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Dental microwear of Neogene cercopithecoids from the Turkana Basin, Kenya

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ABSTRACT

Reconstructions of the diets of individual fossil species can help us better understand the adaptive radiations of higher-level primate taxa. Some researchers have posited that folivory was key to the divergence of cercopithecoids from the catarrhine stem, with bilophodonty reflecting an adaptation for leaf consumption. Others have questioned this model, suggesting that dental functional morphology and wear patterns are more consistent with frugivory and perhaps hard-object consumption. Here, we present new microwear texture data ($n = 22$) that might contribute to the discussion. Specimens were sampled from Buluk (~17 Ma, Early Miocene, *Noropithecus bulukensis*) and Lothagam (~8–4 Ma, Late Miocene to Early Pliocene, *Parapapio lothagamensis*/sp. indet and fossil Colobinae) in the Turkana Basin, Kenya, and compared with a select group of extant taxa. Point clouds were generated from high-resolution replicas of molar teeth using a white light confocal profiler and analyzed using scale-sensitive fractal analysis. Results of dental microwear texture analyses for both fossil samples align with those of extant grass (*Theropithecus*) and leaf (*Trachypithecus*) eaters and differ significantly from those of frugivores/generalists (*Macaca, Papio*) and hard-object specialists (*Cercocebus*). While both *Noropithecus* and *Parapapio* postdate the divergence of the cercopithecoid clade from other catarrhines, these results are largely consistent with previous work on the dietary ecology of the early papionin *Parapapio* from Lothagam and the traditional 'tough-food' model of leaves/grasses. Some previous *Noropithecus* dietary reconstructions indicated a diet of harder objects or fruits. Thus, the discrepancy between the microwear results and previous dietary reconstructions for *N. bulukensis* is unexpected. These results raise hypotheses that may help provide new context and insights into the radiation of this important superfamily of primates.

1. Introduction

Current fossil evidence suggests that cercopithecoids evolved from stem catarrhines sometime during the late Oligocene, with increasing taxonomic diversity and abundance in the Middle to Late Miocene and a concomitant decrease in extent of the non-cercopithecoid catarrhine radiation (i.e., 'apes') through the epoch (Andrews, 1981; Andrews et al., 1985; Harrison, 1989; Leakey et al., 2011; Begun, 2013; Stevens et al., 2013). These changes were associated with the earth's orbital dynamics, tectonic disruptions, and shifting ocean currents that affected regional precipitation and ultimately resulted in expanding open woodland and grassland habitats with abundant C4 grasses (Polissar et al., 2019; Peppe et al., 2023). Changes in available food resources for Oligo-Miocene

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catarrhines in Africa are hypothesized to have led to dietary shifts in multiple taxa over time and space.

Early cercopithecoids have been considered in light of such dietary shifts. Victoriapithecids (von Koenigswald, 1969; Benefit, 1987, 1993) and more basal cercopithecoids such as *Alophe* (Rasmussen et al., 2019), 'document the gradual development of a bilophodont molar bauplan' (Locke et al., 2020: 30). The evolution of bilophodont molars in these stem taxa has been suggested to reflect a specialization for a variable diet that might have included hard objects (Lucas and Teaford, 1994; Ungar and Teaford, 1996; Benefit, 1999, 2000). Subsequent modifications of this morphology later in the Miocene resulted in the classic distinction between colobine and cercopithecine molars, with the former having higher cusps, longer shearing crests, and higher shearing capacity than the latter (Kay, 1975; Kay and Hylander, 1978). However, as morphological variation may mask similarities or differences in dietary preference, the precise path of the paleoecological divergence and subsequent radiation of the clade has been the focus of the great deal of work.

Subtle differences in molar morphology have been used to estimate proportions of fruit and leaves in the diets of some stem cercopithecoid taxa (e.g., *Victoriapithecus* has slightly shorter relative shearing crest lengths than *Noropithecus*; Benefit, 1999), but such studies have tended to suggest that all consumed relatively high proportions of fruit. Moreover, while feature-based analyses of molar microwear (Lucas and Teaford, 1994; Ungar and Teaford, 1996; Palmer et al., 1998) have suggested a diet of fruit and perhaps hard objects, these analyses have been carried out only on *Victoriapithecus*. Even when recognizable colobines began to appear at approximately 12–8 Ma, they still had a relatively conservative molar shearing capacity, like their stem cercopithecoid counterparts (Benefit and Pickford, 1986; Benefit, 1999, 2000; Reitz, 2002; Merceron et al., 2009a, 2009b; Rossie et al., 2013; Suwa et al., 2015). It was not until later (i.e., 7.5–6 Ma) that African colobines began to show the deep lingual notches and shearing capacity characteristic of modern colobines (Leakey et al., 2003; Hlusko, 2007; Frost et al., 2009; Gilbert et al., 2010; Suwa et al., 2015).

Surprisingly, feature-based molar microwear analyses fail to detect significant differences between colobine and cercopithecine molars from the latest Miocene and Pliocene of Africa (Lucas and Teaford, 1994; Leakey et al., 2003; El-Zaatari et al., 2005; Teaford et al., 2008). Even recent dental microwear texture analyses of larger samples show only subtle differences between the subfamilies. However, in the case of Merceron et al. (2021), these analyses revealed microwear textures of large-bodied, Plio-Pleistocene colobines from the Shungura Formation to be more similar to modern papionins than to modern colobines. In essence, we are faced with the challenge of documenting differences in past diets while using forms of evidence of different resolutions—in this case, dental morphology and dental microwear (Teaford et al., 2023). Thus, any new evidence we gather on food preferences of early cercopithecoids will be helpful in clarifying dietary adaptations or variation within the group.

The Turkana Basin, Kenya, provides substantive temporal coverage for African fossil catarrhines, with primate-bearing fossil sites dated from the late Oligocene onward (Brown and McDougall, 2011). While the basin is best known for its Plio-Pleistocene hominin localities, there are many other earlier sites yielding fossil primates. Buluk (Harris and Watkins, 1974; Watkins, 1983; Leakey and Walker, 1985; Watkins, 1989; Locke et al., 2020) and Lothagam (Patterson et al., 1970; Leakey et al., 1996) are two such sites.

Here, we present the first dental microwear texture analysis (DMTA) of an early victoriapithecid from the Early Miocene site of Buluk (*Noropithecus bulukensis*) along with Mio-Pliocene cercopithecids from Lothagam (the Early papionin *Parapapio lothagamensis*/sp. indet. and indeterminate colobine species B and C). The aim is to contribute Turkana Basin catarrhine microwear texture data to the ongoing debates concerning the diets of stem and early crown cercopithecids from eastern Africa. To contextualize the microwear patterns from Buluk and Lothagam, we compare them with other fossil catarrhines from the late Paleogene and early Neogene from the Turkana Basin and with extant cercopithecids representing a broad range of dietary adaptations.

1.1. *Dental microwear analysis*

Dental microwear is a 'foodprint' approach that provides direct evidence for properties of foods eaten by individuals in the past via the marks they impart on teeth (Ungar, 2017; Teaford et al., 2023). By contrast, other lines of evidence for diet, such as gross tooth morphology, provide clues to what an individual could have eaten, but not necessarily its food preferences. In other words, microwear reflects actual behaviors of individuals rather than adaptations of taxa for foods with given material properties.

Primates that habitually crush hard and brittle foods, such as nuts, tend to have complex, pitted enamel surfaces (in terms of DMTA, high complexity but low anisotropy; Teaford and Walker, 1984; Scott et al., 2006; Ungar et al., 2008b; Calandra et al., 2012; Scott et al., 2012). Those that more often shear tough foods, such as many dicotyledon leaves and grass blades, tend to have enamel surfaces dominated by long, parallel striations (low complexity and high anisotropy). Soft-fruit eaters tend to have intermediate microwear patterns, with some scratches and some pits but enamel surfaces not dominated by one over the other (i.e., neither high complexity nor high anisotropy; Teaford and Walker, 1984; Scott et al., 2006; Ungar et al., 2008b; Calandra et al., 2012; Scott et al., 2012). Because morphological adaptation gives an indication of dietary potential and molar microwear gives an indication of actual behavior, these two approaches can provide complementary insights into possible diet differences among early eastern African cercopithecoids.

Of course, the etiology of microwear is complex, and patterning can be affected by factors other than food fracture properties, such as abrasive load and type (Ackermans et al., 2020; Hua et al., 2020; Schulz-Kornas et al., 2020; Teaford et al., 2021). Mandibular mechanics and tooth position may also play a role in observed variation (e.g., Gordon, 1982). Nevertheless, the dietary signal does usually rise above the noise (Rodrigues et al., 2009; Burgman et al., 2016; Merceron et al., 2016; Adams et al., 2020). Mammals that eat hard or tough foods tend to have either pitted or scratchy surfaces depending on their diet. This trend holds true considering a variety of mammalian groups, from marsupials to artiodactyls, carnivorans, primates, and many others (see Ungar, 2015 for review). Evidently, whether grit, dust, or phytoliths are the agents of abrasion, and regardless of the particulars of occlusal form and mechanics, microwear patterns still tend to reflect diet. This is, in large part, because angles of approach between opposing teeth are associated with specific food properties (Hua et al., 2015).

1.2. *Buluk and Lothagam samples*

Buluk is an Early Miocene locality, ~17 Ma based on geochronological and faunal analyses (McDougall and Watkins, 1985; Locke et al., 2020). This site was occupied by a major river system, likely with a riparian forest set within a strongly seasonal subhumid to semiarid open woodland (Lukens et al., 2021). Lothagam, on the other hand, has yielded a series of cercopithecid fossils primarily from the Nawata Formation ~7–6 Ma (Leakey et al., 1996; McDougall and Feibel, 1999; Feibel, 2003). The Nawata Formation was also deposited by a large river system, with intercalated altered tephra (particularly in the Lower Nawata Member) facilitating correlation across the exposures (Feibel, 2003). Vertebrate assemblages at Lothagam are consistent with not only a mosaic habitat of woodlands but also a C4-rich mixed-savanna adjacent to the large river system.

Here, the Buluk sample consists of an early stem cercopithecoid, the victoriapithecid *N. bulukensis*. Victoriapithecids typically possess a mixture of bilophodont dental characteristics that align with extant cercopithecids and stem catarrhine features (Locke et al., 2020). *Noropithecus* postcanine teeth are bunodont compared to other extant and fossil cercopithecoids (Miller et al., 2009), and while its molar occlusal morphology is similar to that of *Victoriapithecus*, the former has slightly longer molar shearing crests (Locke et al., 2020). Based on regressions of various dental variables correlated with diet in extant primates, Benefit (1999, 2000) estimated that *Noropithecus* had slightly higher shearing crests than *Victoriapithecus*, which led to an estimate of slightly more leaves in the diet. This still places both taxa as frugivores though, with over 70% of the diet composed of fruit. This interpretation contrasts with earlier assertions that cercopithecoid bilophodonty evolved for folivory (Napier, 1970). To the best of our knowledge, no microwear texture analysis has been published for any victoriapithecid, although feature-based analyses for *Victoriapithecus* have suggested frugivory or hard-object feeding (Lucas and Teaford, 1994; Ungar and Teaford, 1996; Palmer et al., 1998). Thus, one question to be evaluated in this study is whether *N. bulukensis* differs significantly from extant frugivores by DMTA.

Previous studies of feature-based dental microwear of *Par. lothagamensis* (an early papionin) and colobines from Lothagam, on the other hand, found occlusal facets dominated by long, parallel striations, like those of extant tough food feeders, such as folivorous colobines and grass-eating geladas (Leakey et al., 2003). Indeed, Leakey et al. (2003) and Teaford et al. (2008) found that the microwear patterns of colobines and cercopithecines during the Late Miocene and Plio-Pleistocene were practically indistinguishable, with both suggesting tough food diets. However, despite these results, the shearing crest morphology of Miocene cercopithecoids from Kenya suggests less shear potential than that observed for extant colobines (Rasmussen et al., 2019; Benefit, 2000), although some might be akin to those of tough-seed eaters today (Rossie et al., 2013). Additionally, a recent microwear texture analysis of Plio-Pleistocene colobines from the Shungura Formation, Lower Omo Valley, Ethiopia, suggests diets less focused on leaves than that observed for extant *Colobus guereza* (Merceron et al., 2021). Thus, a second set of questions to be evaluated in this study is whether the papionins and colobines from Lothagam differ from each other and how these compare with extant taxa in terms of dental microwear.

2. Materials and methods

2.1. Fossil samples

This study involved examination of all molar teeth (M^1–M^3 and M_1–M_3) of fossil cercopithecoids from Buluk (*N. bulukensis*) and Lothagam (*Par. lothagamensis*/sp. indet., fossil Colobinae spp.) available for study at the National Museums of Kenya in Nairobi and the Turkana Basin Institute in Turkwel as of June 2022 (total molar teeth: $n = 81$; Supplementary Online Material [SOM] Table S1). While combining molar types might increase within-sample variation and thus decrease discriminatory power of microwear, this is a common practice necessary for fossil taxa represented by smaller samples (Shearer et al., 2015; Ungar et al., 2020). All available supplementary fossil catarrhines from other late Paleogene and early Neogene Turkana Basin localities were also considered for analyses: samples from Topernawi (30–25 Ma, sp. indet.), Locherangan (17.5 Ma, *Afropithecus turkanensis*, *Simiolus enjiessii,* noncercopithecoid catarrhine sp. indet.; Anyonge, 1991), and specimens from the Nachukui Formation (Colobinae sp. indet., Gundling and Hill, 2000). These specimens were available for study at the National Museums of Kenya (Locherangan samples) and Turkana Basin Institute, Turkwel (Topernawi and Nachukui specimens). Additional information regarding the supplementary fossil catarrhines can be found in SOM Table S1.

2.2. Extant comparative samples

Calandra et al. (2022) recently found that the MountainsMap (Digital Surf Corp, Besançon, France) Scale-Sensitive Fractal Analysis (SSFA) module produces slightly, albeit statistically significantly, different texture values from the original ToothFrax (SurFract Corp, Worcester, MA) software package developed for microwear texture analysis. This suggests that direct comparisons of results between the two might introduce noise into the system. While ToothFrax was used to generate the original extant comparative baseline SSFA data, MountainsMap had to be used to generate data for the fossil primates presented here because the former is not available for modern operating systems. It was thus necessary to regenerate texture data for the original baseline point clouds using MountainsMap (version 8.1).

Given the amount of work required to regenerate texture data in MountainsMap from the original point clouds, we selected for our baseline a subset of extant cercopithecoid species representing a broad range of reported food preferences. The original point cloud files used in the studies by Daegling et al. (2011; *Cercocebus atys,* hard-object specialist, $n = 15$ M^1s) and Scott et al. (2012; *Trachypithecus cristatus,* folivore, $n = 12$; *Macaca fascicularis,* frugivore, $n = 20$; *Papio ursinus*, dietary generalist consuming a broad range of savanna foods, $n = 12$; *Theropithecus gelada*, grass-eater, $n = 12$) were reanalyzed accordingly. Point clouds for the Turkana Basin primate study were generated with the same confocal profiler that was used in the original baseline series studies.

2.3. Specimen preparation and surface scanning

First, fossil molars of all primates available for study were examined visually and those with wear facet surfaces obscured by obvious taphonomic damage or by matrix were excluded from molding. Those deemed suitable candidates for microwear analysis from Buluk and Lothagam ($n = 81$) and the supplemental sites ($n = 84$) were cleaned using alcohol-soaked cotton swabs, and high-resolution molds were produced using President Jet regular body dental impression material (Coltene-Whaledent, Alstatten, Switzerland) following standard microwear analysis protocols (Teaford, 1988; King et al., 1999). High-resolution replicas were then prepared for further examination using epoxy resin (Epox-Acast, Macungie, PA) poured into the molds, centrifuged, and allowed to dry. All replicas were then screened for postmortem damage by confocal profilometry following the criteria of Teaford (1988) and King et al. (1999). Those with occlusal facets lacking unobscured antemortem microwear were excluded from further analysis.

The final microwear sample consisted of 22 specimens, six from Buluk and 16 from Lothagam (see SOM Table S1 for tooth positions). Additional samples include four specimens from Topernawi, five from Locherangan, and two from Nachukui (SOM Tables S1 and S2). While this represents only a small fraction of primate teeth recovered from these sites, the microwear ‘hit rate’ for candidate replicas was 27%, which accords well with previous studies of occlusal surfaces of fossil primates from open-air sites, such as those in the Turkana Basin (e.g., Teaford et al., 2008).

Specimens preserving antemortem microwear were analyzed using methods described in the study by Scott et al. (2006). A white-light confocal profiler (Sensofar PLμ Standard, Solarius Development Inc., Sunnyvale, CA) fitted with a 100×/0.70 Super Long Working Distance objective lens was used to generate point clouds for analysis. These point clouds all represented the ‘Phase II’ facet 9 following convention (Teaford and Walker, 1984; Krueger et al., 2008). Four adjacent fields of 102 × 138 μm each were scanned whenever distribution of antemortem microwear allowed, for a total sampled area of up to 204 × 276 μm per specimen. Elevations (z) were sampled at a lateral (x, y) interval of 0.18 μm and a vertical step of 0.2 μm. The resulting point clouds for each specimen included approximately 1.74 million points. Prior to generating microwear texture data, point clouds were leveled using the least-squares plane method, spikes were deleted by thresholding out the upper and lower 0.5% of the data, and minimal surface dust/debris was erased using the retouch (no fill) option in MountainsMap (version 8.1).

2.4. Microwear texture analysis

Resultant point clouds were used for DMTA. We used conventional SSFA protocols (Brown et al., 2018), as have been used in microwear texture analysis since its inception (e.g., Ungar et al., 2003). Where this differs from feature-based microwear analysis is instead of relying on manual counts of pits and scratches on a two-dimensional surface (which can introduce significant interobserver errors; Grine et al., 2002), we use an automated approach to measuring surfaces using three-dimensional point clouds and engineering standard texture characterizations. Five SSFA parameters, area-scale fractal complexity (Asfc), length-scale anisotropy of relief (epLsar), scale of maximum complexity (Smfc), and heterogeneity of complexity measured in 3 × 3 (Hasfc_9) and 9 × 9 (Hasfc_{81}) grids were used in this study, given their efficacy in separating primates by diet in past studies (Scott et al., 2006; Schubert et al., 2010; Scott et al., 2012). Surfaces dominated by pits of various shapes and sizes tend to have high Asfc values, whereas those with uniformly oriented striations tend to have high epLsar values. Those with high heterogeneity vary in texture complexity across a surface parsed into 3 × 3 and 9 × 9 cells. Finally, surfaces with few small features tend to have high Smfc values, whereas those preserving rough texture at fine scales have low Smfc values. Detailed descriptions of these texture variables are presented in the study by Scott et al. (2006). We used the ‘SensoMap 8’ SSFA module in MountainsMap (version 8.1) to calculate these attributes.

2.5. Statistical analyses

A general linear model approach was used to assess significant variation between the fossil and extant samples as well as within the fossil sample. Median values for all attributes were calculated from the scans of each specimen prior to analysis. Since microwear data are typically not normally distributed, all data were rank transformed prior to analysis to mitigate violation of assumptions inherent in parametric statistical analyses (see Conover and Iman, 1981). Ranks were used because logarithmic transformation did not normalize the data for all the variables. A multivariate analysis of variance model was used to compare central tendencies among extant cercopithecoids and fossil taxa from Buluk (*N. bulukensis*, $n = 6$) and Lothagam (*Par. lothagamensis*/sp. indet., $n = 12$; fossil Colobinae sp. $n = 4$) for all SSFA parameters.

Individual analysis of variance (ANOVA) models and post hoc tests (Tukey's HSD (Honestly Significant Difference) and Fisher's LSD (Least Significant Difference) pairwise comparisons) were then used to identify sources of significant variation. Statistically significant results ($p < 0.05$) from Fisher's LSD but not Tukey's HSD tests were considered suggestive or of marginal significance. Both pairwise tests were used to balance risk of type I and type II errors (Cook and Farewell, 1996). All statistical analyses were performed in Systat (version 13.2; Systat Software, San Jose, CA). Given the small samples of fossil specimens from Topernawi, Locherangan, and Nachukui, results for catarrhine taxa from these sites were not included in any statistical analyses but only compared visually with results from Buluk and Lothagam (SOM Figs. S1 and S2).

3. Results

Representative microwear photosimulations of Turkana Basin fossil primates and results are presented in Figures 1–4 and Tables 1 and 2. All raw microwear texture data produced in these analyses can be found in SOM Table S1. The fossil cercopithecoid samples from Buluk and Lothagam produced comparatively low complexity and high anisotropy values. The multivariate analysis of variance result (including both extant and fossil samples) indicates significant variation in microwear surface textures between the taxa (Wilks's $\lambda = 0.286$, $F = 10.421$, df = 14,168, $p < 0.01$; Table 1). Individual ANOVA tests indicated significant variation for Asfc ($F = 24.904$, df = 7, $p < 0.01$), epLsar ($F = 2.978$, df = 7, $p < 0.01$), Smfc ($F = 4.513$, df = 7, $p < 0.01$), and Hasfc_{81} ($F = 4.449$, df = 7, $p < 0.01$). Individual ANOVA tests did not produce significant variation for Hasfc_9 ($F = 1.864$, df = 7, $p = 0.086$).

The new baseline series for extant primates evinces the same pattern of variation between species, as did previously published datasets (Daegling et al., 2011; Scott et al., 2012). For example, *Tr. cristatus* has relatively low Asfc and high epLsar values as expected of a folivore. In contrast, *C. atys* has relatively high Asfc and lower average epLsar values as predicted for a hard-object feeder. Not surprisingly, the frugivore, *M. fascicularis*, has intermediate complexity and anisotropy. For the more open-country (e.g., savanna or grassland) primates, the generalist feeder, *Pap. ursinus*, has relatively high complexity and low anisotropy averages, with high dispersion of values, and the grass specialist, *Th. gelada* has low complexity and high anisotropy. These results are consistent with hard foods leading to higher texture complexity and tough ones leading to higher anisotropy (Table 1). We note that all the extant samples have overlapping ranges for epLsar, though the variance for *Tr. cristatus* was much greater than that in the others (Fig. 2).

Cercocebus, Macaca, and *Papio* each differed significantly in Asfc from the three fossil taxa (Tukey's HSD, $p < 0.5$). Neither *Trachypithecus* nor *Theropithecus* differed from the fossil taxa in texture complexity. Pairwise comparisons for epLsar produced marginal differences (Fisher's LSD, $p < 0.05$) between four extant/fossil primate pairs. *Cercocebus* and *Pap. ursinus* differed from the fossil Colobinae specimens, *Pap. ursinus* differed from *N. bulukensis,* and *Th. gelada* differed from *Par. lothagamensis*/sp. indet. The post hoc pairwise comparisons did not indicate differences in texture values among the three fossil taxa for either Asfc or epLsar (Figs. 2 and 3).

The fossil taxa also tended toward high-median Smfc values but varied in Hasfc_{81}. Fossil Colobinae differed significantly from *C. atys* and *M. fascicularis* and marginally from *Pap. ursinus*, *Th. gelada*, and *Tr. cristatus*. Similarly, *Par. lothagamensis*/sp. indet. differed significantly from *C. atys* and marginally from *M. fascicularis* and *Pap. ursinus* when compared using Smfc. All fossil taxa produced higher Smfc values than the extant samples. For Hasfc_{81}, fossil Colobinae, which yielded the highest values for heterogeneity, differed significantly from *Par. lothagamensis*/sp. indet., and *Th. gelada*. *Par. lothagamensis*/sp. indet, which

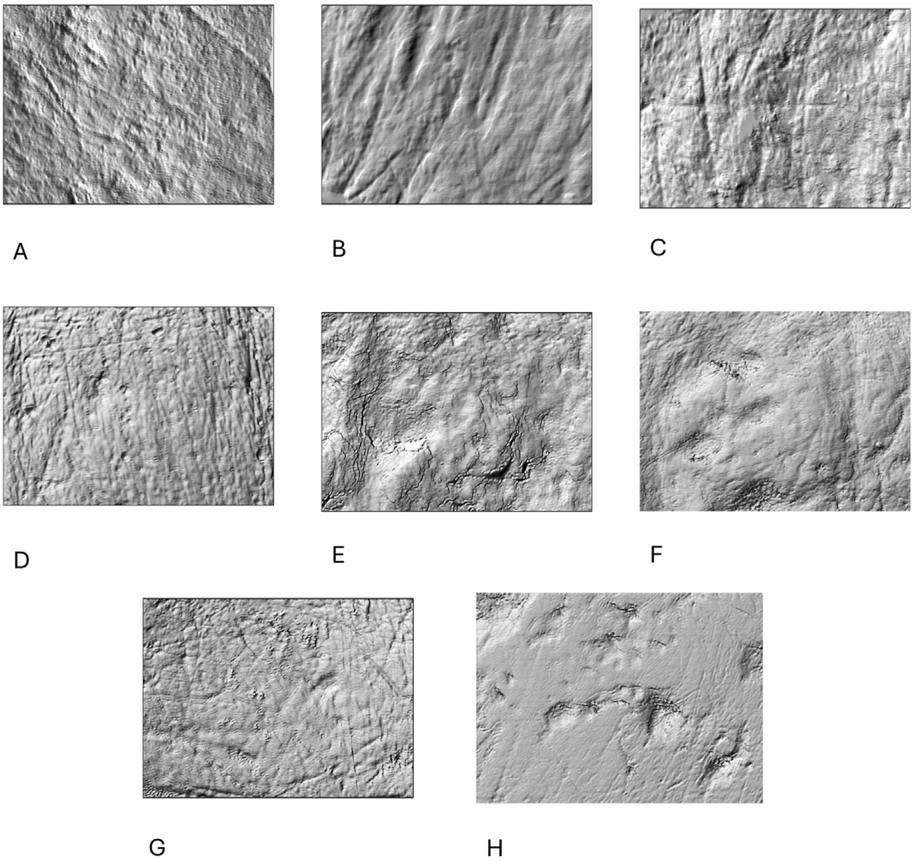

Figure 1. Representative photo simulations of microwear surfaces of sample specimens analyzed using a white light confocal profiler and MountainsMap (version 8.1). A) *Noropithecus bulukensis*, KNM-WS 12638; B) Colobinae sp., KNM-LT 23162; C) *Parapapio lothagamensis* KNM-WS 448; D) *Theropithecus gelada*, Berkeley 1_9Js; E) *Cercocebus atys*, McGraw #94-7; F) *Papio ursinus*, NMNH 197162; G) *Trachypithecus cristatus*, NMH 113171; H) *Macaca fascicularis* NMNH 141145. Each image represents a single field of 102 × 138 µ.

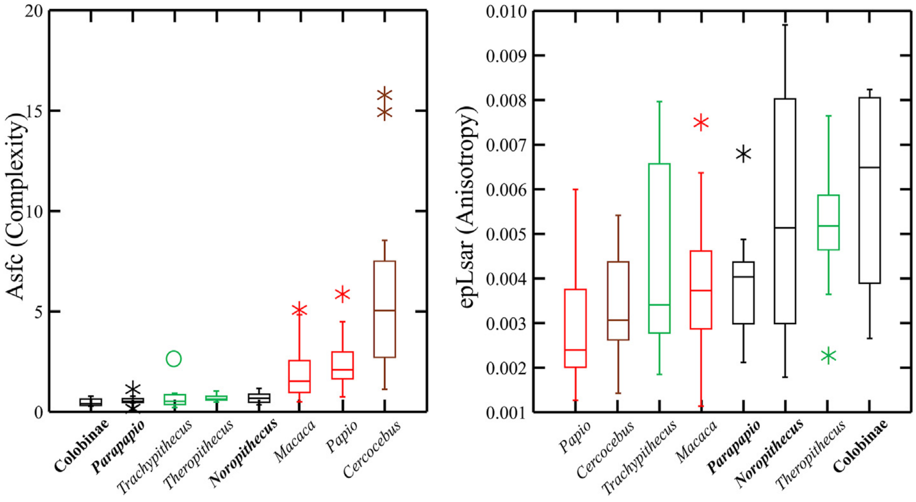

Figure 2. Box and whisker plot of the Buluk and Lothagam Cercopithecoidea specimens compared to extant primates with values for Asfc (complexity; left) and epLsar (anisotropy; right). The top and bottom edges of each box are the first and third quartiles, respectively, the central horizontal line is the median value, and circles are far outliers. *Cercocebus atys* is a hard-object feeder (brown), *Papio ursinus* is a generalist, and *Macaca fascicularis* is a frugivore (red); *Trachypithecus cristatus* is a folivore, and *Theropithecus gelada* is a grass-eater (green). Box and whiskers for the fossil specimens are outlined in black. Abbreviations: Asfc = area-scale fractal complexity; epLsar = length-scale anisotropy of relief. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article).

produced relatively low values for Hasfc_{81}, differed significantly from *M. fascicularis*, the fossil colobines, and *Tr. cristatus* and marginally from *C. atys* and *Pap. ursinus*. *N. bulukensis* differed marginally from fossil Colobinae (Fig. 4).

In sum, when considering Asfc and epLsar, our fossil samples from Buluk and Lothagam all aligned better with extant monocotyledon (grass) and dicotyledon leaf eaters than with fruit and hard-object feeders, with the exception of *Par. lothagamensis*/sp.

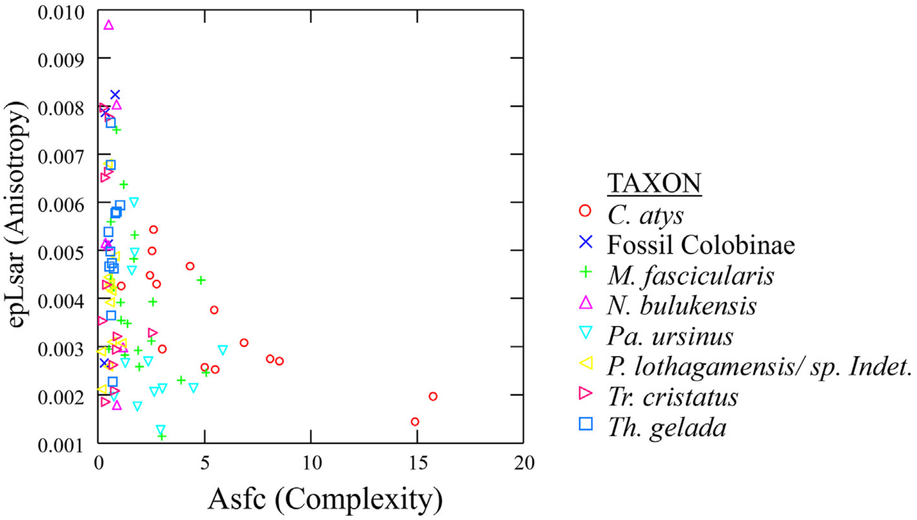

Figure 3. Bivariate plot of epLsar (anisotropy) vs. Asfc (complexity) for fossil and extant specimens. Note the separation of taxa by diet. Abbreviations: Asfc = area-scale fractal complexity; epLsar = length-scale anisotropy of relief; *C. atys* = *Cercocebus atys*; *M. fascicularis* = *Macaca fascicularis*; *Pa. ursinus* = *Papio ursinus*; *P. lothagamensis* = *Parapapio lothagamensis*; *Tr. cristatus* = *Trachypithecus cristatus*; *Th. gelada* = *Theropithecus gelada*. (For interpretation of the references to color in this figure, the reader is referred to the Web version of this article).

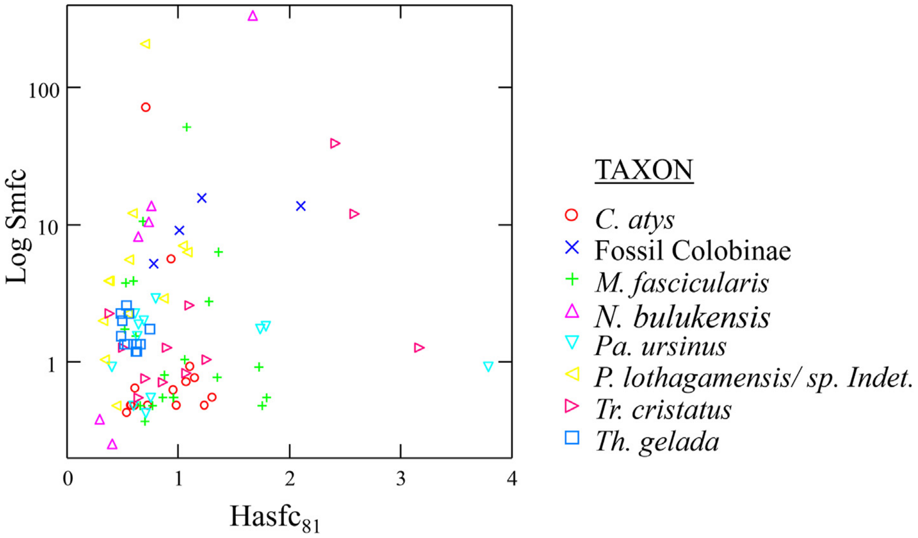

Figure 4. Bivariate plot of Smfc (scale of maximum complexity) vs. Hasfc$_{81}$ (heterogeneity of complexity; 9 × 9) for fossil and extant specimens. Smfc is log-transformed to better illustrate variation among the samples. Note the separation of taxa by diet. Abbreviations: Hasfc$_{81}$ = heterogeneity of complexity (9 × 9 scale); Smfc = scale of maximum complexity; *C. atys* = *Cercocebus atys*; *M. fascicularis* = *Macaca fascicularis*; *Pa. ursinus* = *Papio ursinus*; *P. lothagamensis* = *Parapapio lothagamensis*; *Tr. cristatus* = *Trachypithecus cristatus*; *Th. gelada* = *Theropithecus gelada*. (For interpretation of the references to color in this figure, the reader is referred to the Web version of this article).

indet., which differed marginally from *Th. gelada* when considering anisotropy. As for Smfc, all fossil taxa differed, either marginally or significantly, from the hard-object feeders, and the Lothagam material differs from the frugivore/generalist feeders as well. There also appeared to be some separation between the fossil colobines and the extant folivores, suggesting the possibility that the surfaces of the observed fossil colobines yielded fewer small features by comparison. Unlike the other fossil specimens, *Noropithecus* did not differ from either *M. fascicularis* or *Pap. ursinus* in Smfc. Heterogeneity (Hasfc$_{81}$) separated the fossil taxa, where the fossil colobines produced more heterogeneous surfaces than either *N. bulukensis* or *Par. lothagamensis*. Furthermore, Hasfc$_{81}$ analyses aligned the fossil colobines with the dicotyledon leaf eaters (*Tr. cristatus*) and *Par. lothagamensis* with the grass-eaters (*Th. gelada*). *Noropithecus* did not differ from any extant taxa when considering heterogeneity.

4. Discussion

Our analyses suggest that all fossil cercopithecoids analyzed here (i.e., *N. bulukensis* from the Early Miocene of Buluk, *Par. lothagamensis*/sp. indet. from the Late Miocene and colobines B and C from the Miocene/Pliocene of Lothagam) ate mostly tough foods in the weeks prior to death. This contrasts with microwear texture results previously reported for non-cercopithecoid catarrhines from the Early Miocene, which suggest that these primates were for the most part generalized frugivores (Shearer et al., 2015). On the other hand, the results for the fossil cercopithecoids from Lothagam align well with previous feature-based microwear analyses of the fossil monkey sample from that site (Leakey et al., 2003). That said, the results for *N. bulukensis* were unexpected. While there has been a long-proposed association between the origin of cercopithecoid bilophodonty and folivory (Napier, 1970), more recent studies of

Table 1
Results of statistical tests for central tendencies (rank-transformed data).

A. MANOVA/ANOVA results

		Value	F-ratio	df	p value
Wilks's λ		0.286	10.421	14, 168	**<0.01**
SSFA variables	Type III SS	Mean squares			
Asfc	45053.746	6436.249	24.904	7	**<0.01**
epLsar	13200.1	1885.729	2.978	7	**<0.01**
Smfc	12120.8	2588.69	4.513	7	**<0.01**
Hasfc$_{9}$	8919.76	1274.25	1.864	7	0.086
Hasfc$_{81}$	17972.9	2567.56	4.449	7	**<0.01**

B. Extant paired comparisons

	Cercocebus	*Macaca*	*Papio*	*Trachypithecus*	*Theropithecus*
Asfc					
Cercocebus	/				
Macaca	**23.458**^{a}	/			
Papio	**13.567**^{b}	−9.892	/		
Trachypithecus	**54.150**^{a}	**30.692**^{a}	**40.583**^{a}	/	
Theropithecus	**48.775**^{a}	**25.317**^{a}	**35.208**^{a}	**−5.375**^{b}	/
epLsar					
Cercocebus	/				
Macaca	−6.700	/			
Papio	10.733	17.433	/		
Trachypithecus	−10.433	−3.733	**−21.167**^{b}	/	
Theropithecus	**−27.767**^{b}	**−21.067**^{b}	**−38.500**^{a}	−17.333	/
Smfc					
Cercocebus	/				
Macaca	−14.292	/			
Papio	−16.075	−1.783	/		
Trachypithecus	**−21.742**^{b}	−7.450	−5.667	/	
Theropithecus	**−25.325**^{b}	−11.033	−9.250	−3.583	/
Hasfc$_{81}$					
Cercocebus	/				
Macaca	−4.983	/			
Papio	2.767	7.750	/		
Trachypithecus	−7.067	−2.083	−9.833	/	
Theropithecus	**28.017**^{b}	**33.000**^{a}	**25.250**^{b}	**35.083**^{a}	/

C. Fossil paired comparisons

	Colobinae	*Noropithecus*	*Parapapio*	*Cercocebus*	*Macaca*	*Papio*	*Theropithecus*	*Trachypithecus*
Asfc								
Colobinae	/	−14.917	−5.375	**64.733**^{a}	**−41.275**^{a}	**−51.167**^{a}	−15.958	−10.583
Noropithecus	/	/	9.542	**49.817**^{a}	**26.358**^{a}	**−36.25**^{a}	−1.042	4.333
Parapapio	/	/	/	**59.358**^{a}	**35.900**^{a}	**45.792**^{a}	−10.583	−5.21
epLsar								
Colobinae	/	7.917	23.667	**−30.350**^{b}	23.650	**41.083**^{b}	2.583	19.917
Noropithecus	/	/	15.750	−22.433	−15.733	**33.167**^{b}	−5.333	12
Parapapio	/	/	/	−6.683	0.02	−17.42	**−21.080**^{b}	−3.75
Smfc								
Colobinae	/	24.792	15.958	**−56.242**^{a}	**41.950**^{a}	**40.167**^{b}	**30.917**^{b}	**34.500**^{b}
Noropithecus	/	/	−8.833	**−31.450**^{b}	−17.158	15.375	6.125	9.708
Parapapio	/	/	/	**−40.283**^{a}	**−25.992**^{b}	**−24.208**^{b}	14.958	18.542
Hasfc$_{81}$								
Colobinae	/	**33.083**^{b}	**43.667**^{a}	−18.983	14.000	21.75	**47.000**^{a}	11.917
Noropithecus	/	/	10.583	14.100	19.083	−11.333	13.917	−21.167
Parapapio	/	/	/	**24.683**^{b}	**29.667**^{a}	**21.917**^{b}	3.333	**−31.750**^{a}

Statistically significant differences in bold.

Abbreviations: SSFA = Scale-Sensitive Fractal Analysis; Asfc = area-scale fractal complexity; epLsar = length-scale anisotropy of relief; Smfc = scale of maximum complexity; Hasfc$_{81}$ = heterogeneity of complexity (9 × 9 scale); Hasfc$_{9}$ = heterogeneity of complexity measured in 3 × 3; ANOVA = analysis of variance; MANOVA = multivariate analysis of variance model.

[a] Significant difference ($p < 0.05$) with Tukey's Honestly Significant Difference and Fisher's Least Significant Difference tests.

[b] Significant difference ($p < 0.05$) with only Fisher's Least Significant Difference test.

some early fossil cercopithecoids have suggested a frugivorous or even a harder-food diet (Lucas and Teaford, 1994; Benefit, 1999, 2000; Merceron et al., 2009a, 2009b; Rossie et al., 2013; Rasmussen et al., 2019; Locke et al., 2020). Still, Rossie et al. (2013) proposed that foregut fermentation in colobines evolved for digesting tough seeds and unripe fruits rather than leaves, thus paving the way for increased folivory.

Here, we found that the *N. bulukensis* specimens studied showed a tough-diet DMTA signature with higher anisotropy and lower complexity averages than expected of a fruit or hard-object feeder (Fig. 3). These microwear patterns are more consistent with dicotyledon folivory or monocotyledon grass-eating, like those associated with extant colobines or geladas, respectively.

The patterns for scale of maximum complexity and heterogeneity are more difficult to interpret because, while Asfc and epLsar can be related to the angle of approach between opposing tooth surfaces and by extension to food fracture properties, relationships between Smfc or Hasfc$_{81}$ and aspects of diet are less intuitive

Table 2
Summary statistics for the microwear parameters for fossil and extant primates used in this study.

Species		Variables				
		Asfc	epLsar	SMFC	Hasfc$_{9}$	Hasfc$_{81}$
Trachypithecus cristatus ($n = 12$)	Mean	0.721	0.00439	5.31	0.699	1.3
	Median	0.525	0.00341	1.269	0.614	0.988
	SD	0.632	0.002	11.12	0.44	0.909
Cercocebus atys ($n = 15$)	Mean	5.958	0.00345	5.597	0.535	0.877
	Median	5.045	0.00307	0.548	0.517	0.941
	SD	4.391	0.001	18.117	0.194	0.265
Macaca fascicularis ($n = 20$)	Mean	1.923	0.00389	4.484	0.618	1.007
	Median	1.53	0.00379	0.86	0.488	0.916
	SD	1.361	0.002	11.365	0.292	0.412
Papio ursinus ($n = 12$)	Mean	2.515	0.0029	1.452	0.619	1.096
	Median	2.098	0.0024	1.639	0.518	0.7
	SD	1.444	0.001	0.79	0.35	0.956
Theropithecus gelada ($n = 12$)	Mean	0.684	0.00519	1.675	0.443	0.575
	Median	0.631	0.00518	1.441	0.414	0.549
	SD	0.157	0.001	0.479	0.088	0.081
Noropithecus bulukensis ($n = 6$)	Mean	0.711	0.00546	61.605	0.626	0.751
	Median	0.684	0.00513	9.341	0.421	0.688
	SD	0.315	0.00298	134.831	0.653	0.487
Fossil Colobinae sp. ($n = 4$)	Mean	0.477	0.00597	10.943	0.491	1.276
	Median	0.411	0.00649	11.412	0.474	1.112
	SD	0.227	0.00261	4.716	0.139	0.578
Parapapio lothagamensis ($n = 12$)	Mean	0.542	0.00387	21.314	0.347	0.605
	Median	0.522	0.00404	3.898	0.345	0.553
	SD	0.259	0.00125	58.953	0.167	0.267

Abbreviations: Asfc = area-scale fractal complexity; epLsar = length-scale anisotropy of relief; Smfc = scale of maximum complexity; Hasfc$_{81}$ = heterogeneity of complexity (9×9 scale); Hasfc$_{9}$ = heterogeneity of complexity measured in 3×3; SD = standard deviation.

(Fig. 4). The Lothagam specimens tended toward larger Smfc values, though *Par. lothagamensis*/sp. indet. did not differ significantly from either extant colobine or gelada samples. This may relate to differences in abrasive particle size/shape or masticatory mechanics. *Noropithecus bulukensis* also had relatively higher Smfc values on average, though these were only significantly higher than those of extant mangabeys.

The results for surface heterogeneity are mixed. *Parapapio. lothagamensis*/sp. indet. and *N. bulukensis* tend to have lower values, best aligning them with *Th. gelada*, whereas the few fossil colobines in the Lothagam sample have values more akin to *Tr. cristatus*. However, *N. bulukensis* does not differ in Hafsc$_{81}$ from any extant taxon considered here. Exactly how this relates to diet is not immediately clear, though it may be noted that, again, the fossil cercopithecoids separate best from the extant frugivores and hard-object feeder when considering surface texture as a whole.

The Asfc and epLsar results indicate similar microwear textures for the primates at Buluk and Lothagam despite being separated phylogenetically (victoriapithecids, cercopithecines, and colobines), temporally (by ~10 Myr), and geographically (by >100 km). The similarities in microwear between these fossil cercopithecoid samples are thus surprising, particularly given more forested elements at Buluk and more grassland at Lothagam—though there were likely some similar resources at the sites (e.g., both had woodlands and major river systems; Andrews et al., 1985; Harrison, 1989; Andrews, 1992; Leakey et al., 2011; Begun, 2013; Polissar et al., 2019).

A possible explanation for our findings is that the microwear analyses in this study do not provide sufficient detail to distinguish dietary differences related to habitat and food availability. Our sample sizes, while typical for DMTA, may not be representative of each fossil taxon as a whole. However, it is clear from studies of extant primates that microwear does reflect occlusal dynamics mediated by food fracture properties, that is, pits from crushing hard foods (e.g., nuts) or parallel scratches from shearing/slicing tough ones (e.g., mature leaves; Ungar, 2015). Furthermore, it is also apparent from additional analyses of other catarrhines from the late Paleogene and Neogene (~30–2.6 Ma) in the Turkana Basin that some fossil primates from the region do have quite variable microwear patterning more consistent with soft fruit or even hard object consumption (see SOM Fig. S2).

On the other hand, these results are in line with microwear texture analysis of both *Parapapio ado* and a small sample of colobines (gen. et sp. indet) from Pliocene deposits at Kanapoi in the Turkana Basin (Ungar et al., 2020). That study likewise showed low microwear texture complexity with a narrow range of values, suggesting tough food diets, with grass proposed as an important dietary component for *Parapapio*. It may be noted, however, that Williams (2014) suggested higher complexity values for a small sample of *Parapapio whitei* from the Plio-Pleistocene of South Africa, so this might not hold for all members of the genus.

The split of cercopithecoids and hominoids has long been associated with divergence in food preferences, with the differentiation of cercopithecoids from stem catarrhines linked to a leaf-rich diet in the former (e.g., Napier, 1970; Simons, 1970). The association of the early cercopithecoid radiation with folivory has, however, been questioned. Benefit (1999, 2000) argued that the early cercopithecoid, *Victoriapithecus,* has the low-crowned molars of a frugivore, with subsequent feature-based microwear consistent with that assessment (Lucas and Teaford, 1994; Ungar and Teaford, 1996; Palmer et al., 1998). However, Locke et al. (2020) argued that even though the molar shearing crests of *N. bulukensis* are slightly longer than those of *Victoriapithecus macinnesi*, most *N. bulukensis* specimens still fall within the soft-fruit-eater range.

Despite the relatively bunodont dentition, the microwear textures of *N. bulukensis* specimens considered here (when compared to the extant baseline series) are more consistent with grass and leaf eating or a combination of soft fruits and grasses/leaves. This apparent mismatch between dental morphology and microwear might be explained in a few ways. For instance, while adaptation gives an indication of dietary potential, microwear gives an indication of the foods eaten. As these processes act on different scales (Teaford et al., 2023), it is possible that *N. bulukensis* was adapted to fruit consumption, but the individuals in our study may have consumed mostly leaves, at least in the days before their deaths. A possible example of a similar situation in extant primates might involve modern colobines, where molar crest morphology and predicted dietary behavior do not always align (Wright and Willis, 2012)—with factors such as sex and seasonality also possibly impacting interpretations.

Alternatively, some taxa may have had longer crests than others with similar diets because of phylogenetic inertia. In other words, perhaps early cercopithecoids had shorter molar shearing crests than extant colobines because their immediate ancestors were frugivores. This could be an example of Van Valen's (1973) Red Queen hypothesis at work. Just as Kay and Ungar (1997) suggested that living hominoids have longer crests than their Early Miocene predecessors with a similar range of diets (judging from their microwear) because of competition with cercopithecoids, and perhaps even coevolution with plant mechanical defenses, we propose that the same should hold true for cercopithecoids given competition with apes.

In such cases, microwear may serve as an ‘anchor’ for occlusal morphology when comparing taxa separated in time (see Teaford and Ungar, 2007). From this perspective, even though topographic studies of fossil cercopithecids and victoriapithecids suggest that their molars were capable of processing hard, brittle objects (Benefit, 2000; Hlusko, 2007; Rossie et al., 2013; Thiery et al., 2017; Rasmussen et al., 2019), we should remember that just because an animal is capable of eating something does not mean that is what it consumes from day to day. This interpretation is reminiscent of dental microwear and morphological analyses of *Paranthropus boisei* and *Paranthropus robustus*, where both species have similarly shaped molars but likely had different diets (Sponheimer et al., 2006; Ungar et al., 2008a; Cerling et al., 2011; Grine et al., 2012). In the present case, even though *Victoriapithecus* and *N. bulukensis* dentitions are morphologically similar, the former may have been more frugivorous and the latter more folivorous, or at least processed tougher foods in the weeks before death, if the microwear evidence is an indication.

According to Benefit (1999), cercopithecids retained the dietary behaviors of their victoriapithecid ancestors throughout the Late Miocene and into the Early Pliocene. Our results are consistent with this. However, the results of the present study also suggest more leaf/grass than fruit and hard-object food preferences. Clearly neither feature-based (Leakey et al., 2003) nor texture-based (this study) microwear analyses suggest the colobines from Lothagam consumed harder foods despite larger sample sizes expected to be representative of the population.

This raises another interesting possibility. While the divergence of cercopithecoids from the catarrhine stem was at first hypothesized to involve a dietary shift from fruits to tough leaves in the forest (Napier, 1970), could the radiation of cercopithecoids be tied in part to the spread of tough grasses and more open environments in Africa? If the microwear textures reported here for *N. bulukensis* and *Par. lothagamensis*/sp. indet. reflect the consumption of tougher resources, perhaps increasing grass consumption could have also played a role in the expanding cercopithecoid radiation during the Miocene. Could the leaf-eating adaptations in colobines today even be exaptations (sensu Gould and Vrba, 1982) for folivory in monkey species returning to the forest, rather than for seed or unripe fruit consumption as proposed by Rossie et al. (2013)?

The idea of grass-eating as an exaptation for folivory and a driver of the early cercopithecoid radiation seems unlikely at the first glance. The initial divergence of cercopithecoids and hominoids likely occurred in the late Oligocene, well before the spread of C4 grasslands across eastern Africa (Stevens et al., 2013; Linder, 2017). Nevertheless, MacLatchy et al. (2023) recently claimed evidence of abundant C4 grasses in eastern Africa by 21 Ma, and recent pedogenic carbonate study of $\delta^{13}C$ data suggests that Buluk's habitat, for example, may have been a heterogeneous mix of woodland/brushlands/shrublands, woody grasslands, and grasslands with more C4 grasses on the landscape than previously thought (Peppe et al., 2023). If so, there was likely at least some grass available earlier, and of course, there may well have been more C3 grasses earlier in the Miocene.

On the other hand, mesowear data suggest that most ruminants in the region were likely browsers even during the Early to Middle Miocene (Hall and Cote, 2021), and isotopic analyses of some herbivore tooth enamel samples from Buluk show no evidence of C4 vegetation in the diets of any taxa there (Arney et al., 2024). Thus, if *N. bulukensis* was eating grasses, they were of the C3 variety. Additional paleoecological (e.g., phytoliths or plant wax biomarkers) and dietary data, such as $\delta^{18}O$ from *N. bulukensis* enamel, could help refine vegetation reconstruction at Buluk and victoriapithecid feeding preference, as shown by Nelson (2013). In the end, microwear texture data presented here are not meant as a test of the grass consumption hypothesis, but they are consistent with it and so raise it as a possibility for testing in the future.

For Lothagam, carbon isotope data do point to a somewhat more open setting, particularly moving up section from the Lower to the Upper Members of the Nawata Formation, based on pedogenic carbonate data and tooth enamel data that indicate C4 grazing among bovids, equids, proboscideans, and rhinos (Cerling et al., 2003; Bobe, 2011; Uno et al., 2011). Thus, grass-eating by these cercopithecids seems more likely.

The data presented here raise more questions than they answer, but they lead to new hypotheses involving the ‘Red Queen’ hypothesis (Van Valen, 1973) and perhaps even early grass consumption phenomena. Much more work needs to be done to test these hypotheses, particularly considering that other microwear studies suggest that some fossil cercopithecoids may have been more frugivorous. Future texture-based microwear analyses of *Victoriapithecus* specimens and possibly even feature-based microwear analyses on *N. bulukensis* would likely help us test these new hypotheses. Larger sample sizes of a broader variety of fossil specimens preserving antemortem microwear would also improve our understanding of what these primates ate. It must also be acknowledged that tests of hypotheses concerning the initial divergence of the cercopithecoids will require microwear analyses of the earliest members of the clade, such as *Alophe* and especially *Nsgunwepithecus* (Stevens et al., 2013; Rasmussen et al., 2019). Unfortunately, samples of these taxa are still too small to allow their evaluation by microwear analysis.

Nevertheless, microwear analysis of *Noropithecus* and even *Parapapio* can provide hints and suggest hypotheses concerning the cercopithecoid adaptive radiation in relation to diet. We conclude from this study that individual victoriapithecids from Buluk were not likely frugivores or hard-object feeders, as has been inferred for *Victoriapithecus* or *Alophe* based on occlusal morphology (Benefit, 1999, 2000; Rossie et al., 2013; Rasmussen et al., 2019; Locke et al., 2020). At the very least, our observed specimens likely consumed more tough objects in the weeks before death. Results also suggest that *Par. lothagamensis*/sp. indet., like *Par. ado* from Kanapoi (Ungar et al., 2020), preferred tough foods, tougher on average than that of the extant baboon *Pap. ursinus*, at least as far as microwear signatures indicate.

Author contributions

Leah K. Fehringer: Writing – review & editing, Writing – original draft, methodology, Investigation, Formal analysis, Data curation. **Catherine C. Beck:** Writing – review & editing, Funding acquisition. **Louise N. Leakey:** Resources. **Patricia Princehouse:**

Writing – review & editing, Resources. **John Rowan:** Writing – review & editing, Resources. **Gabrielle A. Russo:** Writing – review & editing, Resources. **Mark F. Teaford:** Writing – review & editing, Writing – original draft, Methodology, Formal analysis. **Kevin T. Uno:** Writing – review & editing, Funding acquisition, Conceptualization. **Peter S. Ungar:** Writing – review & editing, Writing – original draft, Supervision, Project administration, methodology, Investigation, Formal analysis, Data curation, Conceptualization.

Declaration of interests

The authors have no competing interests.

Supplementary Online Material

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