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MOLAR MICROWEAR AND SHEARING CREST DEVELOPMENT IN MIOCENE CATARRHINES

ABSTRACT: The Miocene epoch witnessed an extensive radiation of ape (non-cercopithecoid catarrhine) taxa. In order to appreciate the extent of this radiation, we need to understand something of the dietary diversity of these forms. In this study, we compare the dental microwear of seventeen ape species ranging in time from the Early to the Middle and Late Miocene and in space from Africa to Europe and Asia. While sample sizes are limited by taphonomic damage, the data suggest that Early Miocene African ape species ranged somewhat in their food preferences, whereas Middle to Late Miocene Eurasian ape diets probably varied more than their African predecessors. Most fossil taxa examined were probably frugivorous, though Rangwapithecus, Micropithecus, and especially Oreopithecus may have consumed more leaves. In contrast, Ouranopithecus, unlike any living hominoid, evidently preferred hard, brittle foods. These interpretations accord well with results from molar shearing crest length analyses of many of these same species. Further, comparisons of adaptive morphology and epigenetic dental microwear data may allow us to begin to separate functional from phylogenetic or temporal effects on tooth shape.

KEY WORDS: Diet – Apes – Dental morphology – Shearing quotients

INTRODUCTION

The number of Miocene ape taxa (i.e., non-cercopithecoid catarrhines) recognized has grown to the point that all but the most ardent students of primate evolution have difficulty keeping up with them. About seventy species are now documented (see Hartwig 2002), with new taxa being identified at an increasingly dizzying rate! It is clear that extant hominoids are merely the tip of the colossal iceberg that is, or was, the ape radiation. It is also clear that we cannot appreciate the extent of this radiation, or our place in it, without understanding something of the diversity of adaptations of fossil Miocene catarrhines.

One of the best measures of primate adaptive diversity is variation in diet (Fleagle 1999). Diet underlies many of the behavioural and ecological differences that separate primate species today, and it probably always has. In this paper we add to a growing body of information on fossil primate diets, focusing attention on dental microwear of specimens representing seven species of Early Miocene

apes from Africa. We compare these microwear data to those already published for European Miocene apes (Ungar 1996). The microwear evidence suggests that Early Miocene African catarrhines probably varied somewhat their diets. When these taxa are combined with European samples, it becomes clear that Miocene apes had a range of dietary adaptations greatly exceeding those of their extant counterparts, from hard-object feeding to soft-fruit eating to dedicated folivory.

This paper builds on previous diet reconstructions for many of these same taxa based on molar shearing crest lengths (Kay, Ungar 1997). Those studies showed that phylogeny and temporal effects can affect tooth shape, making it difficult to infer diets, especially for stem fossil species with uncertain phyletic affinities. Nevertheless, ranges of relative shearing crest lengths were suggested to reflect ranges of adaptations. Microwear data presented and reviewed here include twelve of the same species considered by Kay and Ungar (1997). We argue that some differences between taxa in microwear and occlusal

morphology reflect similar aspects of diet, and can be compared directly. Comparisons of these independent datasets allow us to gain a more complete picture of the diets of Miocene apes. Microwear is epigenetic (it is not inherited, but rather, reflects activities of individuals during life), and therefore should allow us to "anchor" ranges of morphology data to control for phylogenetic effects. Residuals from a regression of relative shearing crest lengths over relative microwear pit frequencies, for example, separate Early Miocene African species from Middle to Late Miocene Eurasian forms.

BACKGROUND

While data have been presented for dental microwear and diets of Miocene apes from Europe, no such studies have been published on Miocene apes from Africa (Ungar 1996). This is unfortunate because studies of dental morphology of African Miocene apes have raised some important questions that microwear data might help address (Kay, Ungar 1997).

Molar shearing crest length and diets of African Miocene apes. Researchers have recognized form-function relationships between teeth and diet for a long time, and have focused much attention on deciphering the details of these relationships (e.g., Owen 1840–1845, Gregory 1922, Crompton, Sita-Lumsden 1970, Kay, Hiiemae 1974, Kay 1977, 1978, Rosenberger, Kinzey 1976, Maier 1977, 1984, Kay, Hylander 1978, Kinzey 1978, Seligsohn, Szalay 1978, Lucas 1979). It is clear, for example, that primate folivores have reciprocally concave, highly crested teeth for shearing whereas frugivores and hard-object specialists have rounder, flatter teeth for crushing and grinding.

Kay and colleagues (Kay 1978, Kay, Hylander 1978, Kay, Covert 1984) have recognized that comparisons of occlusal form between extant and extinct species and inference of diet in the latter taxa require a quantitative approach. Their Shearing Quotient (SQ), for example, is calculated as a residual from a regression of the summed length of mesiodistal crests over the length of the occlusal table for a series of closely related species with a given type of diet. The higher the SQ, the longer the shearing crests relative to expectation of a species with that diet. The lower the SQ, the shorter the shearing crests relative to expectation. Comparative studies have confirmed that folivores and insectivores have higher SQs than closely related frugivores, and that among frugivores, hard-object specialists have the lowest SQ values (Anthony, Kay 1993, Strait 1993a, Meldrum, Kay 1997).

Kay (1977) applied SQ studies to the inference of diet in African Miocene apes. He found that *Limnopithecus*, *Dendropithecus* and *Proconsul* species all had less crest development than *Rangwapithecus*. Kay suggested then, based on this evidence, that the latter taxon was folivorous, whereas the former ones were frugivorous. Kay and Ungar

(1997) pointed out, however, that while the range of SQ values among these Miocene apes was similar to that for extant hominoids, most of the fossil taxa had lower SQ values than does any living ape species. Thus, either the fossil species were all frugivores and hard-object specialists, with a different assortment of adaptations than living hominoids, or their range of adaptations was similar to those of apes today, and extant taxa have higher SQ values than did these Miocene catarrhines independent of diet.

Support for the latter hypothesis comes from studies showing that while SQ values accurately track diet differences within hominoids or cercopithecoids, Old World monkeys have relatively better developed molar shearing when diet is controlled for (Kay, Covert 1984). Similar phenomena have also been reported for other lines of dental evidence for diet, such as incisor size (Eaglen 1984) and enamel thickness (Dumont 1995). Differences in values *within* higher-order taxa reflect diet differences, but phylogenetic effects make comparisons of distantly related species difficult.

Kay and Ungar (1997) therefore proposed that *variation* in SQ ranges rather than actual values be compared between higher-order taxa. Comparable SQ variation between Early Miocene apes and extant hominoids, for example, suggest that differences between *Limnopithecus*, *Dendropithecus*, and *Proconsul* species on the one hand and *Rangwapithecus* on the other were comparable to those between frugivorous *Pan* and more folivorous *Gorilla*, or small-bodied frugivorous gibbons and more folivorous *Hylobates syndactylus*. Thus, extant hominoids may have "up-shifted" SQ values relative to African Miocene apes, probably reflecting a phylogenetic or temporal shift with enhanced molar shearing in later taxa. If so, then *Limnopithecus*, *Dendropithecus* and *Proconsul* were probably frugivores, whereas *Rangwapithecus* was more likely folivorous.

Dental microwear analysis. Ungar (1998) noted that it is difficult to test ideas concerning phylogenetic or temporal shifts in ranges of morphology without some independent line of evidence for diet – preferably using data that are not dependent on identifying a morphological starting point. Such an approach would allow us to "anchor" a morphological range for comparisons between higher-order taxa. Dental microwear is well suited to serve this role.

Teaford and Walker (1984) noted that patterns of microscopic use-wear, or microwear, on crushing facets of primate molar teeth could distinguish folivores, soft fruit-eaters, and hard-object feeders from one another – the same diet categories that SQ studies separate. They found that frugivores (*Lophocebus*, *Cebus*, *Pongo*, and *Pan*) evince higher ratios of large pits to scratches than folivores (*Colobus*, *Gorilla*, *Alouatta*), and among frugivores, hard-object specialists (*Lophocebus*, *Cebus apella*) have the highest relative frequencies of large pits. Subsequent

studies by Teaford and co-authors have confirmed these results, and shown that microwear can reflect rather subtle differences in diet (Teaford 1985, 1986, Teaford, Robinson 1989, Teaford, Glander 1995).

Researchers have used relationships between microwear patterns and diet in living species to infer diet from microwear patterns in a broad range of fossil primates from the Eocene (Strait 1993b) and the Oligocene (Teaford *et al.* 1996), to the Miocene (Jacobs 1981, Teaford, Walker 1984, Kelley 1986, Daegling, Grine 1994, Ungar 1996, King *et al.* 1999), to the Pliocene and Pleistocene (e.g., Grine 1981, 1986, Walker 1981, Puech 1986, Grine, Kay 1987, Ungar, Grine 1991, Lalueza *et al.* 1993, Lucas, Teaford 1994, Ungar, Teaford 1996, Pérez-Pérez *et al.* 1999, Ryan, Johanson 1989, Leakey *et al.* 2003). Despite such studies, however, no data have yet been published on molar microwear of African Miocene apes. Such studies would give us a more complete understanding of the fossil catarrhine adaptive radiation, and would allow us to evaluate hypotheses proposed by Kay and Ungar (1997) concerning temporal or phylogenetic shifts toward enhanced molar shearing after the Early Miocene.

This study presents new microwear data for six species of Early Miocene African apes: *Proconsul major*, *P. heseloni*, *P. nyanzae*, *Rangwapithecus gordonii*, *Dendropithecus macinnesi*, and *Micropithecus clarki*. While taphonomic damage limits available samples with unobscured dental microwear (e.g., many of the specimens from Rusinga Island show heavy post mortem etching), some trends are evident. First, pit percentage and feature dimensions suggest that most of these species were probably frugivorous. When compared with microwear data for European Miocene forms, none of the African taxa have pit percentages approaching *Ouranopithecus*, an inferred hard-object feeder, whereas *Rangwapithecus* values fall closest to *Oreopithecus* and the pliopithecids from Castell de Barbera, previously reconstructed as folivores. This suggests that the Early Miocene African catarrhines probably had a range of dietary adaptations similar to that of extant hominoids. Microwear patterns for *Proconsul* spp., and *Dendropithecus* are consistent with a soft-fruit diet, whereas feature shapes for *Rangwapithecus* may be consistent with more leaf-eating (though larger samples are necessary to confirm this). These results are consistent with Kay and Ungar's (1997) interpretation of the shearing crest length data, and may help us "anchor" SQ ranges reported for these same taxa.

MATERIALS AND METHODS

This study combines new data for African Early Miocene catarrhines microwear with previously published results for Middle to Late Miocene Eurasian species (Ungar 1996). Fifteen catarrhine taxa are considered in total. The vast majority of specimens examined for this study were deemed unsuitable for analysis given taphonomic damage

that obscured or obliterated ante mortem microwear (see Teaford 1988a for selection criteria). Those specimens that remained are listed in the Appendix.

SPECIMENS EXAMINED

African Miocene catarrhines. Species of two superfamilies of East African Early Miocene apes from Kenya were examined for this study: 1) dendropithecoids (*Dendropithecus macinnesi*, *Micropithecus clarki*), and 2) proconsuloids (*Afropithecus turkanensis*, *Proconsul heseloni*, *P. nyanzae*, *P. major*, *Rangwapithecus gordonii*). These taxa are diverse, phylogenetically and anatomically. While the individual species may sort into distinct families, there is little consensus concerning their phyletic placements relative to major extant groups (Harrison 2002). While most works consider the small-bodied dendropithecoids to be primitive, basal catarrhines (see Fleagle 1999), proconsuloids have been considered stem catarrhines (Harrison 1993, 2002), stem hominoids (Andrews 1992, Rose 1997, Begun *et al.* 1997, Kelley 1997, Ward 1997, Rae 1999) and even stem great apes (Walker, Teaford 1989, Walker 1997, Rae 1997). Indeed, as Harrison (1993) has written "it may not be possible given the quality of the information available, to determine the nature of the relationships among the genera of fossil catarrhines from the Miocene of East Africa". Nevertheless, most would agree that the dental anatomy of all of these primates is probably primitive for catarrhines as a whole (Andrews 1978, Fleagle, Kay 1983, Kay, Ungar 1997).

Eurasian Miocene catarrhines. Middle to late Miocene European apes examined can also be divided into two superfamilies: 1) pliopithecoids (*Anapithecus hernyaki*, *Epipliopithecus vindobonensis*, *Pliopithecus platydon*, and pliopithecids¹ from Castell de Barbera, Spain) and 2) hominoids (*Dryopithecus branchoi*, *Dryopithecus crusafonti*, *Dryopithecus fontani*, *Dryopithecus laietanus*, *Oreopithecus bambolii*, *Ouranopithecus macedoniensis*). New data are also presented here for the Middle Miocene pliopithecoid *Pliopithecus zhanxiangi* from China. Most agree that the pliopithecoids are late surviving stem catarrhines that retain several primitive dental features expected of the ancestral catarrhine morphotype (Harrison 1987, see Begun 2002a). Further, while most consider all of the European hominoids to be great apes, their phyletic positions within the family remain debated (e.g., Dean, Delson 1992, Moyà-Solà, Köhler 1993, Bonis, Koufos 1997, Harrison, Rook 1997, Begun 2002b).

¹ These specimens, described in Crusafont-Pairo, Golpe-Posse (1981) remain unnamed (see Begun 2002a).

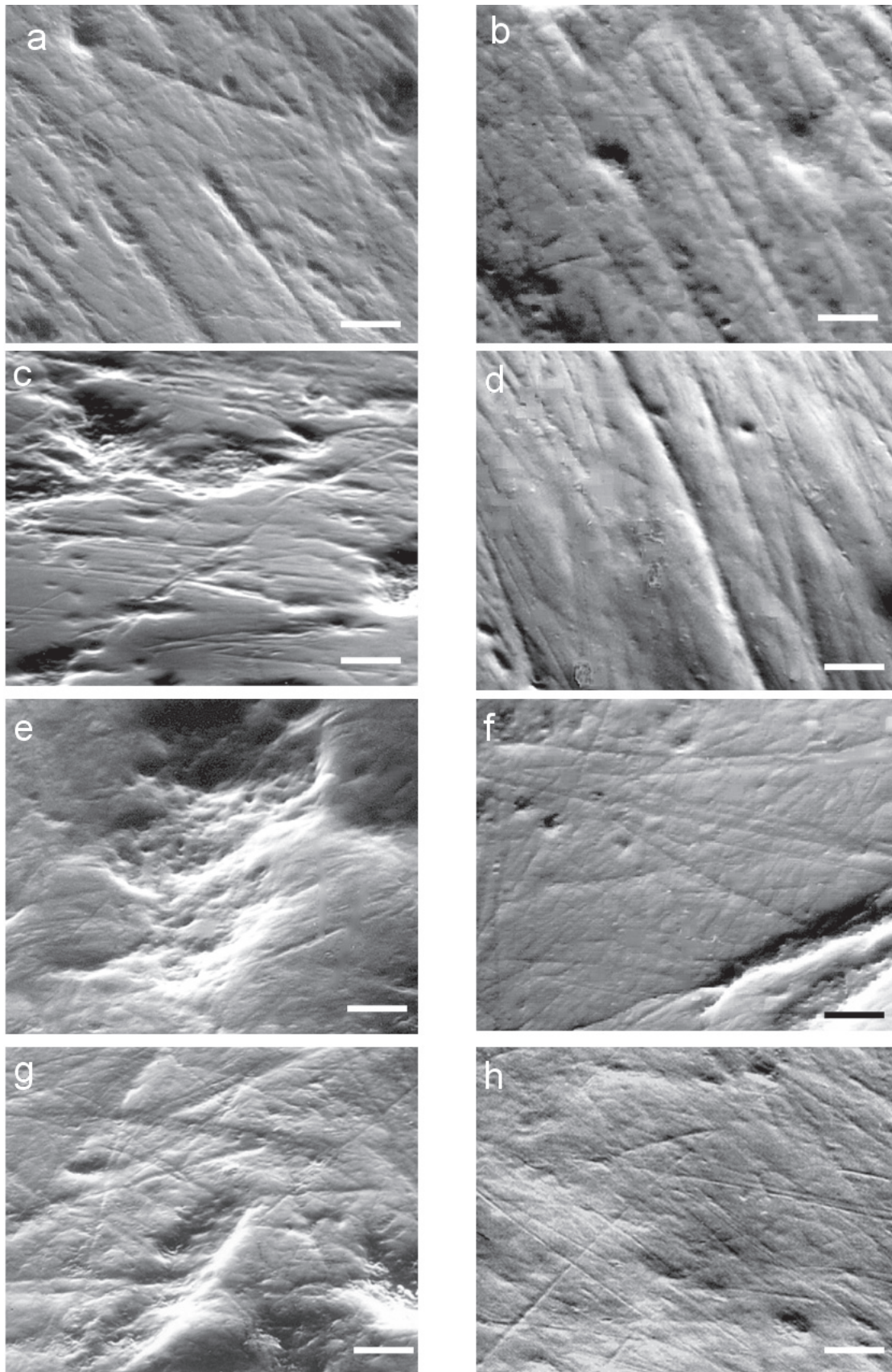


FIGURE 1. Photomicrographs of “Phase II” occlusal facets of various Miocene ape molar teeth. Scale bars = 25 μm . a = *Anapithecus hernyaki* (RUD 108, LM₂), b = *Dendropithecus macinnesi* (KNM-RU 2015, RM₂), c = *Dryopithecus brancoi* (RUD 141, RM²), d = *Oreopithecus bambolii* (BAC 66, RM₂), e = *Ouranopithecus macedoniensis* (RPL 75, RM₂), f = *Pliopithecus platydon* (SK 1453, RM²), g = *Proconsul major* (KNM-LG 45,2 LM₂), h = *Rangwapithecus gordonii* (KNM-SO 907, RM₂).

FIGURE 2. Percentage incidence of pitting by species. The horizontal lines indicate mean values, and the vertical lines above and below are one standard deviation each.

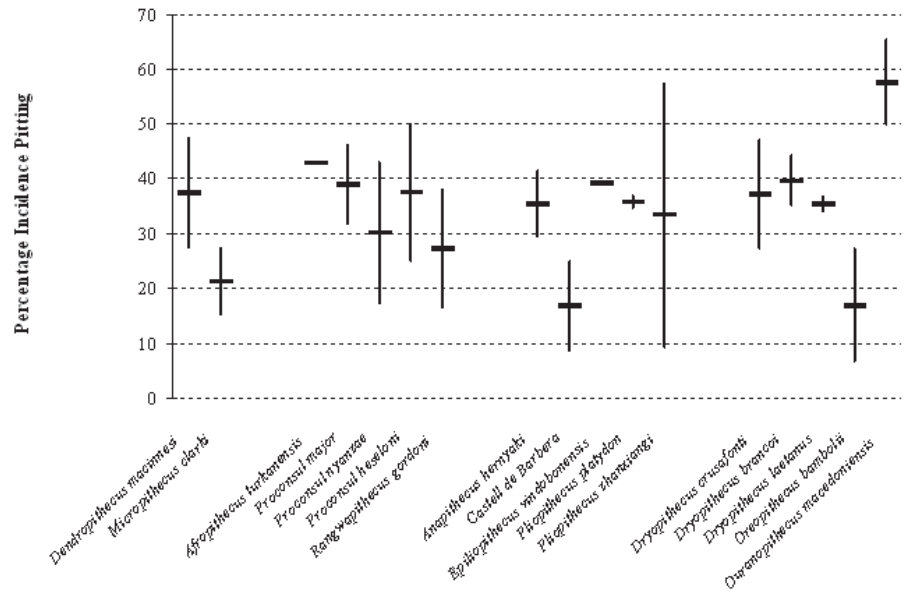
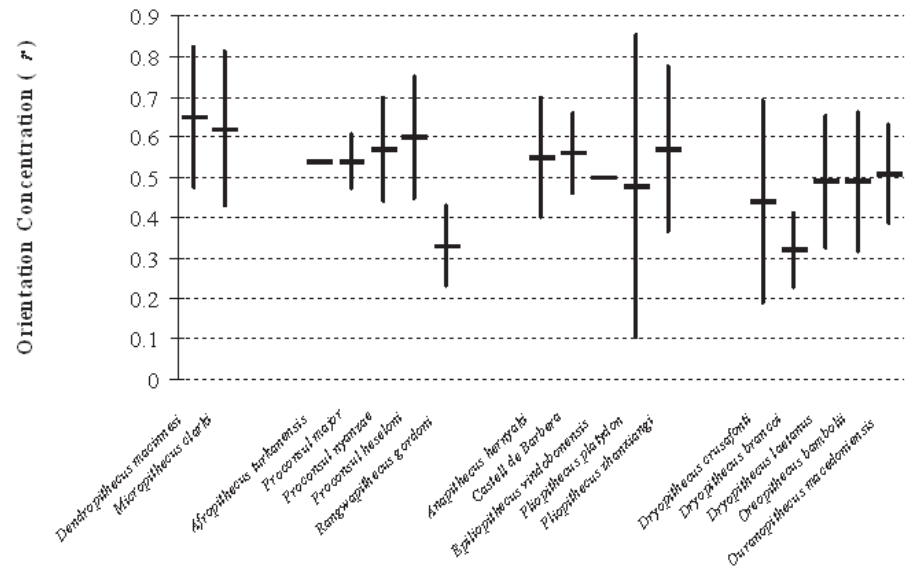


FIGURE 3. Microwear feature orientation concentration by species. The horizontal lines indicate mean values, and the vertical lines above and below are one standard deviation each.



SPECIMEN PREPARATION AND DATA ANALYSIS

Microwear data were collected from high resolution replicas of upper and lower second molars (M2s). Replicas were prepared following usual procedures (Rose 1983, Grine 1986). First, all tooth surfaces were cleaned gently with cotton swabs soaked with acetone and/or ethyl alcohol. Moulds of all available fossil teeth were taken with a hydrophobic polyvinylsiloxane (3M "Express" or Coltène "President Jet") impression material. Such materials reproduce features with resolutions true to a fraction of a micron (Beynon 1987, Teaford, Oyen 1989). Replicas were poured using an epoxy resin and hardener (Epotek 301 or Araldite), mounted on aluminium SEM stubs with silver paint or colloidal graphite to ensure conductivity, and sputter-coated with approximately 20 nm of gold.

Specimens were examined by scanning electron microscopy. M2 Phase II crushing facets were examined

following previous studies (Teaford 1988b, 1994). Specimens were examined at 500x using a scanning electron microscope in secondary mode. All surfaces examined were oriented nearly perpendicular to the electron beam to minimize feature foreshortening. Photomicrographs were taken using Polaroid Type 55 Positive-Negative film of those surfaces that showed unambiguous ante mortem microwear.

A 3.2 by 2.4 inch portion of each photomicrograph was scanned at 200 dpi with 256 grey-levels using a flatbed scanner, yielding a resolution of 0.254 µm per pixel on the display monitor. Resulting images were analysed using Microware 2.1 (see Ungar *et al.* 1991, Ungar 1995). 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, and features were marked by coloured lines on the screen as they were identified to avoid repeated measurement. Because some features were truncated by the edges of images, measurements should be considered

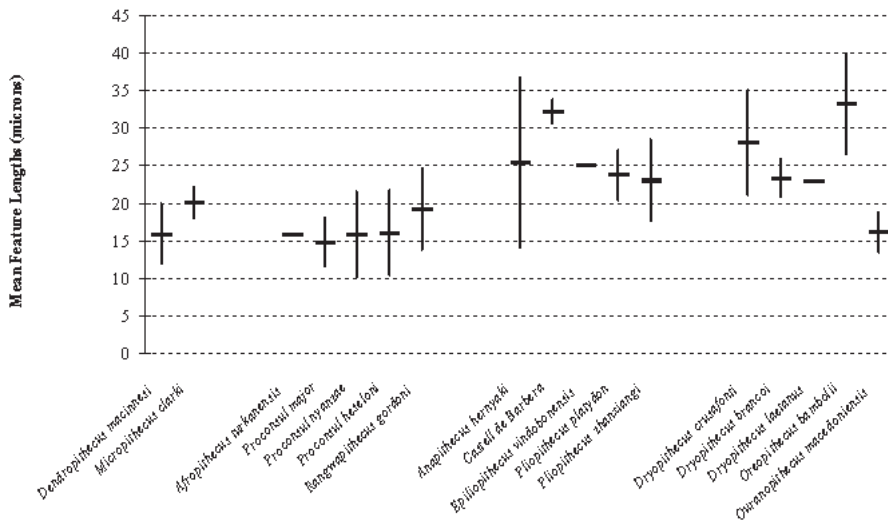


FIGURE 4. Mean feature length by species. The horizontal lines indicate mean values, and the vertical lines above and below are one standard deviation each.

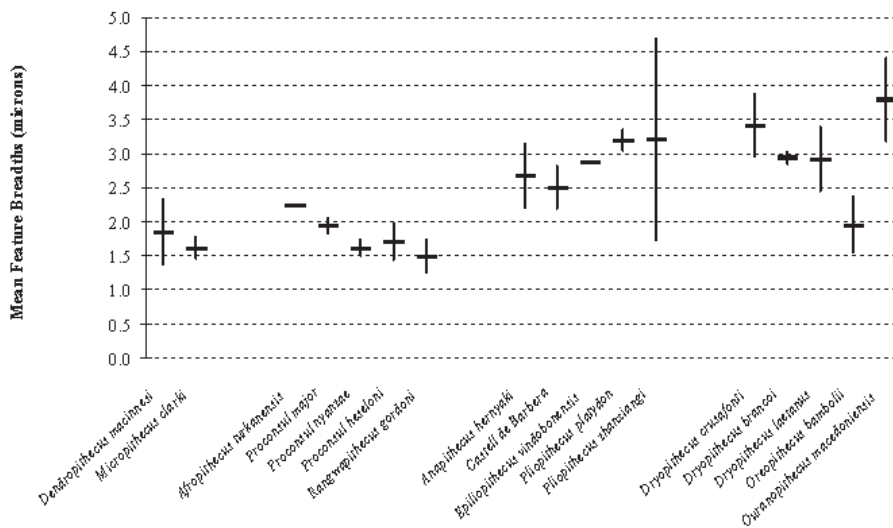


FIGURE 5. Mean feature breadth by species. The horizontal lines indicate mean values, and the vertical lines above and below are one standard deviation each.

minima. Feature lengths, breadths and orientation concentration (mean vector length – see Ungar 1994) were all recorded. In addition, features with lengths more than four times their widths were designated as scratches, whereas those that were relatively shorter and broader were designated as pits, and the percentage incidence of pitting was calculated as the ratio of pits to all features (Grine 1986, Teaford 1988b). All data were rank-transformed to mitigate violation of assumptions associated with parametric statistical tests.

Data were analysed using Analysis of Variance (ANOVA) or general linear models. Analyses were conducted at the generic level because of small sample sizes for most individual species. Those genera with three or fewer individuals were not considered in the statistical comparisons. Genera were initially compared for percentage incidence of pitting in a single classification ANOVA. Genera were then compared for mean feature length, mean feature breadth and feature orientation heterogeneity using a multivariate ANOVA model. Individual ANOVAs were performed for each variable

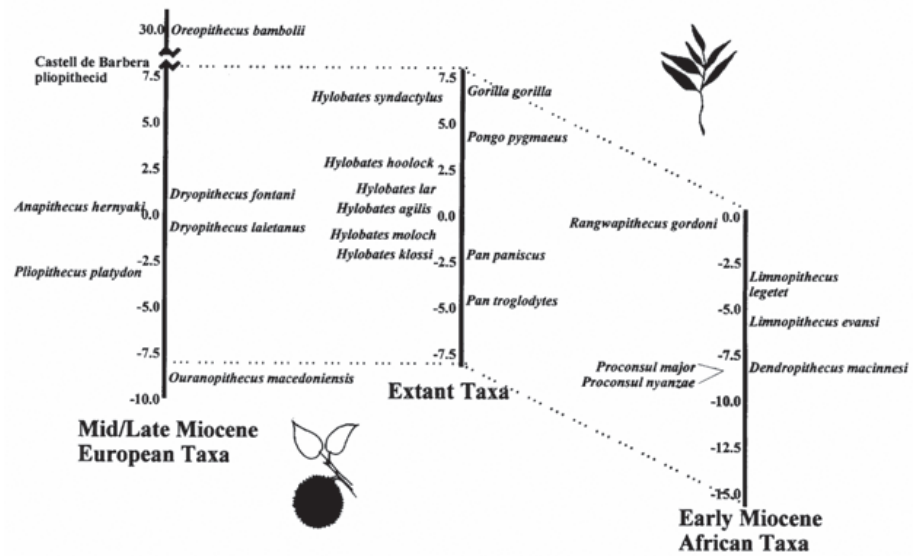
following significant variation in the MANOVA model, and Bonferroni's pair-wise multiple comparisons tests were used to determine the sources of significant variation as warranted.

One final note concerning these analyses should be made. In many cases, small sample sizes (e.g., $n=5$) greatly reduced the power of these tests and made significances of differences difficult to assess (see Sokal, Rohlf 1981). In these cases, failure to reject a hypothesis may still yield insights. In other words, the taxa may differ in an attribute, but sample sizes are insufficient to detect that difference. This is especially the case where differences among fossil groups in mean values are on the same order or greater than those observed for larger samples of extant primates with significant differences in diet and microwear.

RESULTS

Results for the microwear study show considerable variation among taxa. Some sample photomicrographs are

FIGURE 6. Shearing quotient results for extant and fossil Miocene apes.



presented in *Figure 1*. Raw data can be found in the Appendix and summary statistics are presented in *Table 1* and illustrated in *Figures 2, 3, 4* and *5*. Statistical results are presented in *Tables 2* and *3*.

PERCENTAGE INCIDENCE PITTING

Pit percentage averages range from 16.86% to 57.69%. Values for each of the superfamilies show considerable variation, with microwear differences on the same order of magnitude as those separating extant hominoids with known diet differences (Teaford, Walker 1984, Teaford 1988b). The data appear to sort into three groups – those with pit percentage values above 40% those between 30% and 40% and those below 30%. Species with average values less than 30% include *Micropithecus clarki*, *Rangwapithecus gordonii*, the pliopithecoid from Castell de Barbera, and *Oreopithecus bambolii*. Species with average values greater than 40% include *Afropithecus turkanensis* and *Ouranopithecus macedoniensis*. All other taxa, *Dendropithecus macinnesi*, *Proconsul major*, *P. nyanzae*, *P. heseloni*, *Anapithecus hernyaki*, *Epipliopithecus vindobonensis*, *Pliopithecus platydon*, *P. zhanxiangi*, *Dryopithecus crusafonti*, *D. brancoi*, and *D. laietanus*, have intermediate percentage incidence of pitting values.

Statistical analysis was limited to comparisons of the genera *Anapithecus*, *Dendropithecus*, *Dryopithecus*, *Oreopithecus*, *Ouranopithecus*, *Pliopithecus*, *Proconsul*, and *Rangwapithecus* given sample size limitations. The results indicate significant variation in the model, with significant differences reflecting higher pit percentage values for *Ouranopithecus* compared with the other taxa and lower pit percentages for *Oreopithecus* compared with the other taxa.

FEATURE SIZES AND ORIENTATION CONCENTRATION

Taxa also show considerable variation in features size and orientation concentration. Major axis mean length values vary from 14.76 μm to 33.27 μm , and minor axis mean length values vary from 1.62 μm to 3.79 μm . Orientation concentration (0 = evenly distributed about a circle, 1 = all features parallel) varies from 0.32 – 0.65. The Middle and Late Miocene taxa tend to have larger features than the Early Miocene species, though there is some overlap, particularly in feature length. *Rangwapithecus gordonii* and *Micropithecus clarki* have the longest, narrowest feature averages of the African forms, and *Oreopithecus bambolii* and the pliopithecoid from Castell de Barbera have the longest, narrowest feature averages for the Eurasian species. *Ouranopithecus macedoniensis* has the shortest, broadest features. The variation in feature orientation concentration cross-cuts taxa, with some, such as *Dendropithecus* and *Micropithecus* showing considerable orientation homogeneity, and others, such as *Rangwapithecus gordonii* and *Dryopithecus brancoi* showing less.

Statistical analyses were again limited to comparisons of the genera *Anapithecus*, *Dendropithecus*, *Dryopithecus*, *Oreopithecus*, *Ouranopithecus*, *Pliopithecus*, *Proconsul*, and *Rangwapithecus*. MANOVA results indicate significant variation among the taxa, with individual ANOVAs showing this variation in all three variables (major axis length, minor axis length, and orientation concentration). Bonferroni's pair-wise multiple comparisons tests indicate that *Oreopithecus* has significantly longer features than *Dendropithecus*, *Ouranopithecus* and *Proconsul* and that *Dryopithecus* has significantly longer features than

TABLE 1. Summary statistics by species.

| Species | n | Pit % | | Major Axis | | Minor Axis | | r | |
|-------------------------------------|---|-------|--------|------------|--------|------------|-------|------|-------|
| | | Mean | SD | Mean | SD | Mean | SD | Mean | SD |
| Dendropithecoidea | | | | | | | | | |
| <i>Dendropithecus macinnesi</i> | 6 | 37.48 | 9.895 | 15.91 | 3.981 | 1.86 | 0.468 | 0.65 | 0.173 |
| <i>Micropithecus clarki</i> | 2 | 21.30 | 5.982 | 20.05 | 2.100 | 1.62 | 0.163 | 0.62 | 0.191 |
| Proconsuloidea | | | | | | | | | |
| <i>Afropithecus turkanensis</i> | 1 | 43.00 | | 15.77 | | 2.25 | | 0.54 | |
| <i>Proconsul major</i> | 6 | 39.09 | 7.152 | 14.76 | 3.231 | 1.94 | 0.117 | 0.54 | 0.066 |
| <i>Proconsul nyanzae</i> | 4 | 30.25 | 12.823 | 15.87 | 5.776 | 1.62 | 0.121 | 0.57 | 0.128 |
| <i>Proconsul heseloni</i> | 7 | 37.62 | 12.447 | 16.00 | 5.671 | 1.72 | 0.276 | 0.60 | 0.150 |
| <i>Rangwapithecus gordonii</i> | 4 | 27.31 | 10.837 | 19.16 | 5.536 | 1.49 | 0.233 | 0.33 | 0.099 |
| Pliopithecoidea | | | | | | | | | |
| <i>Anapithecus hernyaki</i> | 5 | 35.56 | 6.014 | 25.39 | 11.472 | 2.68 | 0.466 | 0.55 | 0.148 |
| Castell de Barbera | 2 | 16.86 | 7.997 | 32.18 | 1.570 | 2.51 | 0.311 | 0.56 | 0.099 |
| <i>Epilopithecus vindobonensis</i> | 1 | 39.38 | | 25.04 | | 2.88 | | 0.50 | |
| <i>Pliopithecus platydon</i> | 2 | 35.86 | 1.216 | 23.73 | 3.366 | 3.20 | 0.156 | 0.48 | 0.375 |
| <i>Pliopithecus zhanxiangii</i> | 2 | 33.44 | 24.020 | 23.01 | 5.494 | 3.21 | 1.478 | 0.57 | 0.205 |
| Hominoidea | | | | | | | | | |
| <i>Dryopithecus crusafonti</i> | 3 | 37.34 | 9.971 | 28.10 | 7.019 | 3.42 | 0.465 | 0.44 | 0.251 |
| <i>Dryopithecus branchoi</i> | 2 | 39.78 | 4.483 | 23.32 | 2.581 | 2.94 | 0.092 | 0.32 | 0.092 |
| <i>Dryopithecus laetanus</i> | 2 | 35.42 | 1.329 | 22.88 | 0.148 | 2.92 | 0.474 | 0.49 | 0.163 |
| <i>Oreopithecus bambolii</i> | 9 | 16.96 | 10.276 | 33.27 | 6.780 | 1.96 | 0.407 | 0.49 | 0.173 |
| <i>Ouranopithecus macedoniensis</i> | 7 | 57.69 | 7.712 | 16.08 | 2.673 | 3.79 | 0.609 | 0.51 | 0.122 |

TABLE 2. Percentage incidence of pitting analysis.

| I. ANOVA | | | | | | | |
|---|--------------------|-----------------------|---------------------|---------------------|-----------------------|---------------------|------------------|
| | SS | df | MS | F | p | | |
| Hypothesis | 8452.065 | 7 | 1207.438 | 7.113 | 0.000 | | |
| Error | 8657.435 | 51 | 169.754 | | | | |
| II. Bonferroni's matrix of pairwise mean differences. | | | | | | | |
| | <i>Anapithecus</i> | <i>Dendropithecus</i> | <i>Dryopithecus</i> | <i>Oreopithecus</i> | <i>Ouranopithecus</i> | <i>Pliopithecus</i> | <i>Proconsul</i> |
| <i>Dendropithecus</i> | 4.783 | | | | | | |
| <i>Dryopithecus</i> | 2.486 | -2.298 | | | | | |
| <i>Oreopithecus</i> | -18.800 | -23.583** | -21.286* | | | | |
| <i>Ouranopithecus</i> | 25.914** | 21.131 | 23.429** | 44.714** | | | |
| <i>Pliopithecus</i> | 0.200 | -4.583 | -2.286 | 19.000 | -25.714* | | |
| <i>Proconsul</i> | 2.847 | -1.936 | 0.361 | 21.647** | -23.067** | 2.647 | |
| <i>Rangwapithecus</i> | -9.175 | -13.958 | -11.661 | 9.625 | -35.089** | -9.375 | -12.022 |

* $p < 0.1$, ** $p < 0.05$

Proconsul. Further, *Ouranopithecus* has the broadest features, followed by *Dryopithecus* and *Pliopithecus*, which also have significantly broader features than most other taxa.

DISCUSSION

While small sample sizes greatly limit statistical power for most taxa, results presented here can be interpreted, albeit with caution, relative to differences observed among extant primates. Pit percentage differences among these taxa are comparable to those among living catarrhines (Teaford, Walker 1984, Teaford 1988b). Differences

between *Ouranopithecus* and *Oreopithecus* are comparable to those observed between extant hard-object feeders and folivores. Most of the other taxa fall in between these, where one would expect to find soft-fruit eaters. Exceptions to this are the pliopithecoids from Castell de Barbera, *Micropithecus* and *Rangwapithecus*, which all show mean values closer to *Oreopithecus*, but have sample sizes too small to detect significant differences. The single *Afropithecus* individual has a fairly high pit percentage value, but it is still lower than any recorded for *Ouranopithecus*. In sum then, pit percentage results suggest a considerable range of diets for Miocene apes. This suggests that while most of the taxa observed were probably soft-fruit eaters, *Ouranopithecus* was more likely

TABLE 3. MANOVA test results.

| I. MANOVA results | | | | | | | |
|---|--------------------|-----------------------|---------------------|---------------------|-----------------------|---------------------|------------------|
| | Statistic | F | df | p | | | |
| Wilk's Lambda | 0.017 | 965.087 | 3, 49 | 0.000 | | | |
| Pillai Trace | 0.983 | 965.087 | 3, 49 | 0.000 | | | |
| Hotelling-Lawley Trace | 59.087 | 965.087 | 3, 49 | 0.000 | | | |
| II. Individual ANOVAs | | | | | | | |
| | SS | df | MS | F | p | | |
| Major axis | 2445.986 | 7 | 349.427 | 10.804 | 0.000 | | |
| Error | 1649.397 | 51 | 32.341 | | | | |
| Minor axis | 33.757 | 7 | 4.822 | 25.055 | 0.000 | | |
| Error | 9.816 | 51 | 0.192 | | | | |
| <i>r</i> | 0.378 | 7 | 0.054 | 2.306 | 0.040 | | |
| Error | 1.193 | 51 | 0.023 | | | | |
| II. Bonferroni's matrix of pairwise mean differences. | | | | | | | |
| Major axis | <i>Anapithecus</i> | <i>Dendropithecus</i> | <i>Dryopithecus</i> | <i>Oreopithecus</i> | <i>Ouranopithecus</i> | <i>Pliopithecus</i> | <i>Proconsul</i> |
| <i>Dendropithecus</i> | -9.481 | | | | | | |
| <i>Dryopithecus</i> | -0.149 | 9.332 | | | | | |
| <i>Oreopithecus</i> | 7.878 | 17.359** | 8.027 | | | | |
| <i>Ouranopithecus</i> | -9.315 | 0.166 | -9.166 | -17.193** | | | |
| <i>Pliopithecus</i> | -2.025 | 7.456 | -1.876 | -9.903 | 7.290 | | |
| <i>Proconsul</i> | -9.860 | -0.379 | -9.711** | -17.738** | -0.545 | -7.835 | |
| <i>Rangwapithecus</i> | -6.233 | 3.248 | -6.084 | -14.111 | 3.082 | -4.207 | 3.627 |
| Minor axis | | | | | | | |
| | <i>Anapithecus</i> | <i>Dendropithecus</i> | <i>Dryopithecus</i> | <i>Oreopithecus</i> | <i>Ouranopithecus</i> | <i>Pliopithecus</i> | <i>Proconsul</i> |
| <i>Dendropithecus</i> | -0.817* | | | | | | |
| <i>Dryopithecus</i> | 0.466 | 1.282* | | | | | |
| <i>Oreopithecus</i> | -0.713 | 0.103 | -1.179** | | | | |
| <i>Ouranopithecus</i> | 1.117** | 1.934* | 0.651 | 1.830 | | | |
| <i>Pliopithecus</i> | 0.527 | 1.344* | 0.062 | 1.241** | -0.590 | | |
| <i>Proconsul</i> | -0.900** | -0.083 | -1.366** | -0.187 | -2.017** | -1.428** | |
| <i>Rangwapithecus</i> | -1.187** | -0.371 | -1.653** | -0.474 | -2.305** | -1.715** | -0.287 |
| Orientation concentration (<i>r</i>) | | | | | | | |
| | <i>Anapithecus</i> | <i>Dendropithecus</i> | <i>Dryopithecus</i> | <i>Oreopithecus</i> | <i>Ouranopithecus</i> | <i>Pliopithecus</i> | <i>Proconsul</i> |
| <i>Dendropithecus</i> | 0.095 | | | | | | |
| <i>Dryopithecus</i> | -0.135 | -0.230 | | | | | |
| <i>Oreopithecus</i> | -0.060 | -0.156 | 0.075 | | | | |
| <i>Ouranopithecus</i> | -0.045 | -0.140 | 0.090 | 0.015 | | | |
| <i>Pliopithecus</i> | -0.028 | -0.123 | 0.107 | 0.032 | 0.017 | | |
| <i>Proconsul</i> | 0.016 | -0.080 | 0.151 | 0.076 | 0.061 | 0.044 | |
| <i>Rangwapithecus</i> | -0.228 | -0.323* | -0.093 | -0.168 | -0.183 | -0.200 | -0.244 |

* $p < 0.1$, ** $p < 0.05$

a hard-object feeder, and that *Oreopithecus*, and perhaps the pliopithecoid from Spain, *Rangwapithecus*, and *Micropithecus* were more folivorous.

Feature size differences and feature orientation concentration results are more difficult to interpret. *Rangwapithecus* evidently has features oriented more heterogeneously than do other taxa. Because such data have not yet been collected for extant taxa, this is difficult to interpret, though we suspect that this may be related to occlusal mechanics or jaw movements during chewing. *Ouranopithecus* has the widest features, which is consistent with a hard-object interpretation (see Teaford 1988b, Teaford, Runestad 1992). Likewise, *Micropithecus*, *Rangwapithecus*, the pliopithecoid from Castell de Barbera, and *Oreopithecus* all have the narrowest features on average for their superfamilies, which is more consistent with

folivory. On the other hand, there is curious tendency for the Early Miocene African taxa to have smaller features on average than the Middle to Late Miocene Eurasian forms. Comparisons of data presented here with SQ data might better allow us to interpret these microwear results.

COMPARISONS WITH SHEARING CREST RESULTS

Shearing crest data are presented in Table 4 and illustrated in Figure 6. These data (except for *Pliopithecus zhanxiangi*) were first presented in Kay (1977) and Ungar, Kay (1995). It is clear that African Miocene apes have a range of SQ values comparable to that of extant hominoids (10% and 12% respectively), but the Eurasian SQ values (43%) vary

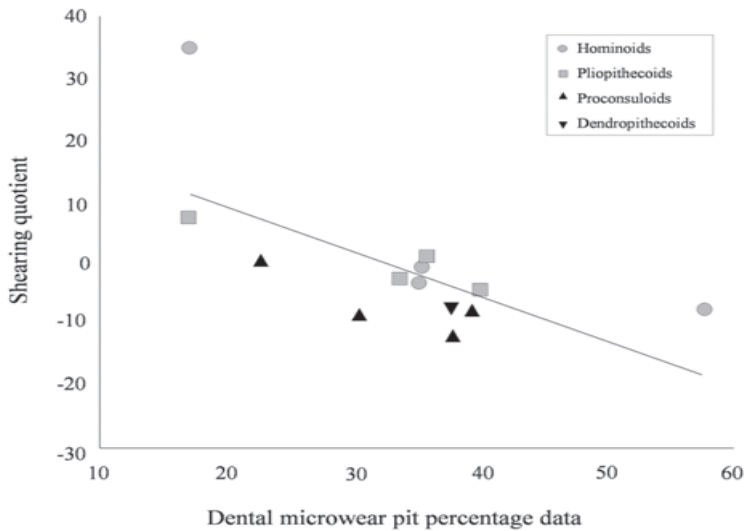


FIGURE 7. Least squares regression of mean shearing quotients and mean percentage incidence of pitting for several taxa. Middle to late Miocene Eurasian taxa are in grey, whereas Early Miocene African species are in black.

considerably more than do those of living apes. Nevertheless, the Eurasian data are easier to interpret (Ungar, Kay 1995). First, *Oreopithecus* and the pliopithecids from Castell de Barbera have higher SQ values than expected of a soft-fruit eating hominoid. These

values exceed even those of gorillas and siamang. This is consistent with a diet dominated by leaves. In contrast, *Ouranopithecus* has a considerably lower SQ than any extant ape. Because hard-object feeding monkeys show lower SQ values than closely related soft-fruit eaters (Fleagle *et al.* 1997), we have posited that *Ouranopithecus* was a hard-object specialist. All other Eurasian taxa analysed in both microwear and SQ studies (*Dryopithecus laietanus*, *Pliopithecus platydon*, *P. zhanxiangi* and *Anapithecus hernyaki*) have intermediate SQs, within the range of frugivorous gibbons and chimpanzees.

TABLE 4. Shearing quotient values* and percentage incidence pitting compared for various Miocene ape taxa.

| | SQ | %-pitting |
|--------------------------------------|--------|-----------|
| Dendropithecoidea | | |
| <i>Dendropithecus macinnesi</i> | -7.56 | 37.5 |
| <i>Limnopithecus evansi</i> | -5.15 | - |
| <i>Limnopithecus legetet</i> | -3.46 | - |
| <i>Micropithecus clarki</i> | - | 21.3 |
| Proconsuloidea | | |
| <i>Afropithecus turkanensis</i> | - | 43.0 |
| <i>Proconsul heseloni</i> | -12.49 | 37.6 |
| <i>Proconsul nyanzae</i> | -8.96 | 30.2 |
| <i>Proconsul major</i> | -8.56 | 39.1 |
| <i>Rangwapithecus gordani</i> | -0.26 | 27.3 |
| Pliopithecoidea | | |
| <i>Epipliopithecus vindobonensis</i> | - | 39.8 |
| <i>Pliopithecus platydon</i> | -4.83 | 38.9 |
| <i>Pliopithecus zhanxiangi</i> | -2.78 | 33.4 |
| <i>Anapithecus hernyaki</i> | 0.61 | 35.6 |
| Castell de Barbera | 7.17 | 16.9 |
| Hominoidea | | |
| <i>Ouranopithecus macedoniensis</i> | -8.43 | 57.7 |
| <i>Dryopithecus brancoi</i> | - | 39.8 |
| <i>Dryopithecus crusafonti</i> | - | 37.3 |
| <i>Dryopithecus laietanus</i> | -1.07 | 35.4 |
| <i>Dryopithecus fontani</i> | 1.32 | - |
| <i>Oreopithecus bambolii</i> | 35.00 | 17.0 |

*Original SQ data from Kay (1977) and Ungar and Kay (1995) except for *Pliopithecus zhanxiangi*, where the value was computed for BPV 261.

The SQ and microwear data for Eurasian Miocene apes accord well with one another. On the basis of both SQ data and microwear pit percentages, *Oreopithecus* and the pliopithecids from Castell de Barbera are reconstructed to have been folivores, *Ouranopithecus* is inferred (in combination with their wide microwear features) to have been a hard-object feeder, and *Dryopithecus laietanus*, *Pliopithecus platydon*, *P. zhanxiangi* and *Anapithecus hernyaki* probably all had diets dominated by soft fruits. The congruence of these results is remarkable, and may be considered testament to the robusticity of these reconstructions despite small sample sizes.

SQ results for the African apes are more difficult to interpret. While the range of their SQ values is more comparable to that of extant hominoids, the living ape range is "upshifted" relative to the Miocene taxa by about 50% (approximately 6 SQ units). Direct comparisons of SQ values suggest, at first glance, that *Rangwapithecus* and *Limnopithecus* were soft-fruit eaters and the other African fossil taxa were extreme hard-object feeders. Kay and Ungar (1997) suggested, however, that these early Miocene forms had overall shorter shearing crests than later apes. This was explained as a phylogenetic or temporal effect, akin to the observation that cercopithecoids as a whole have longer crests than platyrrhines independent of diet. Because folivores still have higher SQ values than

TABLE 4. Appendix. Raw data.

| Taxon | Specimen | N | % pits | Axis Len | | Minor | r | Pits | | Striations | |
|-------------------------|----------|-----|--------|----------|------|-------|-------|------|-------|------------|-----|
| | | | | Major | Len | | | Len | Wid | Len | Wid |
| <i>Afropithecus</i> | WK 16999 | 157 | 43.00 | 15.78 | 2.26 | 0.55 | 6.35 | 3.60 | 22.69 | 1.12 | |
| <i>Anapithecus</i> | RUD 76 | 279 | 37.28 | 19.42 | 2.83 | 0.40 | 8.56 | 5.44 | 25.88 | 1.28 | |
| <i>Anapithecus</i> | RUD 89 | 288 | 43.75 | 19.78 | 2.96 | 0.76 | 9.41 | 4.50 | 27.84 | 1.76 | |
| <i>Anapithecus</i> | RUD 90 | 97 | 29.90 | 45.88 | 3.18 | 0.63 | 9.81 | 5.54 | 61.26 | 2.18 | |
| <i>Anapithecus</i> | RUD 106 | 334 | 29.34 | 21.22 | 2.01 | 0.43 | 6.72 | 4.40 | 27.24 | 1.02 | |
| <i>Anapithecus</i> | RUD 108 | 333 | 37.54 | 20.69 | 2.42 | 0.57 | 6.88 | 4.30 | 28.98 | 1.29 | |
| <i>Dendropithecus</i> | CA 384 | 126 | 49.21 | 14.28 | 2.51 | 0.59 | 7.55 | 3.83 | 20.80 | 1.24 | |
| <i>Dendropithecus</i> | CA 579 | 140 | 31.43 | 16.94 | 1.21 | 0.74 | 3.73 | 1.64 | 23.00 | 1.02 | |
| <i>Dendropithecus</i> | RU 1806 | 166 | 44.58 | 15.25 | 2.12 | 0.74 | 6.27 | 3.12 | 22.47 | 1.32 | |
| <i>Dendropithecus</i> | RU 1850 | 131 | 38.17 | 14.77 | 2.03 | 0.65 | 5.93 | 2.86 | 20.22 | 1.52 | |
| <i>Dendropithecus</i> | RU 1866 | 84 | 21.43 | 23.08 | 1.47 | 0.35 | 4.94 | 2.34 | 28.03 | 1.23 | |
| <i>Dendropithecus</i> | RU 2015 | 202 | 40.10 | 11.18 | 1.84 | 0.85 | 6.77 | 3.04 | 14.14 | 1.04 | |
| <i>Dryopithecus</i> | RUD 77 | 312 | 42.95 | 21.50 | 2.88 | 0.26 | 7.92 | 5.04 | 31.72 | 1.26 | |
| <i>Dryopithecus</i> | RUD 141 | 189 | 36.61 | 25.15 | 3.01 | 0.39 | 8.27 | 5.36 | 34.88 | 1.65 | |
| <i>Dryopithecus</i> | IPS 1798 | 168 | 31.55 | 25.21 | 3.11 | 0.20 | 9.94 | 6.42 | 32.25 | 1.58 | |
| <i>Dryopithecus</i> | IPS 1820 | 98 | 31.63 | 36.11 | 3.21 | 0.70 | 11.46 | 6.04 | 47.51 | 1.89 | |
| <i>Dryopithecus</i> | IPS 1821 | 176 | 48.86 | 23.00 | 3.96 | 0.42 | 9.80 | 5.98 | 35.62 | 2.03 | |
| <i>Dryopithecus</i> | IPS 9000 | 232 | 34.48 | 22.99 | 2.59 | 0.38 | 7.78 | 5.20 | 30.99 | 1.22 | |
| <i>Dryopithecus</i> | IPS 1796 | 154 | 36.36 | 22.78 | 3.26 | 0.61 | 11.16 | 6.04 | 29.41 | 1.67 | |
| <i>Epiplioptithecus</i> | OE 304 | 193 | 39.38 | 25.04 | 2.88 | 0.50 | 8.87 | 5.11 | 35.54 | 1.43 | |
| <i>Micropithecus</i> | MB 11652 | 123 | 17.07 | 21.54 | 1.74 | 0.76 | 11.02 | 4.57 | 23.70 | 1.16 | |
| <i>Micropithecus</i> | MB 11796 | 94 | 25.53 | 18.57 | 1.51 | 0.49 | 6.11 | 3.13 | 22.85 | 0.95 | |
| <i>Oreopithecus</i> | BAC 60 | 167 | 11.38 | 35.50 | 1.82 | 0.40 | 9.72 | 5.89 | 38.81 | 1.29 | |
| <i>Oreopithecus</i> | BAC 66 | 137 | 20.44 | 29.88 | 1.79 | 0.77 | 6.82 | 3.58 | 35.81 | 1.33 | |
| <i>Oreopithecus</i> | BAC 69 | 100 | 15.00 | 38.31 | 2.28 | 0.32 | 8.89 | 6.44 | 43.50 | 1.54 | |
| <i>Oreopithecus</i> | BAC 198 | 143 | 15.38 | 34.69 | 1.79 | 0.71 | 9.88 | 5.09 | 39.20 | 1.19 | |
| <i>Oreopithecus</i> | BAC 104 | 103 | 17.48 | 36.14 | 2.13 | 0.53 | 9.72 | 5.79 | 41.74 | 1.35 | |
| <i>Oreopithecus</i> | MONT 23 | 335 | 20.00 | 23.81 | 1.64 | 0.50 | 6.82 | 4.10 | 28.05 | 1.03 | |
| <i>Oreopithecus</i> | RIB 18 | 196 | 40.31 | 21.47 | 2.81 | 0.49 | 8.11 | 4.79 | 30.49 | 1.48 | |
| <i>Oreopithecus</i> | RIB 21 | 122 | 9.02 | 40.39 | 2.02 | 0.22 | 8.47 | 5.10 | 43.55 | 1.71 | |
| <i>Oreopithecus</i> | RIB 22 | 165 | 3.64 | 39.29 | 1.42 | 0.54 | 9.18 | 4.18 | 40.43 | 1.31 | |

TABLE 4. Appendix. Raw data.

| Taxon | Specimen | N | % pits | Axis Len | | Minor | r | Pits | | Striations | |
|-------------------------------------|----------|-----|--------|----------|------|-------|-------|------|-------|------------|-----|
| | | | | Major | Len | | | Len | Wid | Len | Wid |
| <i>Ouranopithecus macedoniensis</i> | RPL 54 | 193 | 43.01 | 18.89 | 3.03 | 0.69 | 9.38 | 5.08 | 26.07 | 1.48 | |
| <i>Ouranopithecus macedoniensis</i> | RPL 55 | 280 | 63.93 | 14.09 | 3.56 | 0.61 | 7.83 | 4.42 | 25.18 | 2.02 | |
| <i>Ouranopithecus macedoniensis</i> | RPL 75 | 351 | 57.83 | 12.28 | 3.22 | 0.48 | 7.49 | 4.50 | 18.85 | 1.47 | |
| <i>Ouranopithecus macedoniensis</i> | RPL 76 | 251 | 56.57 | 17.01 | 3.70 | 0.52 | 8.66 | 5.08 | 27.89 | 1.91 | |
| <i>Ouranopithecus macedoniensis</i> | RPL 128 | 191 | 60.21 | 19.81 | 4.74 | 0.42 | 10.67 | 6.51 | 33.64 | 2.06 | |
| <i>Ouranopithecus macedoniensis</i> | NKT 21 | 231 | 67.10 | 14.79 | 4.36 | 0.32 | 8.41 | 5.58 | 27.78 | 1.87 | |
| <i>Ouranopithecus macedoniensis</i> | XIR 1 | 221 | 55.20 | 15.71 | 3.97 | 0.55 | 11.00 | 5.88 | 21.52 | 1.62 | |
| Castell de Barbera | IPS ? | 124 | 22.52 | 31.07 | 2.73 | 0.49 | 13.36 | 6.49 | 36.49 | 1.61 | |
| Castell de Barbera | IPS ? | 107 | 11.21 | 33.29 | 2.29 | 0.63 | 9.50 | 5.29 | 36.29 | 1.91 | |
| <i>Pliopithecus platydon</i> | LMJ 2107 | 128 | 36.72 | 21.35 | 3.31 | 0.22 | 9.81 | 6.70 | 28.05 | 1.35 | |
| <i>Pliopithecus platydon</i> | SK 1453 | 220 | 35.00 | 26.11 | 3.09 | 0.75 | 9.29 | 5.31 | 35.16 | 1.89 | |
| <i>Pliopithecus zhanxiangi</i> | BPV 261 | 115 | 50.43 | 19.13 | 4.26 | 0.72 | 11.77 | 6.60 | 26.61 | 1.88 | |
| <i>Pliopithecus zhanxiangi</i> | BPV 1021 | 164 | 16.46 | 26.90 | 2.17 | 0.43 | 10.49 | 5.89 | 30.12 | 1.44 | |
| <i>Proconsul heseloni</i> | RU 7290 | 132 | 39.39 | 19.75 | 1.93 | 0.31 | 5.23 | 2.82 | 29.19 | 1.36 | |
| <i>Proconsul heseloni</i> | RU 2088 | 113 | 41.59 | 17.74 | 1.57 | 0.70 | 4.39 | 2.17 | 27.24 | 1.15 | |
| <i>Proconsul heseloni</i> | RU 1865 | 186 | 51.08 | 10.03 | 1.50 | 0.63 | 4.43 | 2.10 | 15.88 | 0.87 | |
| <i>Proconsul heseloni</i> | RU 1680 | 118 | 39.10 | 11.23 | 1.91 | 0.74 | 9.69 | 3.52 | 12.58 | 1.00 | |
| <i>Proconsul heseloni</i> | RU 5871 | 147 | 35.09 | 15.76 | 1.81 | 0.50 | 6.18 | 3.08 | 20.60 | 1.15 | |
| <i>Proconsul heseloni</i> | RU 2016 | 168 | 11.88 | 25.91 | 1.29 | 0.65 | 5.41 | 2.28 | 28.66 | 1.16 | |
| <i>Proconsul heseloni</i> | RU 2036 | 205 | 45.26 | 11.62 | 2.06 | 0.68 | 5.95 | 3.13 | 16.28 | 1.16 | |
| <i>Proconsul major</i> | SO 542 | 178 | 35.72 | 15.65 | 1.88 | 0.50 | 6.61 | 2.90 | 20.69 | 1.31 | |
| <i>Proconsul major</i> | SO 541 | 111 | 40.54 | 19.99 | 1.96 | 0.64 | 6.41 | 2.91 | 29.25 | 1.31 | |
| <i>Proconsul major</i> | LG 452 | 188 | 29.79 | 14.68 | 1.81 | 0.57 | 7.59 | 3.56 | 17.68 | 1.08 | |
| <i>Proconsul major</i> | CA 1856 | 148 | 48.40 | 11.25 | 2.12 | 0.45 | 5.64 | 3.10 | 16.28 | 1.17 | |
| <i>Proconsul major</i> | CA 568 | 216 | 34.26 | 11.44 | 2.05 | 0.53 | 6.98 | 3.92 | 13.77 | 1.08 | |
| <i>Proconsul major</i> | CA 388 | 157 | 45.86 | 15.59 | 1.87 | 0.57 | 5.61 | 2.41 | 24.05 | 1.41 | |
| <i>Proconsul nyanzae</i> | RU 16000 | 96 | 12.50 | 22.74 | 1.77 | 0.74 | 9.50 | 4.31 | 24.63 | 1.41 | |
| <i>Proconsul nyanzae</i> | RU 2087 | 206 | 42.23 | 10.20 | 1.50 | 0.43 | 4.88 | 2.43 | 14.08 | 0.83 | |
| <i>Proconsul nyanzae</i> | RU 17377 | 249 | 30.13 | 12.12 | 1.56 | 0.57 | 5.85 | 2.78 | 14.64 | 0.98 | |
| <i>Proconsul nyanzae</i> | RU 1982 | 115 | 36.14 | 18.46 | 1.68 | 0.54 | 5.38 | 2.45 | 25.87 | 1.25 | |
| <i>Rangwapithecus gordoni</i> | SO 700 | 56 | 21.43 | 25.62 | 1.75 | 0.24 | 6.70 | 2.97 | 30.78 | 1.42 | |
| <i>Rangwapithecus gordoni</i> | SO 907 | 107 | 42.06 | 12.71 | 1.58 | 0.29 | 4.45 | 2.40 | 18.70 | 0.99 | |
| <i>Rangwapithecus gordoni</i> | SO 1112 | 155 | 28.39 | 17.09 | 1.44 | 0.32 | 4.36 | 2.11 | 22.13 | 1.18 | |
| <i>Rangwapithecus gordoni</i> | SO 1958 | 121 | 17.36 | 21.24 | 1.20 | 0.47 | 4.93 | 2.14 | 24.67 | 1.01 | |

frugivores *within* each of these groups, it may well be that SQ ranges for closely related taxa provide more useful information than do actual values. Accordingly then, perhaps *Rangwapithecus* was still folivorous, and *Proconsul*, *Dendropithecus*, and *Limnopithecus* were soft-fruit frugivores.

The microwear evidence is more consistent with the latter scenario. None of the African Early Miocene taxa considered in the SQ study had microwear pit percentage values of a hard-object feeder. Indeed, most, including all three *Proconsul* species and *Dendropithecus* appear to have been soft-fruit eaters. *Rangwapithecus* values do not differ significantly from those of the other Miocene apes, but this taxon did have the lowest pit percentages and narrowest features of any of the fossil African apes considered in both the SQ and microwear studies. Mean pit percentages and feature breadth differences between *Rangwapithecus* and the other fossil African apes are comparable to those between some extant folivores and soft-fruit eaters. Thus, despite a paucity microwear sample ($n = 4$), the accord between the rank-orders of taxa for the microwear and SQ datasets is sufficiently compelling to suggest that *Rangwapithecus* was probably more folivorous than either *Proconsul* or *Dendropithecus*. If so, we can "anchor" the African Miocene range to an offset of SQ ~ -6 from the extant hominoid range (see *Figure 6*). This is consistent with the notion that there was an overall shift toward increased molar shearing crest lengths in apes following the Early Miocene akin to differences between cercopithecoids and platyrrhines (Kay, Ungar 1997). If this shift was related to changes in occlusal mechanics or tooth function, it might also help elucidate general differences observed in microwear features size between the Early Miocene African apes and Middle to Late Miocene Eurasian forms. More work is needed, however, to explain these differences between samples.

If this "anchor" holds, comparisons of epigenetic microwear patterns with adaptive dental morphology may allow us to separate some functional and phylogenetic components of tooth shape. While microwear variables are best considered together for reconstructing diets, it is possible to compare pit percentages and shearing quotients directly (*Figure 7, Table 4*), as both may be related to the angle of approach into occlusion during mastication and yield similar rank-orders for taxa considered here (see Ungar 1998). Spearman's non-parametric correlation coefficient ($r = -0.64$, $p = 0.018$) shows a negative association between these variables. When a least squares regression is fit to the raw data for illustrative purposes, all of the Early Miocene taxa fall below the line, whereas most of the Middle to Late Eurasian forms fall above. This suggests that the African species have lower SQs for a given percentage incidence of pitting than do the Eurasian species. The residuals themselves therefore provide important information that may ultimately allow us to separate functional aspects of molar shape from those related to phylogeny or temporal trends.

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