes mostly fruits. The sample studied here comes from the Hammon-Todd Osteological Collection at the Cleveland Museum of Natural History. Most specimens were collected near Abong Mbang in eastern Cameroon. Not a great deal is known about this subspecies in Cameroon, but the central African chimpanzee has been the subject of long term study in the Lopé Reserve, Gabon, and the Ndoki Forest, Congo. Diets reported for chimpanzees at Lopé and Ndoki are very similar, and are dominated by fruits (between 70% and 80% of the diet; Tutin and Fernandez, 1985; Kuroda, 1992; Tutin et al., 1997). Other foods eaten include leaves (12%-13%), seeds (5%-10%), and occasionally pith and flowers.

Cebus apella and Lophocebus albigena are commonly included in studies of primate functional morphology (Kay, 1981; Dumont, 1995) and dental microwear (Teaford and Walker, 1984; Teaford, 1988a) as “hard-object” specialists, with adaptations for crushing brittle items, especially nuts. In fact, these primates eat a lot of things, although they do include more hard, brittle foods in their diets than do other primates living in the forests with them. Capuchin and mangabey specimens examined for this study are all housed at the U.S. National Museum of Natural History.

The C. apella specimens analyzed in this study consist of wild-shot individuals from Amazonas in Venezuela and from Demerara-Mahaica and the headwaters of the Essequibo River in Guyana. There is no information on season of capture. Eisenberg (1989) summarized their diets as comprising 66% fruit flesh, 25% seeds, 7% pith, and occasional insects and other prey. While Brown and Zunino (1990) reported that some brown capuchins in Argentina consume more bromeliad leaves and insects, specimens included in the microwear study were restricted to the tropical part of their distribution, where C. apella is noted to consume hard, brittle foods more often than do other sympatric primate species (Terborgh, 1983; Janson and Boinski, 1992).

Lophocebus albigena specimens examined for this study were wild-shot in Congo and Uganda. All specimens examined were collected in the early and middle 20th century during the months of November and December. Grey-cheeked mangabeys are predominately frugivorous, with fruits (including seeds) constituting about 60% of the annual diet at sites ranging from the Dja Reserve in Cameroon to Lopé in Gabon and Kibale in Uganda (Ham, 1994; Olupot, 1998; Poulsen et al., 2001). Insects make up nearly 30% of the diet at these sites, with leaves and flowers each typically constituting about 5% of the diet. While the quantity of hard seeds eaten by L. albigena varies by site and season in some places, seed-eating makes up nearly 60% of feeding observations at the Dja Reserve during the season that includes November and December (Poulsen et al., 2001). Furthermore, recent mechanical properties testing has shown that grey-cheeked mangabeys at Kibale consume more puncture-resistant foods (both seeds and bark) than eaten by sympatric guenons at times of resource scarcity (Lambert et al., 2004). It is no wonder, then, that these mangabeys can frequently be located in the forest by the sound of crushing nuts (Waser, cited in Kay, 1981).

Papio ursinus is often considered a USO specialist, especially in the dry season. The chacma baboon sample used in this study comes from the Transvaal Museum in Pretoria, and has excellent provenience. Details can be found in Daegling and Grine (1999). These individuals were all collected during the dry season from Messina and the D’nyala Reserve in Limpopo Province, South Africa, and the Rustenburg Provincial Nature Reserve in Northwest Province, South Africa.
Hypogeous tubers, bulbs, and roots account for up to 90% of the *Papio ursinus* diet at that time of year (Whiten et al., 1987; Byrne et al., 1993).

The human groups considered here have already been documented to show diet/tooth-use-related differences in incisor microwear (Ungar and Spencer, 1999). All human specimens analyzed are housed at the U.S. National Museum of Natural History. The Aleut included in this study were collected by Hrdlička (1945) during his expeditions to the Aleutian Islands. Most individuals studied are protohistoric, living after AD 1700 (McCartney, pers. comm.). Ethnohistorical accounts of Aleuts record an almost exclusively animal (mostly marine) subsistence base, including both fresh and dried fish, mollusks, and sea mammals. This diet was occasionally supplemented with land resources, including rodents, foxes, and edible tubers (Hrdlička, 1945; Laughlin, 1963). The Aleut are well known for their repetitive, high magnitude tooth-loading of animal tissues. Veniaminov (cited in Hrdlička, 1945) noted, for example, that the Aleut call the month of March *Kisiagnunak*, meaning “when they chew straps.”

Most of the Arikara examined were collected by Stirling from the Mobridge Site (39WW1) and probably date to AD 1600—1700 (Wedel, 1955; Jantz, 1973). The Arikara of the Mobridge Site made ample use of both plant and animal foods. They had a mixed subsistence base, with animal and plant products each representing about half of the yearly diet. Plant foods eaten included wild vegetation (e.g., black cherries, peppers, grapes, pumpkin, and *Chenopodium*) and some cultigens (maize, beans, squash, and sunflowers) (Hurt, 1969; Meyer, 1977; Blakeslee, 1994; Tuross and Fogel, 1994). Still, this Plains group ate large amounts of bison, which were cut into strips and dried (Meyer, 1977). They also hunted smaller game, including deer, antelope, and jackrabbit. Thus, the two foraging groups differed in degree of meat consumption, with the Aleut relying much more on animal tissues than the Arikara.

**Casting procedure**

High resolution replicas of the fossil and baseline specimens were prepared following established procedures (Grine and Kay, 1987; Teaford and Oyen, 1989c; Ungar, 1996). Original teeth were cleaned with cotton swabs soaked in alcohol or acetone to remove dirt and preservatives as necessary. Molds were then made of occlusal crowns using President’s Jet regular body polyvinylsiloxane dental impression material (Coltène-Whaledent Corp., Mawah, NJ), and allowed to degas before casting. Replicas were then poured using Epotek 301 (Epoxy Technologies, Inc., Billerica, MA), a high-resolution epoxy resin and hardener. Resulting casts were mounted on aluminum SEM stubs with glyptal and colloidal graphite (to ensure conductivity) and sputter-coated with approximately 20 nm of gold.

**Specimen imaging**

Molar replicas were then examined using an Amray 1810 SEM at an accelerating voltage of 20—25 keV, a working distance of 12—20 mm, and a magnification of 500 × . Surfaces examined were oriented nearly perpendicular to the electron beam to minimize feature foreshortening (Gordon, 1988).

Crushing surfaces of early *Homo* permanent cheek teeth that preserved antemortem microwear were recorded on Polaroid Type 55 Positive-Negative film. Analyses were restricted to M1s and M2s for the baseline groups, and all available molars (and one P4) for the fossil samples (see Table 1). An ideal study would be restricted to a single tooth type to minimize analytical “noise” (Gordon, 1988; Bullington, 1991), but this was not possible given the small sample sizes available for early *Homo*. Inter-facet variation was controlled by restricting analysis to “Phase II” facets (Gordon and Walker, 1983). These facets have been particularly effective in differentiating primates by diet (Teaford, 1988a).

Specimens examined in this study combined variably worn teeth, following usual practice. Previous analyses of dental microwear in early hominins have failed to find any relationship between degree of gross wear and conventional microwear measurements (Grine, 1986). Furthermore, recent work on a sample of known-age wild primates has demonstrated no age-related effects on microwear patterns (Nystrom et al., 2004).

Photomicrographs were scanned at 200 DPI using a photo scanner and cropped to 640 × 480 pixels. Resulting images had a resolution of 0.25 μm per pixel, and a sample area of 0.02 mm² of the original occlusal surface. Two photomicrographs were taken for each specimen to increase the sample area whenever sufficient microwear was preserved.

**Data collection**

Images were analyzed using Microware 4.02 (Ungar, 2002a). A mouse-driven pointer was used to define four points for each feature: two each to identify the endpoints of the major and minor axes. Axis lengths and orientations were calculated, and standard descriptive statistics were recorded for each image. Pits were distinguished from scratches on the basis of a 4:1 length to breadth ratio (Teaford, 1988a). Descriptive statistics presented here include: 1) overall feature measurements (major and minor axis mean lengths and standard deviations), 2) percentage of all features that are pits; 3) pit measurements (length and width means and standard deviations); and 4) striation measurements (length and breadth means and standard deviations and mean orientation vector length).

All photomicrographs were digitized by three observers (MFT, PSU, and SEZ). Values for individual specimens were averaged to reduce measurement errors inherent in conventional dental microwear analyses (Grine et al., 2002; see discussion above).

**Statistical analyses**

Statistical analyses focused on identifying significant microwear differences among baseline groups with known differences in diet, assessing microwear variation between...
**H. habilis** and **H. erectus**, and determining how data for the fossil species cluster relative to those for the baseline groups. Four variables that have been shown in the past to be useful for distinguishing living species with different diets were considered here: 1) pit percentage, 2) striation breadth, 3) pit width, and 4) mean orientation vector length (Walker and Teaford, 1989; Ungar, 1994; Teaford et al., 2001; Rafferty et al., 2002).

**Analyses of the baseline groups**

All data were rank-transformed before analysis to mitigate the possible effects of violating assumptions associated with parametric statistical tests (Conover and Iman, 1981). Data for the four variables were compared among species (based on specimen values in Appendix II) using a multivariate analysis of variance model (MANOVA) with taxon as the dependent variable and measurement means for each individual as the replicates (Neff and Marcus, 1980). Results indicated whether the taxa differed significantly in overall microwear patterning. Single classification ANOVAs on each variable and multiple comparisons tests were used to determine sources of significant variation (Sokal and Rohlf, 1995). Because baseline groups were chosen for their diet and expected microwear differences, Fisher’s least significant difference (LSD) a priori tests were used to compare species. Tukey’s honestly significant difference (HSD) post hoc tests were also run to balance risks of Type I and Type II errors (Cook and Farewell, 1996).

**Differences between early Homo species**

Rank-transformed microwear data for **H. habilis**, **H. erectus**, and the early **Homo** specimens from Sterkfontein Member 5C and Swartkrans Member I were compared using the same MANOVA scheme described above for comparisons of baseline groups. Only variables that showed significant variation among baseline groups were included in this analysis. The ANOVAs for each variable were used to determine sources of significant variation, and Tukey’s HSD post hoc tests were used to compare pairs of taxa.

**Comparisons of the fossil data and the baseline series**

Hierarchical cluster analyses were performed on the living and fossil taxa, using each of the microwear variables that showed significant variation among taxa in the ANOVA models. Variables were considered separately because they evince different scales. Euclidean distance and complete linkage were used, following Fortelius and Solounias (2000). Specimens assigned to **H. habilis** and **H. erectus** and samples from Sterkfontein Member 5C and Swartkrans Member 1 were considered separately.

**Results**

Raw data for average feature dimensions, pit percentages, and pit and striation measurements for each specimen are presented in Appendix II. Example photomicrographs are illustrated in Fig. 1. Summary statistics are presented in Table 2 and illustrated in Figs. 2–4. Results of statistical analyses are given in Tables 3–4.

**The baseline series**

Results of statistical analyses for the baseline sample are presented in Table 3. All MANOVA test statistics indicate significant variation in the model. In other words, microwear patterns vary among the taxa. Individual ANOVAs show significant variation in feature sizes (both pit width and striation breadth) and pit percentage. The taxa do not differ in striation mean vector length (i.e., orientation homogeneity).

Multiple comparisons tests show the sources of the observed variation. First, pit widths indicate clusters of baseline groups. **Gorilla**, **Cebus**, and **Pan** cluster together as one group, and Arikara, **Lophocebus**, **Papio**, and Aleut cluster in the other. In nearly all cases, each member of one group differs significantly from each member of the other according to both Fisher’s LSD and Tukey’s HSD test results. Striation breadths also discriminate between two groups, which are the same as those for pit width, except that the Arikara cluster with **Gorilla**, **Cebus**, and **Pan** rather than with the Aleut, **Papio**, and **Lophocebus**. Differences between the Aleut and those samples with narrower striations are only marginally significant. These groupings are clearly illustrated by the hierarchical cluster analyses (see Fig. 4).

The multiple comparisons results for the pit percentage analysis indicate three groups, although these are not as clearly separated as are the two groups identified for the feature size variables: 1) **Cebus** and **Lophocebus**, 2) Aleut, **Pan**, and **Papio**, and 3) **Gorilla** and Arikara. **Cebus** and **Lophocebus** have the highest mean pit percentage values, whereas **Gorilla** and Arikara have the lowest values (i.e., the highest proportion of striations). Pit percentages differ significantly between taxa in different groups but not within these groups. Thus, these two groups can be clearly separated. The Aleut, **Pan**, and **Papio** samples have intermediate values. All three differ from **Gorilla** (though **Pan** only marginally). Arikara differs marginally from **Papio**, and **Pan** differs from **Cebus** and **Lophocebus**. The Aleut-**Pan-Papio** group may be considered tenuous because **Papio** does not differ significantly from **Cebus** or **Lophocebus**, and **Pan** does not differ from the Arikara sample. Still, these groupings are supported by the cluster analyses presented in Fig. 4.

In sum, the baseline samples fall into six groups on the basis of pit percentage and feature size (Fig. 3). The mangabeys have high pit percentages and large features, the baboons and Aleuts have intermediate pit percentages and large features, the capuchins have high pit percentages but smaller features, the chimpanzees have intermediate pit percentages and small features, and the gorillas have low pit percentages and small features. The Arikara have low pit percentages, with large pits but narrow striations on average.

**Early Homo comparisons**

Results comparing the four hominin groups are presented in Table 4. The MANOVA results indicate significant
variation in the model. The ANOVA tests indicate significant variation in pit percentage but not pit width or striation breadth. Pairwise comparisons indicate that H. erectus from eastern Africa and Swartkrans Member 2 have higher pit percentages than do H. habilis from eastern Africa and Sterkfontein Member 5A. Likewise, specimens from Swartkrans Member 1 have higher pit percentages than do those from Sterkfontein Member 5C. On the other hand, pit percentages for Sterkfontein Member 5C do not differ significantly from those for H. habilis (from eastern Africa and Sterkfontein Member 5A), and those for Swartkrans Member 1 do not differ significantly from those for H. erectus (from eastern Africa and Swartkrans Member 2).

Figure 4 presents the hierarchical cluster analyses for each variable, including data for the baseline groups and using the fossil specimen attributions listed in Appendix II. There are two distinct clusters for pit width. Papio, Lophocebus, and the Aleut (those taxa with the largest pits) are clearly separate from all other taxa, including the fossil hominins. There may also be a second-order pit width clustering that separates H. habilis, Sterkfontein Member 5C specimens, Arikara, and Pan from Gorilla, Cebus, H. erectus, and Swartkrans Member 1 specimens. This clustering is supported by a significant difference between Arikara on the one hand and Cebus and Gorilla on the other. On the other hand, the lack of significant variation among the hominins, or between Pan, Cebus, and Gorilla makes this unlikely.

There are also two distinct clusters for striation breadth. These clusters accord well with those suggested by statistical analyses of striation breadth for the baseline series. Papio, Lophocebus, and the Aleut all have thicker striations on average than do the other samples. There may, in addition, be a second-order striation breadth cluster separating the Aleut from Papio and Lophocebus. The lack of significant differences between the Aleut and either the baboons or mangabeys makes this unlikely, however. All of the hominins have lower mean striation breadth values, clumping together with Cebus, the Arikara, Pan, and Gorilla.

Finally, there are also two distinct clusters for pit percentage. Homo habilis and Sterkfontein 5C specimens cluster with the Arikara and Gorilla samples, separate from all other groups analyzed. There also appears to be a secondary
clustering of *H. erectus* and the Swartkrans Member 1 specimens with the Aleut, *Pan*, and especially *Papio*. This cluster appears to be distinct from *Lophocebus* and *Cebus*. This second-order clustering does accord well with those suggested by statistical analyses of pit percentage in the baseline series.

**Discussion**

The results presented here for the fossil hominins can be interpreted in terms of relationships between diet and microwear for the baseline series. Interpretations can then be considered relative to those derived from other lines of evidence, and used to evaluate recent models for the diets of early *Homo*.

**Interpretation of the microwear results**

**The baseline series**

The baseline groups varied in microwear pit percentages, pit widths, and striation breadths. Some of these differences provide insights into the relationships between microwear and diet in nonhuman primates and foraging peoples that can be used to infer aspects of diet in early *Homo*.

Pit percentage is the most widely and successfully used microwear attribute for distinguishing mammals with different diets. Theory dictates that microwear feature linearity should reflect the angle of approach of opposing facets, and that the angle of approach should reflect the mechanical properties of foods to be fractured (Grine, 1981). Opposing facets that

**Table 2**

<table>
<thead>
<tr>
<th>Group</th>
<th>Major length</th>
<th>Minor length</th>
<th>Pit width</th>
<th>Scratch breadth</th>
<th>Scratch r</th>
<th>Pit %</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aleut</td>
<td>X 18.5</td>
<td>3.3</td>
<td>6.3</td>
<td>1.5</td>
<td>0.54</td>
<td>45.9</td>
</tr>
<tr>
<td>(n = 5)</td>
<td>s 3.95</td>
<td>0.50</td>
<td>1.07</td>
<td>0.21</td>
<td>0.086</td>
<td>10.01</td>
</tr>
<tr>
<td>Arikara</td>
<td>X 27.0</td>
<td>2.1</td>
<td>4.9</td>
<td>1.3</td>
<td>0.45</td>
<td>30.8</td>
</tr>
<tr>
<td>(n = 5)</td>
<td>s 11.15</td>
<td>0.68</td>
<td>1.30</td>
<td>0.24</td>
<td>0.213</td>
<td>19.37</td>
</tr>
<tr>
<td>Cebus</td>
<td>X 11.1</td>
<td>2.2</td>
<td>3.2</td>
<td>1.2</td>
<td>0.49</td>
<td>59.1</td>
</tr>
<tr>
<td>(n = 5)</td>
<td>s 2.22</td>
<td>0.41</td>
<td>0.65</td>
<td>0.14</td>
<td>0.196</td>
<td>8.74</td>
</tr>
<tr>
<td>Gorilla</td>
<td>X 29.7</td>
<td>1.7</td>
<td>2.8</td>
<td>1.3</td>
<td>0.56</td>
<td>25.5</td>
</tr>
<tr>
<td>(n = 5)</td>
<td>s 4.64</td>
<td>0.44</td>
<td>1.06</td>
<td>0.16</td>
<td>0.185</td>
<td>9.32</td>
</tr>
<tr>
<td>Lophocebus</td>
<td>X 16.0</td>
<td>4.3</td>
<td>5.8</td>
<td>1.9</td>
<td>0.56</td>
<td>59.2</td>
</tr>
<tr>
<td>(n = 5)</td>
<td>s 2.95</td>
<td>1.07</td>
<td>0.97</td>
<td>0.23</td>
<td>0.131</td>
<td>11.03</td>
</tr>
<tr>
<td>Pan</td>
<td>X 18.8</td>
<td>2.2</td>
<td>3.7</td>
<td>1.2</td>
<td>0.49</td>
<td>43.7</td>
</tr>
<tr>
<td>(n = 5)</td>
<td>s 5.98</td>
<td>0.38</td>
<td>1.12</td>
<td>0.09</td>
<td>0.190</td>
<td>5.08</td>
</tr>
<tr>
<td>Papio</td>
<td>X 17.9</td>
<td>3.8</td>
<td>5.9</td>
<td>1.8</td>
<td>0.47</td>
<td>48.4</td>
</tr>
<tr>
<td>(n = 5)</td>
<td>s 3.51</td>
<td>1.40</td>
<td>0.99</td>
<td>0.81</td>
<td>0.083</td>
<td>16.36</td>
</tr>
<tr>
<td><em>H. habilis</em></td>
<td>X 23.8</td>
<td>2.4</td>
<td>4.1</td>
<td>1.3</td>
<td>0.54</td>
<td>37.5</td>
</tr>
<tr>
<td>(n = 6)</td>
<td>s 6.07</td>
<td>0.53</td>
<td>1.06</td>
<td>0.15</td>
<td>0.092</td>
<td>5.99</td>
</tr>
<tr>
<td><em>H. erectus</em></td>
<td>X 15.0</td>
<td>2.2</td>
<td>3.1</td>
<td>1.3</td>
<td>0.48</td>
<td>50.2</td>
</tr>
<tr>
<td>(n = 5)</td>
<td>s 3.34</td>
<td>0.30</td>
<td>0.63</td>
<td>0.12</td>
<td>0.124</td>
<td>4.47</td>
</tr>
<tr>
<td>Sterk M. 5</td>
<td>X 22.3</td>
<td>2.4</td>
<td>4.0</td>
<td>1.4</td>
<td>0.51</td>
<td>36.2</td>
</tr>
<tr>
<td>(n = 3)</td>
<td>s 4.77</td>
<td>0.63</td>
<td>0.86</td>
<td>0.26</td>
<td>0.065</td>
<td>12.68</td>
</tr>
<tr>
<td>Swart M. 1</td>
<td>X 15.8</td>
<td>2.3</td>
<td>3.3</td>
<td>1.3</td>
<td>0.40</td>
<td>50.1</td>
</tr>
<tr>
<td>(n = 4)</td>
<td>s 0.95</td>
<td>0.23</td>
<td>0.14</td>
<td>0.125</td>
<td>0.120</td>
<td>4.88</td>
</tr>
</tbody>
</table>

* Means (X) and standard deviations (s) for feature lengths (major and minor axes), pit and striation breadths, striation orientation concentration (r), and percentage incidence of pitting (taxon averages). All linear measurements are in μm. See Appendix II for information on individual specimens.

![Fig. 2. Microwear pit percentage (top), pit width (middle), and striation breadth (bottom) mean values for baseline groups.](image)

![Fig. 3. Distinguishing microwear criteria for baseline groups.](image)

1. Arikara have large pits; 2. Arikara have broad striations.
shear past one another to slice tough foods should be dominated by scratches from abrasives that are dragged along tooth surfaces. In contrast, opposing facets that approach perpendicular to one another to crush hard, brittle foods should be dominated by pits. Indeed, many studies have shown that mammals that prefer hard, brittle foods have higher pit percentages than those that usually eat soft, tough items (Teaford and Walker, 1984; Teaford, 1988a; Van Valkenburgh et al., 1990; Strait, 1993; Crompton et al., 1998).

The pit percentage results presented here make sense given documented differences in diet and subsistence practices. *Cebus apella* and *L. albigena*, for example, have high pit percentages, as expected for seasonal “hard-object” feeders (Terborgh, 1983; Janson and Boinski, 1992; Poulsen et al., 2001; Lambert et al., 2004). *Gorilla gorilla beringei* specimens have low pit percentages (i.e., high striation counts), as expected for primates with diets dominated by tough leaves and stems (Fossey and Harcourt, 1977; Vedder, 1984; Watts, 1990; Elgart-Berry, 2004). *Pan troglodytes* individuals are intermediate in microwear pit percentage, and are intermediate in the average fracture properties of the foods they consume (Tutin and Fernandez, 1985; Kuroda, 1992; Tutin et al., 1997).

### Table 3

**Extant primate microwear comparisons**

<table>
<thead>
<tr>
<th>Effect</th>
<th>Statistic</th>
<th>df</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wilks’ λ</td>
<td>0.059</td>
<td>24, 88</td>
<td>4.609</td>
<td>0.000</td>
</tr>
</tbody>
</table>

**B. Individual ANOVAS**

<table>
<thead>
<tr>
<th>Effect</th>
<th>SS</th>
<th>df</th>
<th>MS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pit width</td>
<td>2458</td>
<td>6</td>
<td>410</td>
<td>10.313</td>
<td>0.000</td>
</tr>
<tr>
<td>Striation breadth</td>
<td>2083</td>
<td>6</td>
<td>347</td>
<td>6.544</td>
<td>0.000</td>
</tr>
<tr>
<td>Striation r</td>
<td>220</td>
<td>6</td>
<td>37</td>
<td>0.307</td>
<td>0.928</td>
</tr>
<tr>
<td>Pit percentage</td>
<td>2042</td>
<td>6</td>
<td>340</td>
<td>6.239</td>
<td>0.000</td>
</tr>
</tbody>
</table>

**C. Multiple comparisons tests (matrices of pairwise mean differences)**

<table>
<thead>
<tr>
<th>Effect</th>
<th>Aleut</th>
<th>Arikara</th>
<th>Cebus</th>
<th>Gorilla</th>
<th>Lophocebus</th>
<th>Pan</th>
<th>Papio</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pit width</td>
<td>–7.6</td>
<td>–20.2†</td>
<td>–12.6†</td>
<td>–22.1†</td>
<td>–14.5†</td>
<td>–1.9</td>
<td></td>
</tr>
<tr>
<td>Striation breadth</td>
<td>–3.4</td>
<td>14.2</td>
<td>4.2</td>
<td>16.8†</td>
<td>18.7†</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pit percentage</td>
<td>–17.3†</td>
<td>–9.7†</td>
<td>2.9</td>
<td>4.8</td>
<td>–13.9†</td>
<td>–3.6</td>
<td>–0.2</td>
</tr>
<tr>
<td>Striation breadth</td>
<td>–14.2†</td>
<td>–12.6†</td>
<td>1.6</td>
<td>–11.0†</td>
<td>3.2</td>
<td>1.6</td>
<td></td>
</tr>
<tr>
<td>Pit percentage</td>
<td>–11.5†</td>
<td>2.7</td>
<td>11.1</td>
<td>–0.5</td>
<td>–18.2†</td>
<td>1.3</td>
<td>15.5†</td>
</tr>
</tbody>
</table>

† Fisher’s LSD test p ≤ 0.05.
‡ Fisher’s LSD and Tukey’s HSD test p ≤ 0.05.

Fig. 4. Hierarchical cluster analyses for baseline and fossil groups: pit percentage (top), pit width (middle), and striation breadth (bottom) mean values for baseline groups. See Appendix II for fossil specimen designations.
they are hard and brittle or coated with large-grained exogenous grit (Daegling and Grine, 1999). The results for all of these taxa are consistent with previous studies of microwear (Teaford and Walker, 1984; Teaford, 1988a; Daegling and Grine, 1999).

The human samples may also be understood in this context. While pit percentage values do not differ significantly between the groups, the high variance in the Arikara values probably correlates with their greater dietary variation (Hrdlička, 1945; Laughlin, 1963; Blakeslee, 1994; Tuross and Fogel, 1994), which, in turn, may have masked differences between these groups, especially given the small samples analyzed here. The significant difference between the Arikara and Cebus and Lophocebus because repetitive loading and forceful chewing may also cause pits (Puech et al., 1981, 1983b; Teaford and Oyen, 1989a; Teaford and Runestad, 1992; Rafferty et al., 2002). This result may be consistent with Spencer and Ungar’s (2000) suggestion, based on differences in pit size might then help to distinguish between primates whose diets include hard, brittle items and those whose diets comprise tough foods, with the former showing larger microwear pits. More recently, Rafferty et al. (2002) showed high incidences of prism-sized microwear pits for primate species that routinely feed on tough foods.

According to this interpretation, Gorilla and Pan should have smaller pits than Lophocebus and Papio, and they do. On the other hand, C. apella should have larger pits than the apes, as was reported by Teaford (1988a) in an earlier study. They do not. Either pit size is not as good a marker as might be expected—i.e., the large number of features in Cebus apella effectively swamps the signal from large pits—or the individuals studied here were collected at a time or place when they were feeding on tough rather than hard-brittle foods. Small absolute body size (and consequent low maximum occlusal force) does not explain the small pit size in C. apella, as there does not appear to be a relationship between primate body mass and microwear feature dimensions, even within broad dietary categories (e.g., Teaford, 1988a). We expect that studies of larger samples using new 3-D microwear analysis techniques (Ungar et al., 2003) will help resolve this issue.

The Arikara and especially the Aleut have large pits on average, which suggests that their pits were formed as a result of high-impact crushing rather than attritional shearing and slicing. Because the Arikara diet is so varied, it is difficult to parse microwear signals related to specific items. The Aleut, on the other hand, had a diet dominated by meat, which is generally recognized to be tough, requiring substantial work to fracture (Lucas and Peters, 2000). While meat itself is too soft to indent enamel, tooth wear may result from adherent grit (Lalueza et al., 1996; Ungar and Spencer, 1999), or the adhesive effects of tooth-on-tooth contacts during mastication (Puech et al., 1981, 1985). Large microwear pits in the Aleut sample more likely resulted from high occlusal forces (Spencer and Ungar, 2000) in combination with hard abrasives clinging to food, much like the situation posited for coastal hunter-gatherers in North America (Teaford et al., 2001).

The Cebus, Pan, Gorilla, and Arikara samples had narrower striations on average than did the Aleut, Papio, and Lophocebus samples. These differences are likely due to a combination of factors, including the sizes and shapes of abrasive particles, the magnitudes of occlusal forces, and perhaps even differences among the groups in underlying enamel structure (Maas, 1991). The most common way to scratch a tooth is to drag across it an object harder than enamel (Moh’s hardness from 4.5 to 5.0). Two likely culprits are 1) silica in exogenous grit from dust or soil (Moh’s hardness of quartz is 7.0) and 2) opal phytoliths, which are formed as monosilicic
acid is absorbed from groundwater and deposited in the cell walls of plants that are eaten (Moh’s hardness from 5.5 to 6.5) (Baker et al., 1959; Lucas and Teaford, 1995; Ungar et al., 1995; Lucas, 2004; Teaford et al., in press). Microwear striation breadths are likely limited by the sizes and shapes of these abrasives (Ungar, 1994; Ungar and Spencer, 1999). Larger phytoliths could leave broader striations than expected from exogenous grit dominated by smaller, angular clay grains (Ungar, 1994), though larger-grained sand particles could also yield thicker scratches (Daegling and Grine, 1999; Teaford et al., 2001).

Occlusal force likely also plays a role in striation breadth. We know, for example, that hard-object feeders tend to have wider microwear striations than those that prefer softer fruits and leaves (Teaford, 1988a). Ryan’s (1981) attribution of thick gouges in Inuit incisors to “power grasping/pulling” activities is consistent with this notion. This factor might explain why the Aleut have broader striations than the Arikara (Ungar and Spencer, 1999), and perhaps why Papio and especially Lophocebus have broader striations than Pan. On the other hand, it remains unclear why Cebus striations are narrower. Until we better understand the factors that influence striation breadth, interpretations of differences between groups as diverse as those sampled here will remain limited (Teaford and Runestad, 1992).

The fossil groups

The extant baseline data indicate that higher pit percentages should reflect consumption of hard, brittle items requiring heavy masticatory loads. Larger pits suggest hard, brittle items whereas smaller pits more likely point to tougher foods and adhesion of opposing surfaces during shearing. The hominins are well separated from Papio, Lophocebus, and the Aleut in both striation breadth and pit width. The Aleut, chacma baboons, and mangabeys consume foods that evidently require considerable occlusal force for comminution, such as tough mammalian tissues, tough seeds and corns, and, in the case of the mangabeys, at least occasional hard and brittle nuts. This makes sense given inferred relationships between occlusal force and pit size and striation breadth. Compared with the Aleut, Lophocebus, and Papio, the early Homo groups probably did not typically eat foods with considerable fracture strength or puncture resistance. These fossil hominins therefore likely did not specialize on extremely tough foods, such as dried meat, or those with extremely high yield strengths, such as hard USOs.

Likewise, none of the fossil hominin groups have the high pit percentages of L. albigena or C. apella. This result also suggests that early Homo did not often consume hard objects. Homo habilis and Sterkfontein Member 5C specimens have relatively low pit percentages, in line with the figures for the Arikara and Gorilla. This result implies a diet that included some tougher foods, such as those with the mechanical properties of some leaves, woody plants, and perhaps some animal tissues. In contrast, H. erectus and Swartkrans Member 1 specimens had higher but still moderate pit percentages, in line with those of the Aleut, Pan, and especially Papio. This result implies consumption of a range of items and/or those with intermediate fracture properties. These early hominins may have eaten some more resistant foods, such as harder USOs or tough animal tissues than did H. habilis or the hominins from Sterkfontein Member 5C.

The lack of differences in feature size between the early hominin samples suggests that microwear feature “types” may have been formed by similar processes. Small samples and the dietary versatility that might be expected of early Homo (Teaford et al., 2002; Wood and Strait, 2004) would make it difficult to detect differences between the taxa. However, the fact that feature size variation within these samples is not especially large may reflect comparable balances between abrasive particle size and masticatory force rather than Type II statistical errors.

In contrast, the significant differences in pit percentage suggest that the early Homo individuals differed in the fracture properties of their diets. Higher pit percentages for H. erectus and the individuals from Swartkrans Member 1 imply at least occasional consumption of significantly harder or tougher foods on average than those eaten by H. habilis and the individuals from Sterkfontein Member 5C. The fact that these pits tend to be small suggests that they were formed by adhesive wear during shearing and slicing, and therefore that H. erectus and the individuals from Swartkrans Member 1 consumed tougher foods on average than the other samples. Still, because of the small features found in the C. apella sample analyzed for this study, we cannot exclude the possibility that those hominins with higher pit percentages actually consumed some harder foods or ingested larger-grained abrasives as well. Further work on larger samples of extant taxa using 3D microwear texture analysis (Ungar et al., 2003) will hopefully allow us to resolve this issue.

Implications of the microwear results

Changes in diet through time

Comparisons of the early Homo samples to one another allow us to speculate on whether microwear can offer insights into changes in diet through time. Although it is difficult to define ancestor-descendant relationships between specific fossil taxa with precision, H. habilis does make a reasonable ancestral morphotype for the genus Homo, including H. erectus (Chamberlain and Wood, 1987; Strait et al., 1997; Kimbel et al., 1997). In the present context, some features of possible relevance to this argument include retention of larger molars and perhaps thicker tooth enamel than observed for H. erectus (Teaford et al., 2002). Wood and Collard (1999) have even argued that H. habilis is plesiomorphic enough to belong to the australopith adaptive grade, and should be reassigned to the genus Australopithecus.

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2 Occlusal forces required to fracture a food item depend on both mechanical properties of that food and tooth shape (Lucas, 2004). Tough, dried meat, for example, should require more forceful and repeated chewing cycles to fracture by flat Aleut molars than by steeply sloped teeth, such as carnassials designed for shearing and slicing such foods.
In this sense then, a direct comparison of microwear in these species might provide new insights into changes in diet within the genus *Homo* around the time of the Plio-Pleistocene boundary. If so, similarities in feature size suggest that the abrasives causing microwear pits and striations remained consistent over time. However, the material properties of foods eaten may have changed. Higher pit percentages in *H. erectus* suggest that these hominins may have incorporated increasing amounts of fracture-resistant foods (possibly hard, but more likely very tough) compared with *H. habilis*.

**Early *Homo* samples from Sterkfontein Member 5C and Swartkrans Member 1**

Samples from Sterkfontein Member 5C postdate those from Member 5A assigned to *H. habilis* (Partridge, 2000). Indeed, apparent morphological similarities between Member 5C specimens and those from Swartkrans Member 2 have suggested to some that they belong to what we refer to as *H. erectus* (Kuman and Clarke, 2000). In contrast, Swartkrans Member 1 specimens predate those from Member 2 assigned to *H. erectus*. Grine (2005) proposed that Member 1 hominins more closely resemble *H. habilis* than they do *H. erectus*. Regardless of the specific attributions of these samples, there seems to be continuity in microwear pattern within each of these South African localities. In other words, the microwear patterns of *H. habilis* specimens from eastern Africa and Sterkfontein Member 5A are very similar to those from Sterkfontein Member 5C. Likewise, *H. erectus* specimens from eastern Africa and Swartkrans Member 2 have microwear patterns indistinguishable from those of the Swartkrans Member 1 hominins.

**Comparisons with previous studies**

**Previous microwear studies**

Early *Homo* microwear results presented here can also be interpreted within the context of results from previous studies and other lines of evidence for the diets of these hominins. Data presented here may be consistent with the preliminary microwear results presented by Waddle (1988), which suggested that early *Homo* from Swartkrans Members 1 and 2 had a high incidence of small pits. Heavy pitting in *H. erectus* from eastern Africa was also suggested by Walker (cited in Waddle, 1988; Walker and Shipman, 1997). Still, while our results suggest that *H. erectus* and the sample from Swartkrans Member 1 had higher incidences of small pits than did *H. habilis* or the specimens from Sterkfontein Member 5C, none of these hominins showed an extremely high incidence of pitting or remarkably small pits. Thus, the fracture properties of their diets were probably not as challenging as earlier studies suggested. Puech et al. (1983a) and Puech (1984) also studied microwear in some early *Homo* specimens, speculating that evidence of erosion of *H. habilis* molars from Olduvai Gorge (no list of specimens was provided) indicates acidic fruit consumption. However, more recent studies have shown that the pattern of erosion described by these authors suggests taphonomic damage to the part of the tooth examined rather than antemortem tooth use (see Teaford, 1988b; King et al., 1999). The specimens in question are much more severely eroded than any of the extant baseline teeth, and we found evidence of this erosion on both occlusal facets and non-occlusal parts of the teeth, including interstitial facets not exposed to food during life.

**Other lines of evidence**

Bone and tooth chemistry, like microwear, tells us something about what an individual ate. Whereas microwear indicates possibly only a few weeks of diet (Teaford and Oyen, 1989b), tooth and especially bone chemistry reflects food preferences averaged over many months to many years. It is not surprising then, that preliminary results published for the stable isotopes δ¹³C and δ¹⁸O for the Swartkrans Member 1 *Homo* sample suggest a generalized diet (Lee-Thorp et al., 2000; van der Merwe et al., 2003). Indeed, intermediate microwear pit percentages for these hominins accord well with a mixed or generalized diet, as does the lack of large average feature sizes that are seen in some dietary specialists.

The other two commonly cited lines of evidence for diet in early *Homo*, tooth size and shape, provide evidence of what a taxon (or its ancestor) may have been adapted to consume rather than what an individual actually ate. We prefer to leave the studies of dental allometry until larger samples and more precise body weight estimates are available, and relationships between molar size and function are better understood (see Ungar et al., in press). Molar shape, on the other hand, has provided some interesting clues. While sample sizes have necessitated combining taxa, early *Homo* specimens show moderately sloped occlusal surfaces, suggesting an adaptation to a diet tougher than that of their australopith predecessors, and intermediate between those of chimpanzees and gorillas (Ungar, 2004). This is also consistent with the intermediate microwear pit incidences found in early *Homo*.

**Dental microwear and diet models**

The microwear results presented here, combined with other lines of evidence, suggest that early *Homo* ate foods that were neither extremely hard nor exceedingly tough, but instead consumed a rather varied diet. Further, while the diets of different early *Homo* groups probably did not differ dramatically from one another, *H. erectus* and individuals from Swartkrans Member 1 probably consumed some foods that were more difficult to fracture than did *H. habilis* and the individuals from Sterkfontein Member 5C.

These interpretations allow us to comment on popular models for early *Homo* diets. Researchers have long argued that a new resource base made available by the spread of C₄ grasslands and stone tools motivated subsistence changes that led to the origin and early evolution of our genus (for review, see Ungar et al., in press). Workers have suggested a shift from a diet dominated by fruit or other forest resources to savanna animals or xeric plants (especially USOs). In this light, the lack of microwear evidence for dietary specialization is instructive. None of these hominins probably limited their diets to either tough
meat or hard USOs. On the other hand, microwear differences between *H. habilis* and *H. erectus* may be of some significance, especially if the higher incidences of pitting in the latter reflect consumption of more foods resistant to fracture.

Ungar (2004) suggested that the diets of early *Homo* and their immediate predecessors differed largely in fallback foods consumed during times of resource stress. He measured the average difference in occlusal slope between *Australopithecus afarensis* and early *Homo* molars at a given stage of wear to be 4.1 degrees. This is comparable to that between sympatric chimpanzees and lowland gorillas (with an average difference of 4.3%; Ungar, 2004), taxa that overlap greatly in their diets except at “crunch” times. The intermediate pattern of microwear makes sense in this light because features may turn over rapidly (Teaford and Oyen, 1989b), and thus should reflect more commonly eaten foods. Extant primates often prefer foods that are easy to fracture, leaving tougher or harder items as occasional fallback resources (e.g., Remis, 1997; Lambert et al., 2004). It is reasonable to hypothesize, then, that early *Homo* species had versatile diets, but preferred foods that were easy to consume. These hominins, especially *H. erectus* and the individuals from Swartkrans Member 1, would probably have resorted to harder or tougher items mostly when other foods were unavailable. We speculate that, given environmental dynamics during the Plio-Pleistocene (Cerling, 1992; Behrensmeyer et al., 1997; Potts, 1998), changes in the fracture properties of fallback foods consumed by early *Homo* might relate to changes in resources available to these hominins.

**Conclusions**

A study of early *Homo* from the Plio-Pleistocene of eastern and southern Africa reveals antemortem microwear on molars or premolars of 18 of 83 specimens examined. Microwear data for these specimens cluster with data for baseline groups of protohistoric human foragers and extant nonhuman primates that prefer less fracture-resistant foods. This finding suggests that none of the early *Homo* groups specialized on very tough or very brittle items. Still, *H. erectus* and Swartkrans Member 1 specimens do have more small pits than do those of *H. habilis* and specimens from Sterkfontein Member 5C. This result suggests some dietary variation among these early hominins such that *H. erectus* and individuals from Swartkrans Member 1 ate, at least occasionally, more tough or brittle foods than did *H. habilis* and individuals from Sterkfontein Member 5C.

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**Appendix I. Fossil specimens examined for this study**

<table>
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<th>Group Specimen*</th>
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<th>Axis lengths</th>
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