Dental microwear profilometry of African non-cercopithecoid catarrhines of the Early Miocene

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INTRODUCTION

The early Miocene of eastern Africa was home to a number of primate taxa. Their phylogenetic relationships and ecological niches have been much discussed, but not often agreed upon. Among the taxa present in these areas are two commonly recognized superfamilies, Proconsuloidea and Dendropithecoidea, along with a number of genera of uncertain taxonomic affiliation (*e.g.*, *Limnopithecus*, *Kalepithecus*.) [1, 2]. These primates existed from approximately 23 Ma - 16 Ma and represent a sizable part of the east African Miocene fossil record.

Previous analyses of these primates have focused on cladistics[3,4] ,postcranial functional morphology [5,6,7], and dental morphology [8,9,10,11,12]. A less thoroughly explored area is the direct analysis of diet as a proxy for paleohabitat and paleobiology.

Here we examine the diets of east African Miocene non-cercopithecoid primates using dental microwear texture analysis, which has been widely used to reconstruct the diets and paleohabitats of a broad range of taxa [13,14,15,16,17].

For this study we have assembled the largest microwear database of African Miocene catarrhines to date (n = 83), and have included *Limnopithecus*, a genus not analyzed in previous studies. This is the first direct comparison of the microwear *within* the African Miocene catarrhines, although some fossils have been used as comparative material for broader studies of Miocene primate paleoecology and paleobiology [18].

MATERIALS AND METHODS

Post-canine teeth for all available Early Miocene non-cercopithecoid catarrhine primates with potential microwear were collected from the Kenya National Museum in Nairobi, Kenya following standardized protocols [15,19,20].

Phase II crushing/grinding facets were inspected with a Sensofar PLμ confocal imaging profiler (Solarius, Inc) 100x objective lens. Point clouds were generated from 4 adjacent fields of 102 x 138 µm with a lateral sampling interval of 0.18 µm and vertical resolution of 0.005 µm.

Point clouds were analyzed using scale-sensitive fractal analysis [21]. This technique uses fractal geometry to analyze 6 variables to describe surface texture: Area scale fractal complexity (*Asfc*), Scale of maximum complexity (*Smc*), Anisotropy (*epLsar*), Textural fill volume (*Tfv*), and Heterogeneity (*HAsfc*) based on two grid densities, 3 x 3 ($HAsfc_9$) and 9x9 ($HAsfc_{81}$). See Figures 1 and 2 for graphical depictions of texture surfaces.

Microwear texture variables were collected from 83 individuals, encompassing 7 genera. Texture attributes were rank transformed and compared using conservative non-parametric statistical tests. Pairwise multivariate analysis of variance (MANOVA) tests were run within the fossil sample. An additional MANOVA was performed to compare 5 fossil genera (taxa with sample sizes >1)with a diverse group of extant primates from Scott *et al.*, 2012 [20]. Principal components analysis (PCA) was used for visualization co-variation and correlation of variables in n-dimensional space.

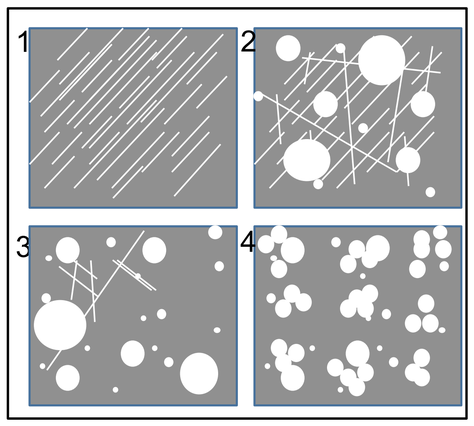


Figure 1 – Diagrammatic rendering of microwear surfaces modified from Scott *et al.*, 2006 [22]. Fields depict: 1. anisotropic texture, 2. complex texture, 3. heterogeneous texture, 4. homogeneous texture.

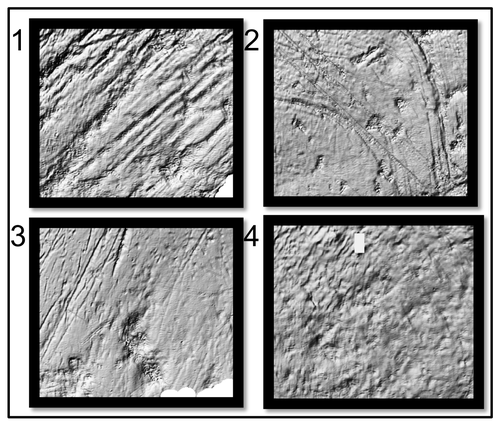


Figure 2 – Photosimulations of microwear surfaces depicting examples of different texture types. Fields depict: 1. anisotropic texture, 2. complex texture, 3. heterogeneous texture, 4. homogeneous texture.

RESULTS

• Statistical tests show no significant difference among any of the fossil primates (Table 1), although there are significant differences between fossil microwear variables for the fossil taxa and those of extant primates (from Scott *et al.*, 2012) [20] (Table 2).

– Fossil genera are more commonly different from extant specialist feeders than from generalists

– Fossil genera are more commonly different from Platyrrhini and Cercopithecoidea than they are from Hominoidea.

•PCA/CVA analyses fail to show consistent differences in the morphospace of microwear texture variables in fossil genera and species

Genus	*Dendropithecus*	*Limnopithecus*	*Micropithecus*	*Proconsul*	*Rangwapithecus*
Dendropithecus		0.942568	0.359036	0.810114	0.61569
Limnopithecus			0.15656	0.49194	0.469933
Micropithecus				0.257787	0.697534
Proconsul					0.616872
Rangwapithecus					

Wilks' lambda:	0.7277
df1:	24
df2:	248.9
F:	0.9894
p(same):	0.4808
Eigenvalue 1:	0.1968
Eigenvalue 2:	0.08411

Pillai trace:	0.2985
df1:	24
df2:	296
F:	0.9947
p(same):	0.4731
Percent:	57.98
Percent:	24.78

Table 1 – MANOVA table describing comparisons between fossil genera. P=0.05

Genus	*Dendropithecus*	*Limnopithecus*	*Micropithecus*	*Proconsul*	*Rangwapithecus*
Gorilla	0.779	0.126	0.129	0.744	0.077
Pan	0.165	0.022*	0.254	0.165	0.037*
Pongo	0.705	0.200	0.511	0.523	0.269
Lophocebus	0.062	$2.88E^{-04}$*	0.091	0.021*	0.004*
Alouatta	$3.48E^{-05}$*	$4.21E^{-08}$*	$4.10E^{-03}$*	$1.26E^{-06}$*	$1.05E^{-04}$*
Ateles	0.111	0.003*	0.175	0.226	0.042*
Cebus	$2.91E^{-04}$*	$2.16E^{-08}$*	0.009*	$1.63E^{-04}$*	$1.66E^{-05}$*
Cercocebus	0.001*	$1.23E^{-07}$*	0.009*	0.002*	$3.26E^{-05}$*
Colobus	0.036*	$2.13E^{-04}$*	0.004*	0.009*	0.001*
Macaca	0.311	0.014*	0.117	0.206	0.017*
Papio	0.020*	$5.18E^{-05}$*	0.042*	0.048*	0.001*
Presbytis	0.126	0.011*	0.390	0.069	0.159
Procolobus	0.025*	$2.00E^{-04}$*	0.021*	0.017*	0.002*
Semnopithecus	0.019*	0.001*	0.199	0.003*	0.011*
Theropithecus	0.013*	$1.28E^{-04}$*	0.033*	0.001*	0.002*
Trachypithecus	0.146	0.028*	0.218	0.019*	0.055

Table 2 – MANOVA table describing comparisons between fossil and extant genera. P=0.05. Significance indicated by *

DISCUSSION

• Results suggests that these fossil taxa were filling the common primate niche of generalized (and perhaps opportunistic) frugivory, though some differentiation may have existed (Figure 7).

• The possibility of exogenous grit (e.g., dirt, ash, or other wind blown abrasives) affecting the microwear signature of the primate fossils is unlikely, as a recent study of fossil Tragulidae (*Dorcatherium*), from the same deposits indicate clear distinctions among 4 species [24] (Figure 4).

• While no significant differences were seen among the fossils, PCA analyses show a possible dietary restriction of *Proconsul* on Songhor (possibly due to competition with *Rangwapithecus?)* (Figures 5 and 6).

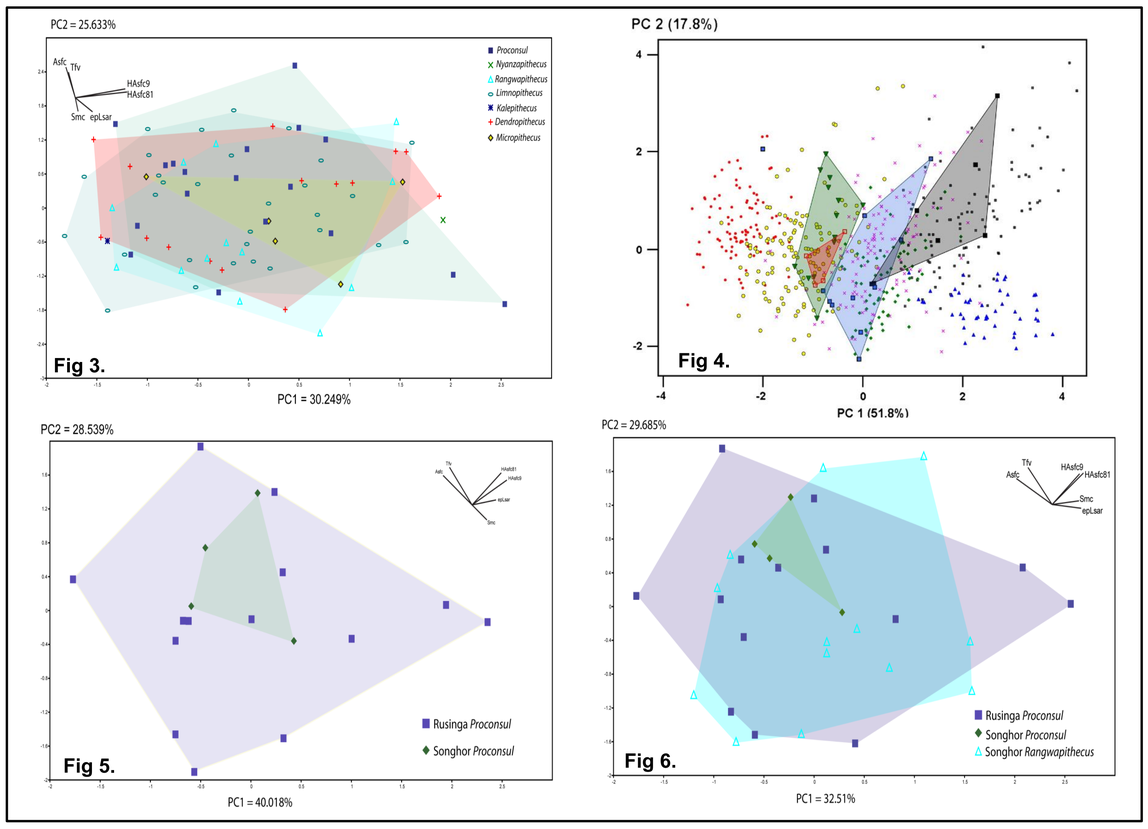


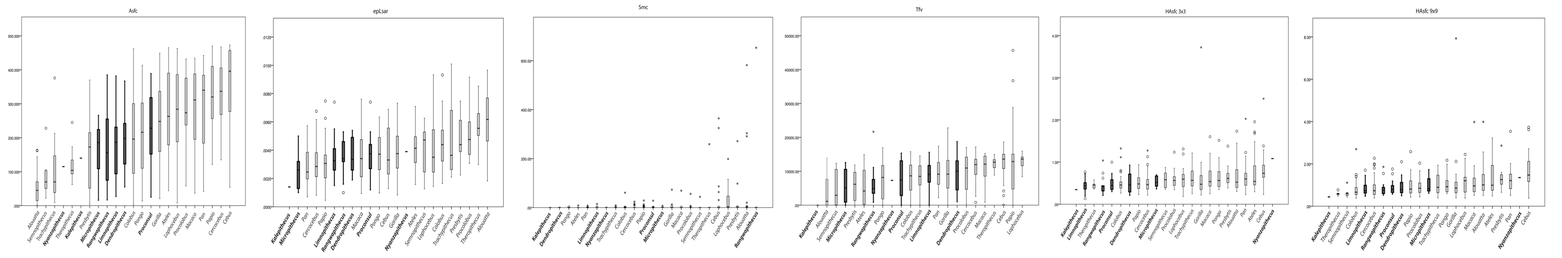
Figure 3 – PCA of all fossil taxa. Significant overlap suggests no statistical difference in microwear texture variables.

Figure 4 – PCA plot showing separation of species from Rusinga and Songhor Island **Tragulidae (*Dorcatherium*)** [24].

Figure 5 – PCA of *Proconsul* microwear texture variables on Rusinga and Songhor.

Figure 6 – PCA of *Proconsul* and *Rangwapithecus* microwear texture variables on Rusinga and Songhor.

Figure 7 -- Microwear texture variables of fossils (bold) and extant primates. Outliers indicated by º. Extreme values indicated by *.



CONCLUSIONS

• Here we present results of the first dental microwear texture analysis performed exclusively within African Miocene non-cercopithecoid catarrhines. Results corroborate previous studies in revealing no significant differences found in the microwear patterns among any of the fossil taxa tested herein [18].

• Our results suggest that despite differences in body size and dental complexity, the non-cercopithecoid primates of the early-mid African Miocene were consuming foods that had similar mechanical properties, at least for available individuals shortly before death [23] , which therefore caused similar microwear patterns.

• Obscuration of microwear by exogenous grit is unlikely, as fossil tragulids from the same deposits exhibit clear species differences in their microwear textures [24].

• The microwear signatures of these fossil primates does not indicate that they were consuming identical foods, merely that they were eating mechanically similar types of foods, and plants with similar phytolith or dietary grit content, in the weeks before death.

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