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Community Niches and Evolution of Generalist Primates: A Preliminary Assessment of Plio-Pleistocene Cercopithecidae in Africa

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ABSTRACT

Niche construction theory has increasingly received attention in paleoanthropology as a new focus for considering the evolutionary consequences of hominin tool-use and cultural adaptation starting in the Pleistocene. Modern humans excel at dramatic landscape modification, allowing us to regulate the effects of natural selection on our own species while simultaneously imposing novel selective forces on other living organisms. The long-standing effects of this current and past niche construction by our species make it challenging to explore the timing and effects of hominin behavioral adaptations using modern analogues alone. In this paper I employ a community ecological approach to address evolutionary trends within a group of generalist primates—the Cercopithecidae—from Pliocene and early Pleistocene localities in Ethiopia, Kenya, and South Africa. Principal component analysis is used to model the dental ecomorphological niches of fossil cercopithecid species and taxocenes (a closely related subset of the faunal community), along with a comparative sample of extant cercopithecids from sub-Saharan Africa. Differences in the dental morphological niches of modern cercopithecid taxocenes can be attributed to variation in habitat conditions. Taxocenes appear more similar at local scales and co-occurring cercopithecids are relatively evenly dispersed in their dental morphological niche space, suggesting that they are able to maximize their available niches while avoiding competition within these taxocenes. Fossil taxocenes in eastern Africa (Hadar, Shungura, and Koobi Fora formations) also tend to occupy similar niches to one another and exhibit minimal spatial or temporal variation in their dental morphological niches. These eastern African taxocenes are distinct from those in South Africa (Makapansgat, Sterkfontein, Swartkrans, and Kromdraai), both in their overall niche positions and in measures of dispersion. Despite high species richness, cercopithecid taxocenes in the early Pleistocene of South Africa occupied restricted niches with more closely packed species, a pattern with no modern African analogue. The loss of this South African niche and an overall niche shift between early Pleistocene and modern cercopithecid taxocenes in Africa likely reflect a combination of climatic and habitat factors along with increasing influences from tool-using hominins during the later Pleistocene. These results provide an important comparative pattern for considering how Pliocene hominins may have responded to environmental and habitat variation. Further, given the challenges of interpreting hominin behavioral evolution during this period, community paleoecological approaches like the one taken here can be useful for identifying changes in other mammalian groups in response to an expanded hominin niche.

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INTRODUCTION

Cercopithecid primates have long been used as an analogue for exploring how different biotic and abiotic factors may have influenced hominin evolution (Elton 2006; Elton et al. 2001; Foley 1994; Frost 2007; Jolly 2009). Relatively larger-bodied colobine and cercopithecine taxa appear in the fossil record during the late Miocene before peaking in their taxonomic and ecological diversity over the Pliocene and Pleistocene as fossil species and lineages migrated, speciated, and adapted to different environmental conditions in eastern and southern Africa (Elton 2007; Frost 2007; Jablonski and Frost 2010). Extinct species and genera of hominins and cercopithecids also shared biogeographic dispersal patterns and convergent adaptations to terrestrial substrates, larger body size, and the exploitation of new dietary resources through the Pliocene and Pleistocene (Elton 2006; Hughes et al. 2008; Levin et al. 2015; Strait and Wood 1999).

Environmental change and competition with other cercopithecids are commonly cited as a conjoined cause of extinction of larger-bodied fossil lineages, including *Theropithecus oswaldi* spp. and the terrestrial colobine genus *Cercopithecoides* (Leakey 1982; Pickford 1993). Similar declines in other fossil African mammal groups have been attributed to climate or habitat changes (Faith 2014; Faith et al. 2018), hominin impacts (particularly for carnivores—Werdelin and Lewis 2013), and other biotic factors (Faith et al. 2018; Fortelius et al. 2016). Analyses of speciation and extinction patterns have found no evidence for a correlation between cercopithecid turnover events and global environmental change (Frost 2007), although the exact timing and causes of later extinctions are difficult to assess with a sparse middle and late Pleistocene fossil record.

Examining changes in the paleoecological niches of fossil cercopithecids provides an additional way to examine whether and how these species may have interacted with each other and with their environments. A species' niche can be defined through its environmental requirements (Grinnell 1917; Hutchinson 1957), influence on its own environment (Elton 1927; MacArthur and Levins 1967), or a combination of these extrinsic (environmental) and intrinsic (adaptive) factors (Chase and Leibold 2003; Leibold 1995). These factors can vary across time and space, and a distinction can therefore be made between a species' fundamental niche—defined as all possible conditions under which that species can survive—and the realized niches of individuals and discrete populations that exist at any one place or time (Hutchinson 1957). For example, the introduction or removal of an ecological competitor may cause a local population to exhibit character displacement or release (Dayan and Simberloff 2005; Grant 1972), which would appear as an intrinsic niche shift occurring within those competing populations but leaving their combined niche intact. An apparent shift could also result from niche contraction following environmental change. The effects of such an extrinsic niche shift could be limited to one or two populations or affect all species within a local community, resulting in widespread ecological retreat or niche collapse (Crowley et al. 2012; Layman et al. 2007; Miller et al. 2005).

Many species of extant Cercopithecidae are characterized as ecological generalists (i.e., having a large fundamental niche). Members of the tribes Papionini and Cercopithecini occupy a wide range of habitats and exploit a variety of dietary resources across different sites (Butynski et al. 2013; Eeley and Lawes 1999; Fleagle 2013). Populations exhibit variable diets in response to fluctuation in resource availability due to seasonal or geographic effects or to interspecific competition (Alberts et al. 2005; Barton et al. 1992; Buzzard 2006; Chapman et al. 2002; Hemingway and Bynum 2005; Hill and Dunbar 2002; Lambert 2002). Stable isotope and dental microwear analyses provide evidence for potential dietary niche partitioning and local variation in species diets for fossil cercopithecid taxa (Carter 2006; Cerling et al. 2013; El-Zaatari et al. 2005; Fourie et al. 2008; Leakey et al. 2003; Lee-Thorp et al. 1989; Levin et al. 2015; Martin et al. 2018; Negash et al. 2020; Proctor 2007; Robinson et al. 2017; Shapiro et al. 2016; Teaford et al. 2008; van der Merwe et al. 2003; Wynn et al. 2016). Extant populations may also respond to variation in resource availability through differences in group size, activity budgets, and/or range size (Arseneau-Robar et al. 2021; Chapman and Chapman 1999; Gogarten et al. 2014; Kane and McGraw 2017; Korstjens and Dunbar 2007; Korstjens et al. 2018; McLester et al. 2019; Miller et al. 2020). Similar social and behavioral adaptations likely helped buffer fossil cercopithecids from changing climates and resource availability in ways undetectable in the fossil record. While much of the research on niche construction in hominin evolution has focused on aspects of social learning and tool-use in the Pleistocene that is captured in the archaeological record (Antón et al. 2014; Fuentes 2013; Laland et al. 2000; Potts 2012; Thompson et al. 2021), early hominins would have likely deployed a similar range of social and behavioral adaptations during the earlier Pliocene that would be less immediately visible. Modeling contemporaneous cercopithecid niches therefore provides a baseline of generalist primate responses to environmental variation that can be used to determine how and when hominins began to diverge from this pattern.

Ecological and behavioral flexibility among cercopithecids also enables them to co-exist at sites throughout sub-Saharan Africa today, including in high-latitude and seasonal regions in eastern and southern Africa. However, it is unclear how much extant cercopithecids and other primates have been affected by modern human activity (Cowlishaw 1999; Ellwanger and Lambert 2018; Kühl et al. 2019; van Schaik 2002), raising the possibility that these fossil communities have no modern analogue (Faith et al. 2019). While modern human niche construction has been implicated as a major driver of ecological change across the globe (Andermann et al. 2020; Boivin et al. 2016), analyses of ancient African ecosystems have provided mixed results for potential hominin influence (Faith et al. 2018; Fortelius et al. 2016; Werdelin and Lewis 2003). In order to test the potential effects of hominin activity on cercopithecid primate ecologies and evolution, an important first step is modeling cercopithecid niches to identify when and how they may have changed through time or in response to different environmental conditions.

This study, therefore, provides an important comparative analysis of potential ecological dynamics among these generalist primates which make up the cercopithecid taxocene—a closely phylogenetically related subset of the broader mammalian community. I note that unlike other common community subsets (e.g., an ecological guild), this taxonomic grouping does not assume that members are resource competitors. Given the shared adaptations of many cercopithecid species, this provides a useful example for considering whether and how taxocene niches are influenced by local environmental conditions today and in the past. Specifically, this study addresses the hypothesis that the morphological and behavioral flexibility of extant and extinct cercopithecid species makes this taxocene resilient to variation in resource availability, resulting in a pattern of niche stasis within Africa (H_0: no change). Alternatively, cercopithecids may exhibit a taxocene niche shift (H_1: positional change) and/or niche reduction (H_2: size change) from sites with high to low resource availability (in response to local environmental conditions) or from fossil to modern sites (in response to hominin influences or past environmental change).

MATERIALS AND METHODS

The cercopithecid niche was modeled from the dental morphologies of living and fossil African cercopithecid primates. Teeth serve as an important point of contact between organisms and their environments through their role in processing food resources, and dental adaptations within the Cercopithecidae are correlated with a range of dietary behaviors. Dental metric data were collected from over 1,000 fossil cercopithecid specimens housed in the National Museum of Ethiopia, National Museums of Kenya, Evolutionary Studies Institute at the University of Witwatersrand, and Ditsong National Museum of Natural History (summarized in Table S1 in the supplementary material). A comparative sample of modern sub-Saharan cercopithecid primates included 532 specimens from the National Museum of Ethiopia, the Smithsonian National Museum of Natural History, Carnegie Museum of Natural History, Academy of Natural Sciences of Philadelphia at Drexel University, and American Museum of Natural History in New York.

Mesiodistal length and buccolingual breadth measurements were taken on the occlusal surfaces of the fourth premolar and all molar teeth for both the maxillary and mandibular dentition using Mitutoyo digital calipers. Lengths of maxillary incisors were taken from the root at the alveolus, or on the alveolus directly if the root was not preserved. The root length measurements are strongly correlated with incisor crown lengths in extant cercopithecids (I1: $n=160$, $p<0.001$, adjusted $R^2=0.90$; I2: $n=159$, $p<0.001$, adj. $R^2=0.87$) and were used in place of the latter since many fossil and extant specimens had heavily worn, broken, or absent incisors. Buccal/lingual and occlusal tooth surfaces were photographed using a digital microscope and measured in ImageJ software (Rueden et al. 2017; Schindelin et al. 2012) for two-dimensional shear crest and enamel thickness measurements on unworn to lightly-worn M2s and moderately-worn M1 teeth, respectively. Dental measurements are depicted in Figure 1.

All analyses were performed using R Statistical Software (R Core Team 2020). Variable subsets from the maxillary and mandibular dentitions were analyzed separately to account for differences in data availability within the incomplete fossil sample. For each, M1 occlusal lengths were included to reflect body size variation and control for any lingering effects of allometry (Jungers et al. 1995). Remaining dental metrics were converted to ratios capturing aspects of tooth shape and relative sizes associated with dental function, listed below in Table 2. These included relative maxillary incisor proportions (Deane 2009; see also Hylander 1975; Shellis and Hiiemae 1986), buccal M^2 and lingual M_2 shearing ability (Kay 1975), M1 protocone/id enamel thickness (Kay 1981; Shellis et al. 1998), premolar size (Daegling et al. 2011; Scott et al. 2018; Strait et al. 2013), and inter- and intra-tooth proportions (Kay 1975; Lucas et al. 1986).

TAXOCENES

I considered all of the cercopithecid taxa found within the same fossil deposits to represent a complete taxocene (see Table S1). Fossil analyses were first performed at the member level for taxocenes from the Hadar Formation (Lower Awash Valley, Ethiopia) Shungura Formation (Omo Valley, Ethiopia), Koobi Fora Formation (East Turkana, Kenya), and South African cave deposits at Makapansgat, Sterkfontein, Swartkrans, and Kromdraai. Site members were also grouped into larger regional taxocenes for the Pliocene (ca. 4.0–2.6 Ma) and early Pleistocene Gelasian (ca. 2.6–1.8 Ma) and Calabrian (ca. 1.8–0.8 Ma) stages in the Lower Awash Valley, Omo Valley, East Turkana, and South Africa. Following Bobe (2011), here I use Omo-Turkana Basin to refer to these combined taxocenes and distinguish between the respective Omo Valley (Ethiopian) and Turkana Basin (Kenyan) components to account for potential differences between the two. To avoid biasing fossil comparisons, some members were excluded based on taxocene size, completeness, and species overlap with other nearby sites. The final set of fossil taxocenes considered at the member level included the Sidi Hakoma and Kada Hadar Members (Hadar Fm.), Members C, E, and G of the Shungura Formation, Tulu Bor, Upper Burgi, KBS, and Okote Members of the Koobi Fora Fm., and Makapansgat Members 3 and 4, Sterkfontein Member 4, Swartkrans Member 1, and Kromdraai A. Where appropriate, regional taxocenes were supplemented with additional fossils from other members at these sites and from the sites of Ledi-Geraru (Leadu) in Ethiopia, West Turkana, Laetoli, and Kanapoi in Kenya, and Cooper's A, Bolt's Farm, and Skurweburg in South Africa.

Extant cercopithecid taxocenes were initially drawn from 177 modern localities in sub-Saharan Africa based on museum records and published species lists in Rowan et al. (2020). Species lists from these localities were aggregated

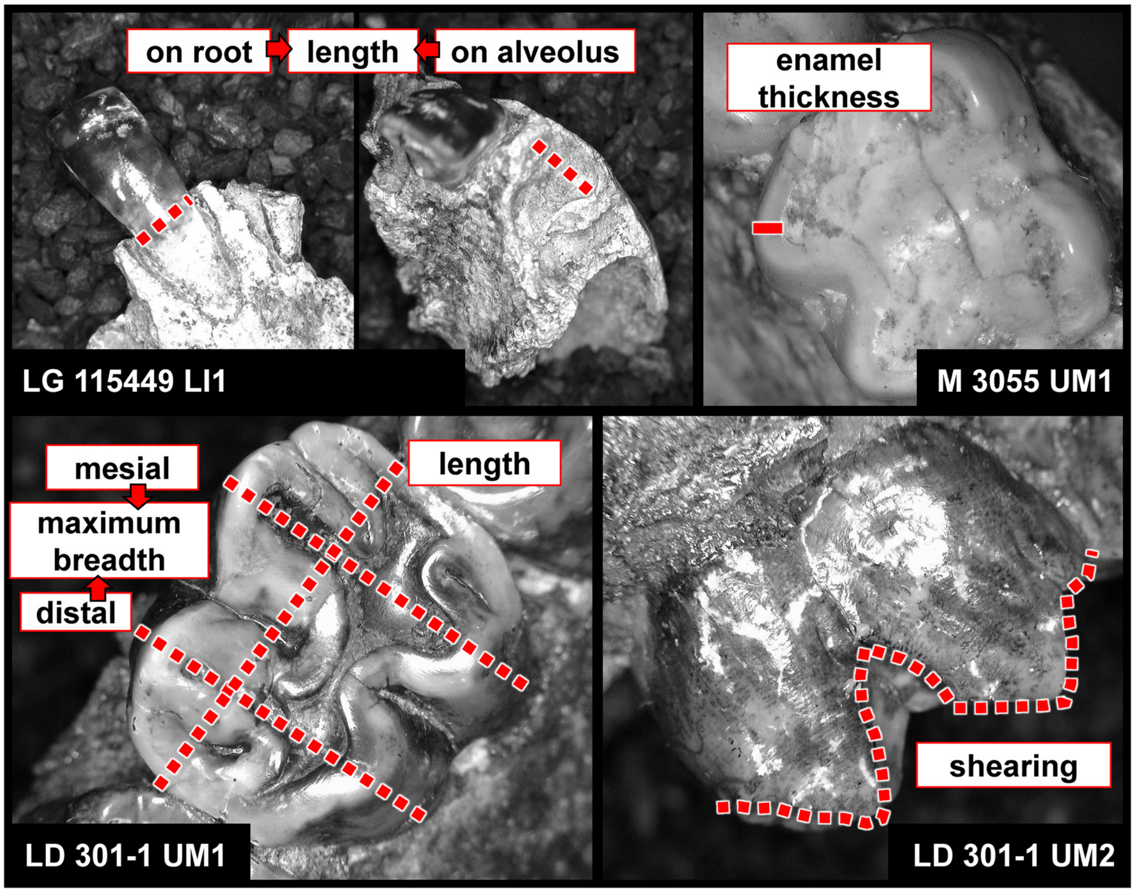

Figure 1. Example microscope image showing dental measurements taken.

into twelve habitat types based on the vegetation zones and mapping units of White (1983; summarized in Table 1) and by fifteen modern country boundaries to approximate some of the potential spatial or temporal averaging that may be present within the fossil sample (Du and Behrensmeyer 2018). These habitat- and country-based taxocenes included some taxa that were not in the modern measurement sample and were instead resampled by genus for these broader comparative analyses, as described below. For local comparisons, 34 representative sites were chosen containing species in the dental dataset. Only sites with three or more cercopithecids were considered, and sites with identical species lists or in close spatial proximity to one another were excluded to avoid biasing taxocene comparisons. Although care was taken to choose example sites from each of the different habitat types, some habitats were not represented at this level due to low species richness. The distribution of modern sites and countries are shown in Figure S1, and a full species list for each country, habitat, and local site taxocene are included in Table S2.

RESAMPLING

Despite efforts to target relatively complete and large cercopithecid collections, the availability of dental variables for all modern and fossil specimens was still limited by sample availability and preservation at appropriate wear stages. Dental variables were resampled with replacement to allow for the inclusion of more fragmentary specimens and poorly represented taxa, and to control for differences in abundance. This resampling workflow is visualized in Figure 2. For each modern taxocene, a blank dataframe was created for one male and one female individual per species based on target maxillary or mandibular measurements. Sex- and species-specific values were resampled where available to fill over 65% of this target dataset (Step 1). Modern cercopithecid taxa were next resampled by species regardless of sex (Step 2), then by genus (Step 3) to complete over 98% of the modern taxocene sample. Some monospecific taxa or otherwise poorly represented genera were still missing enamel thickness or shearing variables after this step, and these values were filled using higher-taxon resampling as necessary until the target dataframe was complete (Step 4). Missing values for the cercopithecins *Allenopithecus nigroviridis* (all shearing and enamel thickness) and *Miopithecus ogouensis* (maxillary enamel thickness) were filled by resampling other species in the tribe Cercopithecini. *Procolobus verus* (all enamel thickness) and *Piliocolobus* spp. (maxillary enamel thickness) were resampled from extant *Colobus* species (shared tribe Colobini). For the large papionins *Theropithecus gelada* (mandibular enamel thickness) and *Mandrillus leucophaeus* and *M. sphinx* (mandibular shearing; maxillary shearing and enamel thickness), missing values

TABLE 1. MODERN HABITAT CLASSIFICATIONS BASED ON WHITE (1983).
(Mapping units in *italics* had no representative sites in the sample.)

Habitat	Description and mapping units adapted from White (1983)
Acacia Woodland	Woodland and bushland (>40% cover) dominated by *Acacia* species, including transition zones. These habitats are found in drier regions below the Sahara (43) and in eastern (35a, *35b*, *37*, 42, 45) and southern Africa (35a, 35c, 44).
Afro-Alpine	High-elevation peaks occurring on isolated mountains in eastern (65) and southern (*66*) Africa. Vegetation is variable, but all experience nighttime temperatures that can fall below freezing year-round.
Desert	Extreme arid conditions found in the Sahara (*67*, *69*, *72*, *73*) and Namib (74) deserts, as well as in coastal deserts along the Atlantic and Red Sea (*68a*, 68b).
Edaphic Grassland	Grass and herb vegetation on waterlogged soils that inhibit the growth of woody species (typically <10% woody cover). Found in areas receiving strongly seasonal rainfall (*59*, 60, *61*, 62, 63, 64).
Forest Mosaics	Transitional zones where rainforest intersects with woodland and grassland habitats. Found at the periphery of the Guineo-Congolian rainforest (11a, *12*, *13*, *14*) and along the eastern coast of Africa (16a, 16b, 16c).
Miombo Woodland	Woodland (>40% cover) dominated by *Brachystegia* and related species. Can experience higher mean annual rainfall than acacia or mopane woodlands, but tree growth remains limited due to shallow soils. Found in the Zambezian region of central, southern, and eastern Africa (25, 26).
Montane (secondary) Grassland	Secondary grassland found on lower (non-alpine) mountain elevations and maintained by fire, grazing, and human activity. May also include remnant patches of forest and woodland (*17*, 19A, 20).
Mopane Woodland	Woodlands in southern Africa (28, *36*) dominated by the mopane tree. These habitats are considered distinct from other woodland types (e.g., acacia, miombo) because of their vegetative homogeneity.
Sedge and Reed Swamp	Papyrus-dominated freshwater swamps associated with lakes and rivers, including regions around Lake Chad and the Okavango Delta (75). Grasslands and small trees may occur in these regions, but this habitat does not include heavily forested swamps like those found in the Guineo-Congolian basin.
Shrubland and Grassy Semi-desert	Arid regions capable of sustaining limited vegetation, found along the periphery of the Sahara (54a, 70, 71) and Namib deserts (51, *53*, 56, *57a*, *57b*). Additional pockets of semi-desert are found in parts of eastern Africa with low mean annual rainfall (54b).
Tropical Lowland Rainforest	Evergreen and semi-evergreen forest found in central and western Africa (1a, 2, 3, *4*). This habitat grouping also includes swamp forests located along the Congo River and Atlantic coastal regions (8, 9).
Woodland (other)	Open-canopy woodlands (>40% cover), allowing for the development of grasses. Found in western and central Africa north of the transitional forest mosaic (27, 29a, 29b, *30*) and in southeastern Africa (29c, 29d, *29e*, *31*).

were resampled from other large papionins only (*Mandrillus, Theropithecus, Papio*) due to potential size effects between these taxa and the smaller *Cercocebus* and *Lophocebus*.

Resampling for fossil cercopithecids followed a similar taxonomic pattern (species, genus, higher taxon group), but these steps were further subdivided based on temporal, spatial, and phylogenetic proximity. Too few fossil specimens were attributable to sex, so two individuals per fossil species were resampled first by their specific taxocene (i.e., by member) independent of sex (Step 1). This initial step filled 18% of the target maxillary dataset and 24% of the mandibular. After the next phase of resampling by fossil site or formation (Step 2a), approximately one-third of the resampled dataset was filled with strong spatial and moderate to strong temporal restriction. Beyond this, spatial and temporal restrictions were progressively relaxed as

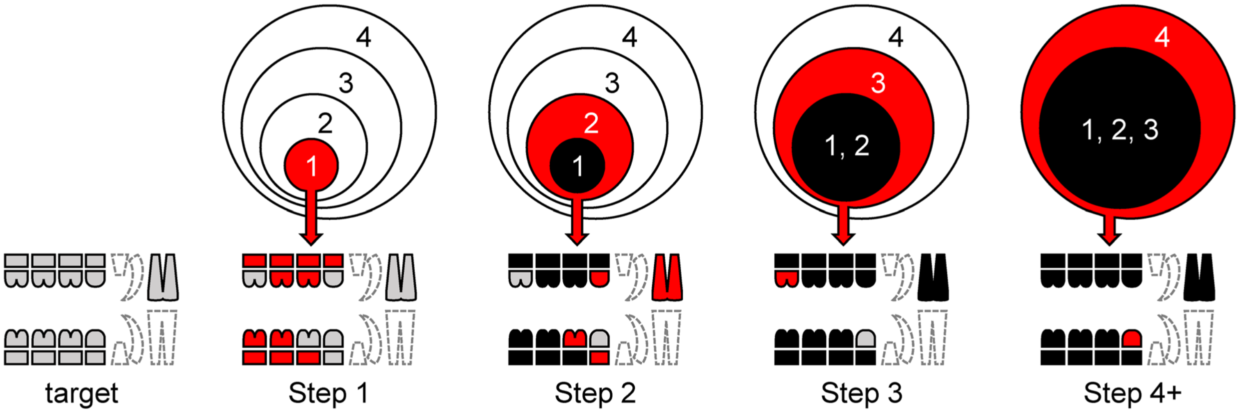

Figure 2. Schematic of resampling workflow.

fossil species were resampled by region and time period (Step 2b), by time period alone (Step 2c), then by all available fossils of that species (Step 2d). A similar pattern was repeated for fossil genera (Step 3: regional and temporal restrictions; temporal only; unrestricted), filling over 80% of the maxillary sample by fossil genus (90% for mandibular). As an example, the wide-ranging fossil colobine *Cercopithecoides williamsi* from Makapansgat Member 3 would have been resampled stepwise from 1) the MLD3 sample, 2a) all of Makapansgat, then 2b) the earlier Pleistocene (Gelasian) of South Africa. Had the *C. williamsi* sample remained incomplete at this point, resampling would have proceeded to 2c) all Gelasian *C. williamsi* in both eastern and South Africa, 2d) *C. williamsi* regardless of time period, 3a) Gelasian South African *Cercopithecoides*, 3b) Gelasian *Cercopithecoides* in both eastern and South Africa, 3c) all *Cercopithecoides*, and finally 4) all large-bodied fossil colobines.

As with the modern species, some monospecific fossil genera, indeterminate species, or otherwise poorly represented taxa required resampling beyond the genus level. These included the large papionins *Dinopithecus ingens* (all enamel thickness and shearing), *Gorgopithecus major* (mandibular shearing), and *Soromandrillus quadratirostris* (mandibular enamel thickness and shearing), which were resampled with other large fossil papionins. Missing values for *Paracolobus mutiwa* (maxillary incisors and enamel thickness) and *Rhinocolobus turkanaensis* (maxillary incisors and shearing) were filled with those from other large fossil colobines. An indeterminate fossil colobine (Omo Mbs. C and G) and papionins (various sites) were necessarily resampled by tribe and size class for most measurements. Finally, fossil guenons including *Nanopithecus browni* and indeterminate species from Koobi Fora and the Omo were supplemented with extant African cercopithecins after all available fossil measurements were exhausted.

Although the use of resampling at these higher taxonomic levels is not ideal, this is preferable to removing these taxa entirely. Many of these traits are under phylogenetic control and given the scale of differences between groups such as small-bodied fossil cercopithecins, large-bodied papionins, and colobines, resampling within these groups is not expected to have an outsized impact on the overall taxocene analyses. To further control for potential intraspecific variation within the sample as a result of either natural (e.g., sexual dimorphism) or artificial variation introduced by the resampling procedure, each taxocene was resampled 1,000 times for use in subsequent analyses. I note, however, that as a result of the resampling protocol, taxocenes with greater proportions of resampled species may appear artificially more similar to one another than they actually are. This would potentially make it more difficult to reject the null hypothesis of niche stasis (H_0).

ASSESSING NICHE STRUCTURE

Principal component analysis was used to model the cercopithecid dental morphological niche in multidimensional space (Hutchinson 1957; Stroik 2014). Separate analyses were run on the maxillary and mandibular dentition to account for differences in data availability, and only extant and fossil species with complete dental data were used to generate the initial models. Species-averaged dental ratio data and size variables were first run in scaled principal component analyses using the *prcomp* function in the stats R package (R Core Team 2020) to approximate the fundamental maxillary and mandibular niches of African cercopithecid primates. Resampled individuals were then projected into this fundamental niche space to calculate the local, realized niches of cercopithecid taxocenes based on the first two principal component (PC) axes.

For each modern and fossil taxocene, PC1 and PC2 niche centroids were calculated as the average position of all constituent taxa along that principal component axis. This provides a rough measure of how close or far taxocenes may be from one another and from the fundamental cercopithecid niche, relevant for identifying potential positional change (H_1). Taxocene niche volumes (for H_2) were calculated from a maximum convex hull placed around the edges of each taxocene in two-dimensional principal component space, using the *convhulln* function from the geometry R package (Roussel et al. 2019). This captures how much of the fundamental niche space is occupied by a given taxocene, and a larger niche volume therefore indicates greater

TABLE 2. PROPORTIONS OF VARIANCE AND VARIABLE LOADINGS FOR THE FIRST TWO PRINCIPAL COMPONENT AXES.

	Maxilla		Mandible	
	PC1 (50.8%)	PC2 (18.4%)	PC1 (42.7%)	PC2 (31.3%)
Body size (M1 length)	0.43	-0.03	0.49	-0.04
Incisor proportions (I1:I2)	-0.34	0.29	n/a	
Relative enamel thickness (M1)	-0.13	0.61	-0.08	0.61
Relative shearing ability (M2)	-0.01	-0.54	0.06	-0.53
P4 shape (breadth:length)	0.08	0.36	0.33	0.43
Relative P4 size (P4:M1-M3 length)	-0.42	-0.14	n/a	
Relative P4 size (P4:M2 area)	-0.34	-0.3	-0.38	-0.26
Molar proportions (M1:M3 length)	-0.44	0.06	-0.54	0
Molar proportions (M1:M3 breadth)	-0.43	-0.05	n/a	
M3 shape (breadth:length)	n/a		-0.45	0.31

total ecomorphological diversity than a small niche volume. Taxocene niche centroids and volume metrics are not controlled for species richness, nor do they account for the degree to which species within a taxocene occupy dissimilar or overlapping niches. To first assess whether taxocenes occupy static (H_0) or changed niches (H_1/H_2), direct comparisons between taxocene niches were performed through analysis of multivariate homogeneity of groups dispersions and permutational multivariate analysis of variance using the respective *betadisper* and *adonis* functions in the vegan R package (Oksanen et al. 2019).

Taxocene dispersion metrics are based on the distance of each individual from the taxocene centroid. Smaller dispersions therefore indicate that individuals within a taxocene are more densely packed within their combined niche space. This could occur in small taxocenes where few species contribute to a lower niche volume, or in larger taxocenes where many species overlap with one another regardless of the total niche volume. In contrast, more diverse taxocenes with ecomorphologically distinct species would be characterized by greater average distances between individuals and the group centroid. Permutational MANOVA assesses niche similarity or dissimilarity from both the relative positions of taxocene centroids (how close are groups on average) and the level of niche overlap observed between groups within their available niche space based on both taxocene volumes and dispersions (Anderson 2001; Anderson and Walsh 2013). Where appropriate, post-hoc pairwise comparisons were performed using the *TukeyHSD* function in the stats R package (R Core Team 2020) and *pairwise.perm.manova* from the RVaideMemoire R package (Hervé 2020).

RESULTS

THE CERCOPITHECID DENTAL MORPHOLOGICAL NICHE

Each data subset performed similarly in the initial principal component analyses used to model the cercopithecid maxillary and mandibular dental ecomorphological niches. The first two components captured over 65% or more of the total variation (Table 2; Figures 3 and S2). Species used to generate the respective models are shown in Figures 4 and S3. Body size was represented along the first principal component opposite relatively larger central incisors (maxillary) and P4 and M1 size. At the species level, this primarily reflected a gradient from small-bodied guenons to mangabeys, extant colobines, fossil colobines, and extant and fossil large-bodied papionins. Tropical forested sites with multiple small-bodied *Miopithecus* and *Cercopithecus* monkeys (e.g., Massif du Ziama, Mbam et Djerem) had taxocene centroids pulled towards the negative axis of PC1, more seasonal, higher-latitude sites and habitats in the modern sample (e.g., Lac Fitri, Nairobi) with larger-bodied *Papio* and few small guenons had less negative centroids. Fossil taxocene centroids along PC1 were clearly distinguished from modern sites in being strongly positioned towards the positive axis, indicating larger overall body sizes than observed in modern taxocenes. This is driven by both the larger absolute sizes of some fossil taxa (e.g., fossil vs. modern colobines or *Theropithecus* species) and by the greater proportional representation of large-bodied fossil papionins and colobines relative to small cercopithecines.

Fossil and modern taxocenes exhibited a more similar range of variation in PC2 centroid position where molar

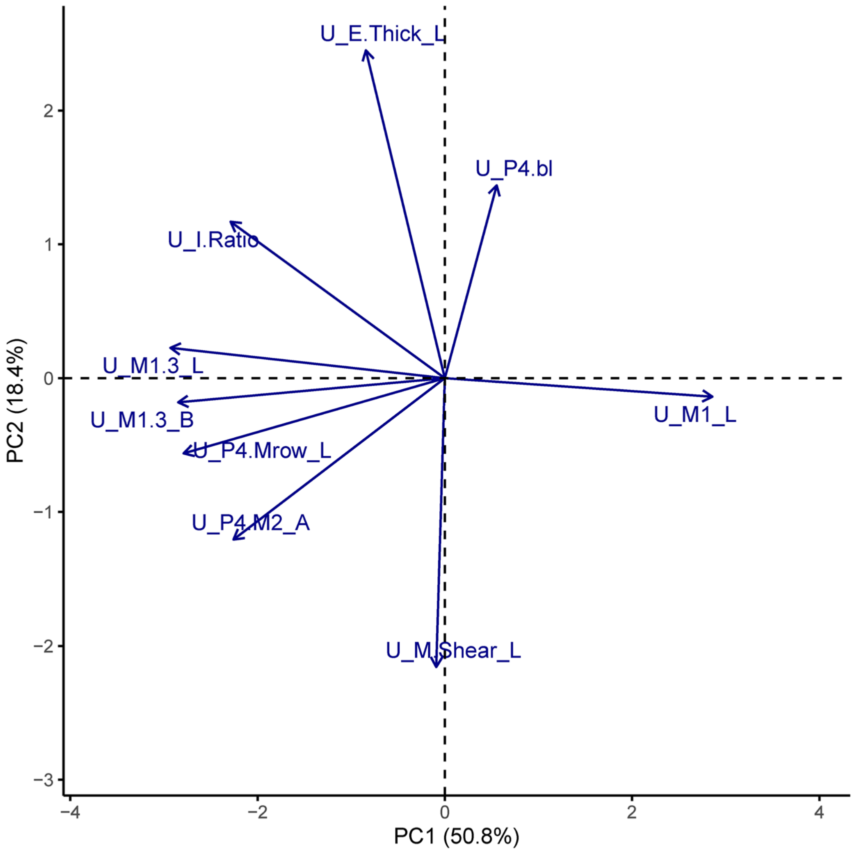

Figure 3. Biplot of maxillary variables in principal component space.

shearing loaded opposite enamel thickness and broader postcanine teeth. This axis generally separated folivorous colobines, frugivorous guenons and papionins, and hard-object feeding mangabeys and papionins. For modern taxocenes, sites with greater proportions of folivorous and frugivorous taxa had more negative centroid positions along PC2 (e.g., Akagera, Badiar), while sites with more omnivores and hard-object feeders had more positive centroids (e.g., Campo Maan, Fernan Vaz). Fossil taxocenes occupied among the more extreme niche centroid positions on PC2, differentiating some of the Omo-Turkana sites (negative) from those in South Africa (positive).

A summary of taxocene comparisons for measures of niche similarity and dispersion is included in Table 3, where significance indicates that some taxocene pairs exhibit differences in dispersion or occupy dissimilar niches. Proportional significant results ($p<0.05$) were calculated from the 1,000 resampled taxocene comparisons and results in **bold** are also accompanied by an average $p<0.05$. Summary results for averaged taxocene niche volumes, dispersion metrics, and centroid positions from the maxillary niche are included in Table 4 (select modern taxocenes) and Table 5 (all fossils); complete results for all modern taxocenes (maxillary and mandibular) are included in Table S3 and fossil mandibular results in Table S4. Example taxocene volumes and centroids within the maxillary ecomorphological niche space are shown in Figures 5, 6a, and 6b for the combined sample, modern habitats, and fossil members, respectively. Note that since taxocene volumes are calculated from the periphery only and centroids are based on the average of all individuals, the centroids in these figures are not necessarily located at the visual center of each hull.

MODERN TAXOCENES

For the 34 modern localities, taxocene niche volumes were correlated with overall species richness ($p<0.001$, $R^2=0.76$–0.77), but taxocene dispersions were not. Similar effects were observed for habitat- and country-based taxocenes. Potential support for H_2 is therefore interpreted with some caution to account for differences in species richness. In direct pairwise comparisons, results for modern African cercopithecids were relatively consistent. In both the maxillary and mandibular analyses, taxocenes at different analytical scales (site, habitat, country) exhibited similar patterns of dispersion, but different niche positions at the habitat level, in support of H_1. Post-hoc pairwise comparisons of significantly different habitats indicate that tropical lowland rainforest, montane (secondary) grassland, and other woodland habitats are most different from edaphic grassland, mopane woodland, and shrubland and grassy semi-desert. Shrubland and grassy semi-desert habitat is also distinct from forest mosaics. Desert habitats were often significantly different from tropical lowland rainforest, forest mosaics, and montane grasslands in post-hoc

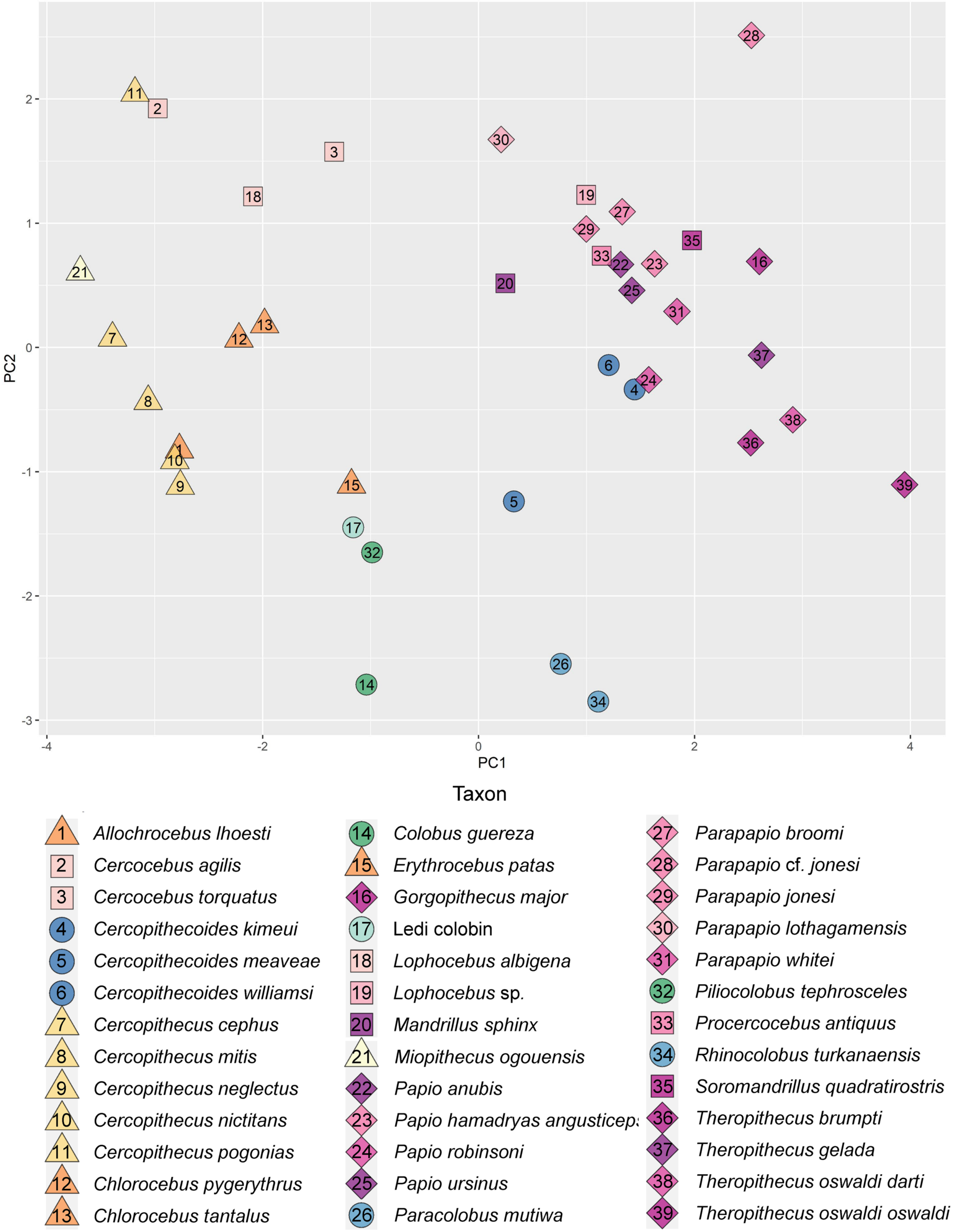

Figure 4. Species positioning within the principal component niche space based on averaged maxillary dental variables.

TABLE 3. PROPORTIONS OF SIGNIFICANT RESULTS ($p<0.05$) FROM RESAMPLED TAXOCENE COMPARISONS.

Modern	Maxilla		Mandible	
	Dispersion	Similarity	Dispersion	Similarity
Site	3.4%	**65.9%**	13.9%	53.2%
Habitat	0.1%	**100%**	0.0%	**97.9%**
Country	7.8%	28.9%	1.4%	10.3%

Fossil	Maxilla		Mandible	
	Dispersion	Similarity	Dispersion	Similarity
Member	**100%**	**74.2%**	**88.2%**	**98.9%**
Region	**92.2%**	27.0%	53.2%	50.9%

comparisons. Differences in species richness and taxocene niche volumes alone cannot account for these results. Instead, small-scale variation between taxocenes in different habitats becomes more pronounced when grouping the most similar sites together. These two main habitat groups exhibit distinct centroid positions, with desert, semi-desert, edaphic grassland, and mopane woodland having more positive centroids on PC1 and—to a much lesser extent—PC2 (see Figure 6a).

Post-hoc pairwise comparisons further suggest that the significant differences observed between modern sites are related to habitat differences, although no specific site pairs were statistically significant after controlling for multiple comparisons. Modern site pairs approaching significance typically consisted of one more forested site (Mont Fouari – tropical rainforest; Fernan Vaz and Tsoulou – forest mosaics; Campo Maan and Rio Muni - tropical lowland rainforest) and one more open woodland or grassland site (Abijatta-Shalla, Akagera, Ngorongoro, Nairobi – acacia woodland; Lac Fitri - edaphic grassland; Deux Bales, Equatoria, Kidepo Valley, Mount Assirik, Omo, Parc W Niger, Zemongo – other woodland; Aberdare, Mount Nimba - montane grassland). One forest mosaic site (Badiar) was also included in the latter group, being different from other forested sites. This highlights that local variation in habitat structure is not always captured in categorical classification systems, which may explain the more mixed results of modern site-based niche comparisons. Centroid position again varied across these two groups, with the less-forested sites occupying a more positive position along PC1 but

TABLE 4. AVERAGE RESAMPLED MAXILLARY NICHE METRICS FROM EXAMPLE MODERN SITES AND *HABITATS*.

	Number of Taxa	Volume	Dispersion	PC1 Centroid	PC2 Centroid
Massif du Ziama	10	19.99	2.03	-1.82	-0.64
Rio Muni	9	16.91	1.92	-2.50	0.34
Tropical lowland rainforest	*41*	27.49	1.88	-2.02	-0.34
Mbam et Djerem	8	18.45	1.91	-1.86	0.00
Badiar	5	10.51	1.83	-0.85	-1.14
Forest mosaics	*31*	*27.83*	*2.03*	*-1.68*	*-0.21*
Akagera	7	15.12	2.00	-1.42	-0.89
Nairobi	4	9.96	2.04	-1.26	-0.25
Acacia woodland	*23*	21.60	1.98	-1.26	-0.46
Gombe	6	12.99	1.98	-1.78	-0.54
Miombo woodland	*11*	*19.13*	*2.15*	*-1.13*	*-0.21*
Lac Fitri	3	5.77	1.84	-0.64	-0.13
Edaphic grassland	*7*	*10.52*	*1.97*	*-0.43*	*-0.20*
Desert	*3*	*3.38*	*1.83*	*0.20*	*0.40*

TABLE 5. AVERAGE RESAMPLED MAXILLARY NICHE METRICS FROM FOSSIL SITE MEMBERS AND *BASINS*.

	Number of Taxa	Volume	Dispersion	PC1 Centroid	PC2 Centroid
Sidi Hakoma	4	7.19	2.03	1.54	-0.53
Kada Hadar	3	4.88	2.33	1.62	-0.27
Pliocene Hadar Formation	*4*	*6.79*	*2.01*	*1.54*	*-0.34*
Shungura Mb. C	6	13.41	2.02	0.95	-1.15
Pliocene Omo Valley	*7*	*14.77*	*2.01*	*1.06*	*-0.87*
Shungura Mb. E	5	7.32	1.75	1.89	-1.2
Shungura Mb. G	7	16.37	2.09	1.21	-0.96
Gelasian Omo Valley	*8*	*16.79*	*2.04*	*1.17*	*-0.78*
Tulu Bor	6	15.51	2.19	0.87	-0.19
Pliocene East Turkana	*6*	*15.26*	*1.97*	*0.94*	*0.26*
Upper Burgi	6	10.46	1.74	1.85	-1.23
Gelasian East Turkana	*6*	*10.39*	*1.84*	*1.62*	*-0.77*
KBS	9	24.08	2.29	0.94	-0.66
Okote	6	20.90	2.67	0.87	-0.08
Calabrian East Turkana	*9*	*24.13*	*2.28*	*0.95*	*-0.62*
Makapansgat Mb. 3	7	6.80	1.27	1.63	0.33
Makapansgat Mb. 4	5	3.95	1.34	1.7	0.39
Sterkfontein Mb. 4	6	3.87	1.00	1.48	0.65
Gelasian South Africa	*9*	*6.20*	*1.11*	*1.53*	*0.37*
Swartkrans Mb. 1	5	6.17	1.41	2.15	-0.08
Kromdraai A	3	2.02	1.03	1.67	0.56
Calabrian South Africa	*7*	*6.93*	*1.27*	*2.00*	*-0.02*

more negative position along PC2. This pattern is opposite that seen at the habitat scale but can be attributed to the effect of averaging more speciose, often allopatric colobines and guenons in forested habitats, overemphasizing their contribution at this scale compared with the local site level. Although modern taxocenes were not found to exhibit different patterns of dispersion at the site level, the two taxocenes at Mont Fouari and Tsoulou (1.1) stand out in having very low dispersions compared with other sites (1.7–2.3), while Knysna and Ngorongoro have slightly elevated dispersions (2.5) in the maxillary analysis. Finally, there were no significant differences between modern taxocenes when aggregated by country. Overall, these results indicate that modern cercopithecid taxocenes exhibit little variation in measures of niche dispersion, as species tend to be evenly distributed within their collective dental morphological niche space regardless of taxocene niche size. Taxocenes at local scales occupy distinct niches from one another, reflecting different habitat types. These differences are emphasized when sites are grouped by habitat but become obscured when sites are grouped spatially across multiple habitats.

FOSSIL TAXOCENES

As with the modern cercopithecid taxocenes, fossil taxocene niche volumes at the member level were also correlated with species richness, albeit less strongly ($p<0.01$, $R^2=0.48–0.49$). Dispersion was again not correlated with species richness for the fossil taxocenes. Compared with modern sites, some of those in the Omo-Turkana Basin exhibited elevated niche volumes per taxocene size while South African sites exhibited reduced niche volumes (Figure 7), indicating potential support for H_2.

Direct niche comparisons of fossil cercopithecids revealed a distinct pattern from their modern counterparts. Fossil taxocenes exhibited significant differences in dispersion, as well as a pattern of niche dissimilarity at the member level (see Figure 6b). Most of these significant differences involved pairwise comparisons between eastern and South African taxocenes with few exceptions. Differences in dispersion were driven largely by more highly-dispersed taxocenes at Hadar (Kada Hadar Mb.), the Omo Valley (Shungura Mbs. C and G), and East Turkana (Tulu Bor, KBS, Okote Mbs.) compared with South African taxocenes at Sterkfontein (Mb. 4), Swartkrans (Mb. 1), and Kromdraai

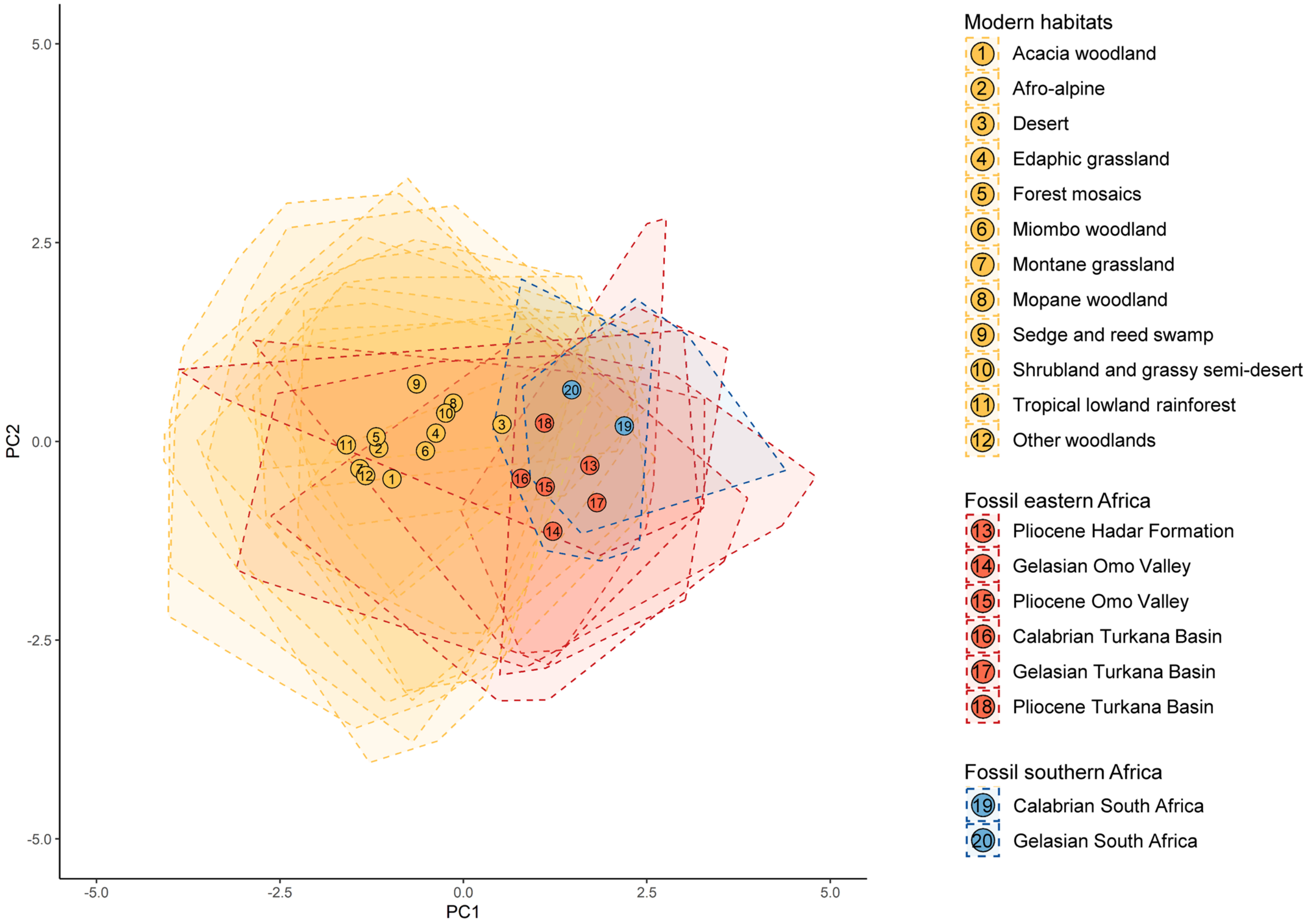

Figure 5. Example taxocene niche volumes and centroid positions from a representative maxillary permutation.

A. Of these, the Okote Member and Sterkfontein appeared in the most significantly different pairwise comparisons. In contrast, patterns of niche dissimilarity most often involved the Upper Burgi taxocene and, to a lesser extent, the Shungura Formation (Mbs. C, E, and G) compared with Sterkfontein (Mb. 4) and Makapansgat (Mbs. 3 and 4). Despite similar species richness across these members, the three taxocenes from South Africa have much lower niche volumes and a more positive PC2 centroid position, in support of both H_1 and H_2. In some instances, the Sterkfontein taxocene was also found to be dissimilar to that from Swartkrans, which occupies the most extreme position along PC1. When fossil members were grouped together by region and time period, the resulting taxocene comparisons were not found to occupy distinct niches and produced mixed results for differences in dispersion.

Modern and fossil taxocenes were not directly compared but would almost certainly have exhibited significant niche differences as all fossil taxocenes are shifted positively on PC1 relative to modern sites and habitats (see Figure 5). In other niche measures, fossil taxocenes show a similar range of variation to that seen across modern sites and habitats. The Upper Burgi and Shungura Members C, E, and G exhibit a more negative position along PC2, along with modern sites like Mount Assirik and Badiar. Taxocenes from Makapansgat, Sterkfontein, and Kromdraai have a more positive PC2 centroid, like Zinave, Lake Manyara, Rio Muni, and Fernan Vaz. East Turkana sites exhibit slightly elevated niche volumes relative to the number of cercopithecids, but which are still in the range of modern sites like Massif du Ziama. The reduced taxocene niche volumes of South African fossil sites (especially relative to species richness) are most similar to those seen at Tsoulou, Mont Fouari, and Zinave. The small dispersions of South African sites are again similar to modern Tsoulou and Mont Fouari, while the larger dispersions in eastern Africa are comparable to sites like Knysna or Ngorongoro.

DISCUSSION

Many previous studies of African primate community structure have included members of the Hominoidea and Strepsirrhini in addition to Cercopithecidae and focused on more species-rich tropical forest sites. These have shown that primate species richness in Africa exhibits a strong latitudinal and weak longitudinal gradient, with the greatest number of species concentrated in tropical forested regions of equatorial Africa (Chapman et al. 1999; Eeley and Lawes 1999; Reed and Bidner 2004). A similar pattern can

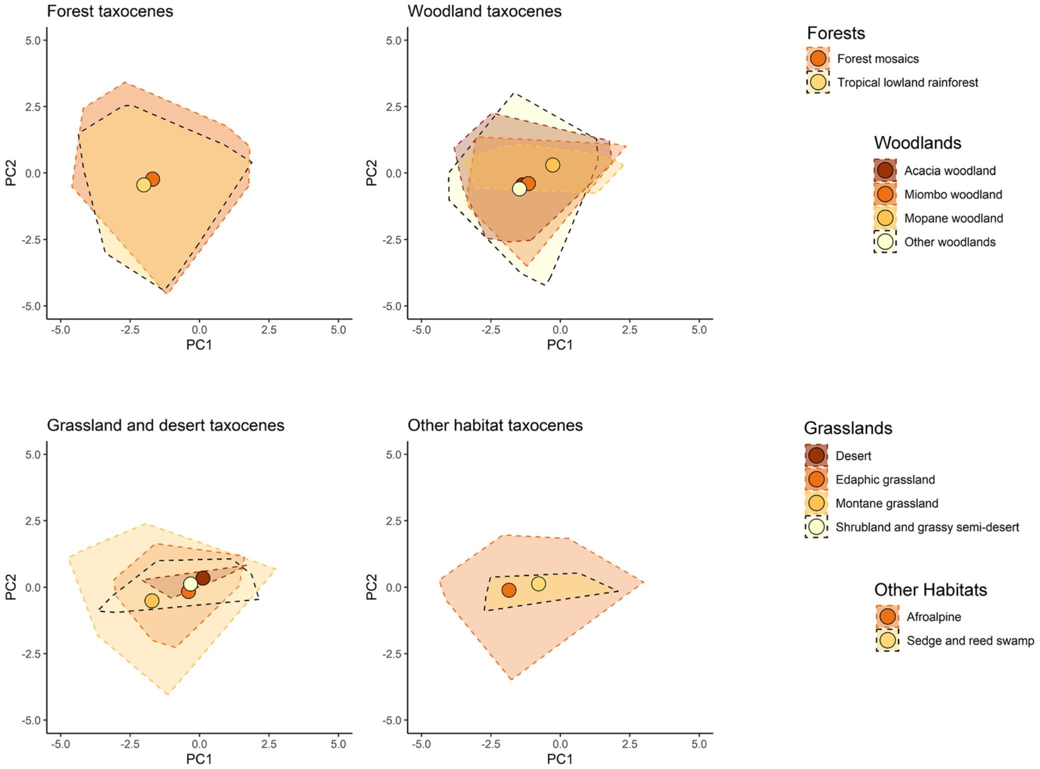

Figure 6a. Example distribution of modern taxocenes within the maxillary ecomorphological niche space from a representative permutation.

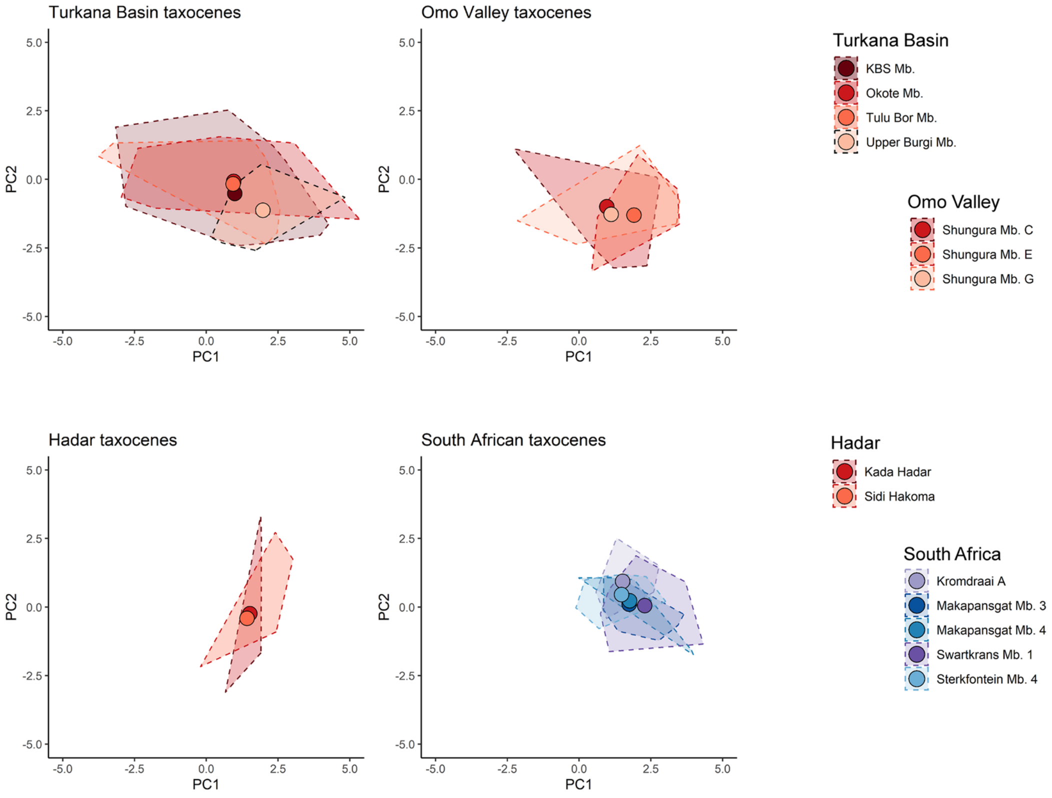

Figure 6b. Example distribution of fossil taxocenes within the maxillary ecomorphological niche space from a representative permutation.

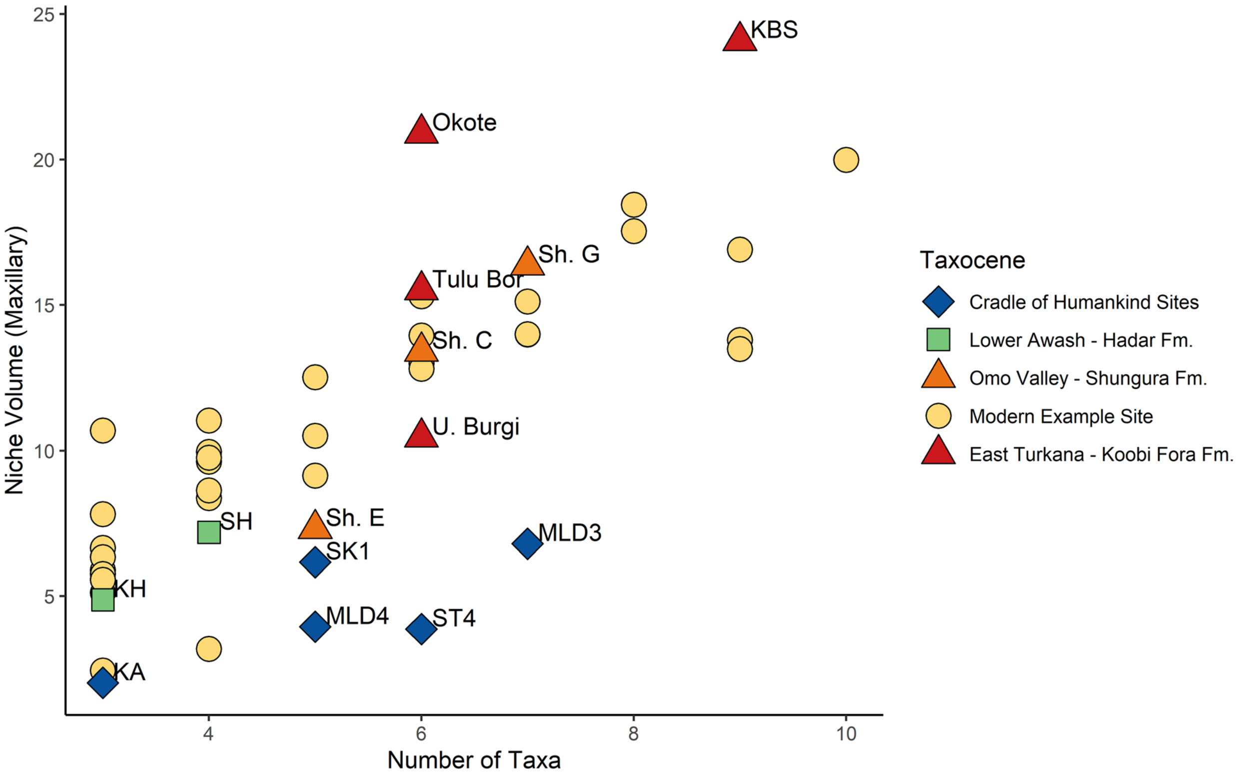

Figure 7. Plot of taxocene species richness and maxillary niche volumes.

be observed when focusing only on the cercopithecid component of these primate communities, resulting in greater taxocene niche volumes for sites in more forested regions of Africa today. Pairwise differences are most pronounced when comparing habitat-based taxocenes from seasonal and higher-latitude habitats (e.g., desert, shrubland and grassy semi-desert, mopane woodland) with those from lower-latitude habitats (e.g., tropical lowland rainforests or forest mosaics). In particular, the presence of multiple species of smaller-bodied guenons and colobines in forested regions contributes to lower average body sizes and a proportional increase in adaptations for folivory and frugivory rather than hard-object feeding and omnivory. This is consistent with findings that factors such as rainfall and historical biogeography have led to a greater concentration of small-ranged ecological specialists in western and central Africa (Beaudrot et al. 2014; Cowlishaw and Hacker 1997; Eeley and Foley 1999; Lawes and Eeley 2000; Reed and Fleagle 1995).

In addition to the clear differences between more closed (forest) and open (desert, shrubland) habitats, there were also differences between habitats that fell intermediate to these two extremes. Although the four woodland habitat categories included in this study all share vegetative features like 40% or more woody cover, an open canopy, and a grass layer, these habitats and the sites within them did not necessarily exhibit a consistent cercopithecid taxocene. At the site level, localities associated with acacia woodlands tended to have slightly higher dispersions than those in other woodland habitats, despite similar species richness. Mopane woodlands consistently had the smallest taxocene niche volumes and most positive PC2 centroid positions at both the site and habitat level, distinguishing them from other woodland habitats as observed in the post-hoc comparisons. This again highlights the complex relationship between local habitat conditions and taxocene composition, and cautions against the use of simplified environmental measures (e.g., canopy height, percent woody cover) that may ignore otherwise meaningful differences between sites and thus local faunal communities. While exploring the potential biogeographic, climatic, anthropogenic, or other factors driving these differences is beyond this scope of this study, future studies focusing on primate communities in woodland habitats specifically may be especially helpful for interpreting taxocene differences observed within the fossil sample.

As always, reconstructing species paleoecologies is limited by the availability of adequately preserved fossil samples and our ability to interpret this fragmentary record. Despite efforts to target well-represented collections and dental morphological variables, all fossil taxocenes considered here included a taxon represented by only one or two specimens. Measures of shearing ability and enamel thickness (contributing to variation along the second niche axis) were further limited by the need for specific wear stages of the M1 and M2. It is therefore worth acknowledging the resampling methods used to overcome this incomplete record may have produced more similar taxocene niches than were actually present. Specifically, resampling endemic taxa such as such as *Paracolobus*, *Rhinocolobus*, and

Soromandrillus in eastern Africa and *Dinopithecus* in South Africa could have exaggerated some of the variation seen across these two regions. At the same time, resampling for the wide-ranging *Theropithecus*, *Papio*, and *Cercopithecoides* as well as indeterminate papionins from the Koobi Fora Formation involved taxa from both eastern and South Africa. The lack of significant effects at the regional level further supports the interpretation that differences between fossil taxocenes cannot be solely a result of these methods or of purely biogeographic effects.

Differences between fossil cercopithecid taxocenes in eastern and South Africa place a greater emphasis on variation in proportions of adaptations rather than body size differences. The reduced role of body size variation in the fossil sample can be attributed to a combination of taphonomic biases against smaller-bodied taxa (i.e., Cercopithecini and Colobini) and towards more open and arid habitats like those found in parts of eastern and southern Africa today. Small-bodied cercopithecin monkeys are found at all of the modern sites included in this analysis and in five fossil taxocenes: Shungura Mbs. C and G, and the Tulu Bor, KBS, and Okote Members in East Turkana. In pairwise comparisons, these fossil members exhibited different dispersions from South African deposits without Cercopithecini. The guenon fossil record is very limited but does attest to the longevity and presence of these monkeys in the Plio-Pleistocene of eastern Africa (Arenson et al. 2022; Frost et al. 2020; Jablonski et al. 2008; Plavcan et al. 2019). In South Africa, the oldest known specimens of *Chlorocebus* come from middle Pleistocene deposits at Sterkfontein (Ogola 2009; see also Arenson et al. 2022), and arboreal guenons (*Cercopithecus*) may have arrived in southern Africa even more recently (Lawes 1990). However, differences between eastern and South African taxocenes cannot be entirely attributed to an absence—real or artificial—of cercopithecins in South Africa, since significant pairwise comparisons between these regions implicated the Upper Burgi taxocene from East Turkana, which has neither guenons nor small-bodied Colobini. Future studies focusing on modern Asian cercopithecids may provide a natural comparison to some of these fossil sites, as Asian taxocenes also lack cercopithecins.

Paleoecological and paleoclimate studies indicate a consistent trend throughout the Pleistocene towards aridification and corresponding expansion of grassland habitats across Africa (Marlow et al. 2000; deMenocal 2004). Similar changes have been documented through time in the Omo-Turkana Basin (Bibi et al. 2013; Bobe 2011; Fortelius et al. 2016; Levin et al. 2011) and between older (Makapansgat, Sterkfontein) and younger (Swartkrans, Kromdraai) sites in South Africa (Avery 2001; Hopley et al. 2006; Reed 1996; Vrba 1974). Despite this and other evidence for habitat differences between more open and closed habitats in the modern sample, this study found no clear pattern of temporal variation in the fossil cercopithecid taxocenes from the Pliocene and early Pleistocene considered here. Pairwise comparisons of fossil taxocenes from eastern and South Africa instead indicate significant differences between taxocenes' dispersions or a significant pattern of niche dissimilarity across these two regions reflecting different dental morphological adaptations. Since the modern sites and habitats in this study did not show significant differences in dispersion, it is unclear whether these results within the fossil sample could be attributable to habitat differences from non-analogue conditions (Faith et al. 2019) or hominin activity. Further studies are needed to explore the factors that could be responsible for these effects.

One of the few exceptions to the eastern vs. southern distinction can be seen in the significantly different niche positions observed between Sterkfontein Mb. 4 and Swartkrans Mb. 1, driven by both dental morphology and body size differences. Other analyses of temporal change in fossil Cercopithecidae have suggested a pattern of gradual rather than sudden changes in Pliocene and early Pleistocene cercopithecid diversity (Elton 2007; Frost 2007). Extending these analyses further into the Pleistocene may help capture a longer record of change, as Elton (2007, 2012) found for South African cercopithecid taxocenes after Swartkrans Mb. 1 and Kromdraai. The small cercopithecid samples from Swartkrans Members 2 and 3 were not included separately in this study but as cercopithecid remains continue to be recovered and studied from younger sites in this region, expanding these analyses to include sites like Cooper's D (Berger et al. 2003; DeSilva et al. 2013; Folinsbee and Reisz 2013) and Haasgat (Adams 2012; McKee and Keyser 1994; McKee et al. 2011) may shed light on the nature of this potential niche shift.

Direct comparisons between the modern and fossil cercopithecid taxocenes are also complicated by potential taphonomic biases and unbalanced habitat representation. Tropical forest sites in western and central Africa today are absent from the Pliocene and early Pleistocene fossil record, while many localities in eastern and southern Africa today that may represent similar habitat conditions to some fossil sites were excluded from analysis for having fewer than three cercopithecid taxa. The Hadar Formation and sites in the Omo-Turkana Basin have typically been reconstructed as heterogeneous habitats, either because they supported a mosaic of open grassland to woodland habitats or because of temporal averaging across homogeneous environments at the submember or smaller scale (Bobe 2011; Bonnefille et al. 2004; Fortelius et al. 2016; Reed 2008). South African sites have also been reconstructed as having a mix of grassland and woodland components (Avery 2001; Hopley et al. 2006; Reed 1996), although some authors suggest that these deposits represent more restricted climate periods—and thus habitat conditions—than previously thought (Pickering et al. 2019). These paleoenvironmental reconstructions suggesting a potential role for woodland or otherwise mixed habitats reinforce the need to further explore potential taxocene differences between modern cercopithecids in woodland areas that are distinct from one another despite apparent similarities in habitat structure.

Despite potential taphonomic differences, modern and fossil cercopithecid taxocenes in this study nonetheless exhibit a similar range of centroid positions along the dental morphological axis (PC2) and a similar range of niche volumes. However, while modern sites were found not to exhibit differences in dispersion, fossil taxocenes showed a clear split in dispersion metrics, which again distinguished sites in eastern and South Africa. Of the modern sites, Tsoulou and Mont Fouari in the Congo were most similar in volume and dispersion to fossil South African taxocenes. Both are small parks with areas of forest next to fire-maintained grassland (Verschuren 1989). Compared with other forested sites, they contain few cercopithecid species and are the only two sites in the entire modern sample without papionins. South African fossil taxocenes show a similar level of taxonomic skew, being dominated by papionins (especially *Parapapio* spp. at Makapansgat and Sterkfontein) and having few or no colobines and no small-bodied cercopithecins. Eastern African fossil sites had high dispersions similar to those today at Knysna or Ngorongoro. These two modern sites have only three species each, but these taxa occupy distinct positions within the cercopithecid dental morphological niche space. Something similar may occur in the Kada Hadar member where the three cercopithecid taxa present—*Theropithecus darti*, *Parapapio* cf. *jonesi* and cf. *Rhinocolobus turkanaensis*—are commonly reconstructed to have very distinct ecologies (Benefit and McCrossin 1990; Leakey 1987; Wynn et al. 2013, 2016). In the more species-rich Omo-Turkana sites, high dispersions may in part be driven by size differences between large papionins on one extreme of the first niche axis and small cercopithecins and *Colobus freedmani* on the second.

Finally, it is worth returning to the broader primate communities that would have shared the paleolandscape with the cercopithecid taxocenes studied here. Great ape species are important contributors to primate ecological diversity in Africa today (Fleagle and Reed 1996) and may directly impact cercopithecid populations where they co-occur (Boesch 1994; Stanford 1995; Watts and Amsler 2013). Pliocene sites from the Hadar, Usno, and Koobi Fora Formations preserve evidence of *Australopithecus afarensis* (Johanson 2017; Kimbel 1988; Kimbel and Delezene 2009; Wood and Leakey 2011), followed by co-occurring *Paranthropus* and *Homo* lineages in the early Pleistocene of the Omo-Turkana Basin (Alemseged et al. 2002; Bobe and Carvalho 2019; Brown et al. 1985; Grine et al. 2019; Leakey and Walker 1988; Leakey et al. 2012; Prat et al. 2005; Suwa et al. 1996; Ward et al. 2015; Wood and Constantino 2007; Wood and Leakey 2011). Cave sites in South Africa include fossils of *Au. africanus* in the older Makapansgat and Sterkfontein deposits (Cadman and Rayner 1989; Dart 1925; Grine 2013; Stratford 2018) followed by co-occurring *Paranthropus* and *Homo* at Swartkrans Member 1 and possibly Kromdraai B (Braga and Thackeray 2003; Grine 1989, 2005; Vrba 1981). The archaeological record from this time period includes the earliest known stone tools (~3.3 Ma) (Harmand et al. 2015), consistent Oldowan technology by 2.6 Ma (Braun et al. 2019; Semaw et al. 2003), and evidence for meat consumption by early Pleistocene hominins (Ferraro et al. 2013). However, hominins may not have engaged in a major niche shift at this time (Barr et al. 2022), and the analyses presented here did not detect any temporal changes in cercopithecid taxocenes that could be attributed to hominin activity during the Pliocene and early Pleistocene. Later hominins may have had a greater impact on cercopithecids, either directly through hunting them (Shipman et al. 1981) or indirectly by altering the landscape and potential food availability. As more fossils continue to be recovered from later Pleistocene sites, it would be helpful to expand these analyses to examine the potential timing of a later niche shift between fossil and modern taxocenes, which was not detected in the period studied here.

CONCLUDING REMARKS

This study confirms that extant cercopithecid taxocenes in sub-Saharan Africa today exhibit variable niches based on local habitat conditions, and that cercopithecids today appear to maximize their available niches while balancing within-taxocene competition. Like their extant counterparts, fossil cercopithecid taxocenes also occupied distinct niches, reflecting broad habitat differences across eastern and South African fossil sites. The high species richness of fossil South African sites remains unusual, especially as greater taxonomic diversity in this region does not correspond to increased taxocene niches or within-taxocene dispersion. Fossil eastern African sites appear to combine elements seen in both tropical and in more seasonal sites and habitats today, although it is unclear how much these patterns could be affected by temporal and spatial averaging in the fossil sample. Evidence for smaller-scale variation is more limited, with mixed results for niche differences at modern sites and little evidence for fossil taxocene differences within regions. Gradual environmental changes and hominin activity during this period may not have had enough of an impact on cercopithecids to produce a measurable taxocene niche shift in these generalist primates.

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DATA AVAILABILITY

Raw dental measurement data (from calipers and ImageJ measurements) and R code used in these analyses are available upon request to the author.

STATEMENT ON USE OF AI

No AI was used.

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Special Issue: Niche Construction, Plasticity, and Inclusive Inheritance: Rethinking Human Origins with the Extended Evolutionary Synthesis, Part 1

Supplement 1: Community Niches and Evolution of Generalist Primates: A Preliminary Assessment of Plio-Pleistocene Cercopithecidae in Africa

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SUPPLEMENT 1

This file includes: Figures S1–S3 and Tables S1–S4.

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TABLE S1. FOSSIL TAXOCENE COMPOSITION.

Regional Taxocene	Member Taxocene	Taxon	Reference	Sample[1]	
				Max	Mand
Pliocene **Hadar Fm.** Ethiopia (3.42–2.90 Ma)[2]	**Sidi Hakoma** Hadar Fm. (3.42–3.24 Ma)	*Theropithecus oswaldi darti*	Eck 1993	xx	xxx
		Parapapio cf. *jonesi*	Frost and Delson 2002	xx	xx
		cf. *Rhinocolobus turkanaensis*	Frost and Delson 2002	x	xxx
		Cercopithecoides meaveae	Frost and Delson 2002	xxx	xxx
	Kada Hadar Hadar Fm. (3.20–2.90 Ma)	*Theropithecus oswaldi darti*	Eck 1993	xx	xxx
		Parapapio cf. *jonesi*	Frost and Delson 2002	xxx	xxx
		cf. *Rhinocolobus turkanaensis*	Arenson et al. 2022	x	xx
Pliocene **Omo Valley** Ethiopia (~3.3–2.53 Ma)[3]	Usno Fm. (~3.3–3.0 Ma)[4]	*Soromandrillus quadratirostris*	Gilbert 2013	xx	
	Mb. C Shungura Fm. (3.07–2.53 Ma)	*Theropithecus brumpti*	Eck and Jablonski 1987	xxx	xxx
		Theropithecus oswaldi darti	Eck 1987a	x	x
		Cercopithecini indet.[5]	Eck 1987b		
		Rhinocolobus turkanaensis	Leakey 1987	x	xx
		Paracolobus mutiwa	Leakey 1987		xx
		Colobinae indet.[6]	Leakey 1987		
early **Pleistocene** **(Gelasian)** **Omo Valley** Ethiopia (2.53–1.87 Ma)[3]	**Mb. E** Shungura Fm. (~2.4–2.32 Ma)	*Soromandrillus quadratirostris*	Gilbert 2013	xxx	
		Theropithecus brumpti	Eck and Jablonski 1987	xx	xxx
		Theropithecus oswaldi oswaldi	Eck 1987a	x	xx
		Rhinocolobus turkanaensis	Leakey 1987	x	xx
		Paracolobus mutiwa	Leakey 1987		xx
	Mb. F[4]	cf. *Cercopithecoides williamsi*	Frost 2001	x	x
	Mb. G Shungura Fm. (2.27–~1.9 Ma)	*Soromandrillus quadratirostris*	Gilbert 2013	xx	
		Theropithecus brumpti	Eck and Jablonski 1987	xx	xxx
		Theropithecus oswaldi oswaldi	Eck 1987a	x	xx
		Cercopithecini indet.[5]	Leakey 1987		
		Rhinocolobus turkanaensis	Leakey 1987	x	xxx
		Paracolobus mutiwa	Leakey 1987		xx

		Colobinae indet. [6]	Leakey 1987		
Pliocene **East Turkana** Kenya (3.60–2.64 Ma)[3]	Lokochot Mb. (3.60–3.44 Ma)[7]	Papionini indet. (large)[8]	Jablonski et al. 2008a		
	Tulu Bor Mb. Koobi Fora Fm. (3.44–2.64 Ma)	*Theropithecus brumpti*	Jablonski et al. 2008a	x	x
		Theropithecus oswaldi darti	Jablonski et al. 2008a	x	x
		Papionini indet. (small)[9]	Jablonski et al. 2008a		
		Nanopithecus browni[10]	Plavcan et al. 2019		
		Cercopithecoides kimeui	Jablonski et al. 2008b		
		Cercopithecoides williamsi	Jablonski et al. 2008b	xx	xx
early Pleistocene (Gelasian) **East Turkana** Kenya (~2.0–1.87 Ma)[3]	**Upper Burgi** Koobi Fora Fm. (~ 2.0–1.87 Ma)	Papionini indet. (large)[11]	Jablonski et al. 2008a		
		Theropithecus oswaldi oswaldi	Jablonski et al. 2008a	xxx	xxx
		Rhinocolobus turkanaensis	Jablonski et al. 2008b	xx	xx
		Paracolobus mutiwa	Jablonski et al. 2008b		x
		Cercopithecoides kimeui	Jablonski et al. 2008b		
		Cercopithecoides williamsi	Jablonski et al. 2008b	xxx	xxx
early Pleistocene (Calabrian) **East Turkana** Kenya (1.87–1.38 Ma)[3]	**KBS** Koobi Fora Fm. (1.87–1.53 Ma)	Papionini indet. (large)	Jablonski et al. 2008a		
		Papionini indet. (medium)	Jablonski et al. 2008a		xxx
		Theropithecus oswaldi oswaldi	Jablonski et al. 2008a	xx	xx
		Lophocebus sp.	Jablonski et al. 2008a	xx	xx
		Cercopithecini indet.[4]	Jablonski et al. 2008a		
		Rhinocolobus turkanaensis	Jablonski et al. 2008b	xxx	xxx
		Cercopithecoides kimeui	Jablonski et al. 2008b		
		Cercopithecoides williamsi	Jablonski et al. 2008b	xx	xx
		Colobus freedmani	Jablonski and Leakey 2008		xx
	Okote Koobi Fora Fm. (1.53–1.38 Ma)	Papionini indet. (large)	Jablonski et al. 2008a		
		Papionini indet. (medium)	Jablonski et al. 2008a		xxx
		Theropithecus oswaldi oswaldi	Jablonski et al. 2008a	xx	xxx
		Lophocebus sp.	Jablonski et al. 2008a	xxx	xxx
		Cercopithecini indet.[4]	Jablonski et al. 2008a		

		Colobus freedmani	Jablonski and Leakey 2008		xxx
early Pleistocene (Gelasian) Cradle of Humankind South Africa	**Mb. 3** Makapansgat	*Theropithecus oswaldi darti*	Eisenhart 1974	xxx	xx
		Parapapio broomi	Eisenhart 1974	xxx	xxx
		Parapapio jonesi	Eisenhart 1974	xx	xx
		Parapapio whitei	Eisenhart 1974	xxx	xx
		Papionini indet. (small)	Eisenhart 1974		xx
		Cercopithecoides williamsi	Eisenhart 1974	xx	xx
		Cercopithecoides (large)	Eisenhart 1974		
	Mb. 4 Makapansgat	*Theropithecus oswaldi darti*	Eisenhart 1974	xx	xxx
		Parapapio broomi	Eisenhart 1974	xx	xxx
		Parapapio jonesi	Eisenhart 1974	xx	xx
		Parapapio whitei	Eisenhart 1974	xx	xx
		Cercopithecoides williamsi	Eisenhart 1974	xx	xx
	Mb. 4 Sterkfontein (2.61–2.07 Ma)[12]	*Parapapio broomi*	Eisenhart 1974	xxx	xxx
		Parapapio jonesi	Eisenhart 1974	xxx	xxx
		Parapapio whitei	Eisenhart 1974	xx	xxx
		?*Papio izodi*	Gilbert et al. 2018		
		Papio sp.	Gilbert et al. 2018		
		Cercopithecoides williamsi	Freedman and Stenhouse 1972	xx	xx
early Pleistocene (Calabrian) Cradle of Humankind South Africa	**Mb. 1** Swartkrans (~2.0–1.8 Ma)[13]	*Dinopithecus ingens*	Freedman and Brain 1977		
		Gorgopithecus major	Freedman and Brain 1977	xx	xx
		Theropithecus oswaldi oswaldi	Freedman and Brain 1977	x	x
		Papio robinsoni	Gilbert et al. 2018	xx	xx
		Papionini indet. (small)	Freedman and Brain 1977		xx
	Kromdraai B[14]	*Cercopithecoides* (large)	Freedman 1976	xxx	xxx
	Kromdraai A	*Gorgopithecus major*	Freedman and Brain 1972	xxx	xxx
		Papio hamadryas angusticeps	Gilbert et al. 2018		xx
		Papionini indet. (small)	Freedman and Brain 1972		

Fossil cercopithecid taxa included in analyses at the member and regional level, with notes on sample completeness. All specimens were measured from the following museums: National Museum of Ethiopia (Hadar Fm. and Omo Valley, Ethiopia); National Museums of Kenya (East Turkana, Kenya); Evolutionary Studies Institute at the University of Witwatersrand (Makapansgat and some Sterkfontein, South Africa), and Ditsong National Museum of Natural History (some Sterkfontein, Swartkrans, and Kromdraai, South Africa). A full specimen list is available from the author on request.

1. "xxx" = complete at Member level, "xx" = complete within basin, "x" = complete by fossil species.
2. Campisano and Feibel 2008.
3. McDougall et al. 2012.
4. The Unso Fm. and Shungura Mbs. A, B, D, and F were not analyzed separately, but specimens were included in the regional Omo samples.
5. Where necessary, fossil Cercopithecini were supplemented with resampled values from other fossils and extant guenons.
6. Where necessary, this indeterminate colobine was supplemented with resampled values from other eastern African fossil colobines.
7. The Lokochot Mb. was not analyzed separately due to small samples, but specimens were included in the Pliocene Turkana sample.
8. Includes "*Parapapio* sp. B" and "*Parapapio* sp. C" from Jablonski et al. (2008a).
9. "*Parapapio* cf. *ado*" in Jablonski et al. (2008a).
10. Where necessary, *Nanopithecus* was supplemented with resampled values from extant *Miopithecus*, and other fossil and extant guenons.
11. Includes "*Parapapio* sp. A" and "*Parapapio* sp. B" from Jablonski et al. (2008a).
12. Pickering and Herries 2020.
13. Pickering et al. 2019.
14. Kromdraai B was not analyzed separately, but specimens were included in the Calabrian Cradle of Humankind sample.

TABLE S2. MODERN TAXOCENE COMPOSITION.

		Sample[1]	
Taxocene	Taxon (museums)	Max	Mand
Countries (& included habitats)			
Angola (edaphic grasslands, semi-desert, miombo woodland, other woodland, *mosaics*)	*Cercopithecus ascanius* (CMNH, NMNH)	x	xx
	Cercopithecus mitis (AMNH, CMNH, NMNH)	xx	xx
	Chlorocebus cynosuros	x	x
	Colobus angolensis (CMNH, NMNH)	x	x
	Papio cynocephalus (NMNH)	x	x
	Papio ursinus (NMNH)	xx	xx
Cameroon (forest mosaics, tropical rainforest, other woodland)	*Allochrocebus preussi*	x	x
	Cercocebus agilis (AMNH, CMNH)	xx	xx
	Cercocebus torquatus (AMNH, CMNH, NMNH)	xx	xx
	Cercopithecus cephus (CMNH, NMNH)	xx	xx
	Cercopithecus erythrotis	x	x
	Cercopithecus mona (ANSP, NMNH)	x	xx
	Cercopithecus neglectus (CMNH, NMNH)	xx	xx
	Cercopithecus nictitans (AMNH, CMNH, NMNH)	xx	xx
	Chlorocebus tantalus (AMNH, CMNH)	xx	xx
	Colobus guereza (AMNH, CMNH, NMNH)	xx	xx
	Colobus satanas (NMNH)	x	x
	Colobus vellerosus (NMNH)	x	x
	Erythrocebus patas (AMNH, ANSP, NMNH)	xx	xx
	Lophocebus albigena (AMNH, CMNH, NMNH)	xx	xx
	Mandrillus leucophaeus	x	x
	Mandrillus sphinx (AMNH, CMNH)	xx	xx
	Miopithecus ogouensis (CMNH, NMNH)	xx	xx
	Papio anubis (AMNH, NMNH)	xx	xx
	Piliocolobus badius (NMNH)	x	x
	Piliocolobus preussi	x	x
Central African Republic (tropical rainforest, other woodland)	*Cercocebus agilis*	xx	xx
	Cercocebus galeritus	x	x
	Cercopithecus ascanius	x	xx
	Cercopithecus cephus	xx	xx
	Cercopithecus mona	x	xx
	Cercopithecus neglectus	xx	xx
	Cercopithecus nictitans	xx	xx
	Chlorocebus tantalus	xx	xx
	Colobus guereza	xx	xx
	Erythrocebus patas	xx	xx
	Lophocebus albigena	xx	xx
	Papio anubis	xx	xx
	Piliocolobus oustaleti (CMNH, NMNH)	x	x

Republic of Congo (forest mosaics, tropical rainforest)	*Allenopithecus nigroviridis* (AMNH, CMNH, NMNH)		xx
	Cercocebus agilis	xx	xx
	Cercocebus torquatus	xx	xx
	Cercopithecus ascanius	x	xx
	Cercopithecus cephus	xx	xx
	Cercopithecus mona	x	xx
	Cercopithecus neglectus	xx	xx
	Cercopithecus nictitans	xx	xx
	Chlorocebus cynosuros	x	x
	Colobus guereza	xx	xx
	Colobus satanas	x	x
	Lophocebus albigena	xx	xx
	Mandrillus sphinx	xx	xx
	Miopithecus ogouensis	xx	xx
	Piliocolobus bouvieri	x	x
	Piliocolobus oustaleti	x	x
Ivory Coast (tropical rainforest, other woodland)	*Cercocebus atys* (NMNH)	x	x
	Cercocebus lunulatus	x	x
	Cercopithecus diana (NMNH)	x	x
	Cercopithecus lowei (NMNH)	x	x
	Cercopithecus nictitans	xx	xx
	Cercopithecus petaurista (NMNH)	x	x
	Chlorocebus sabaeus (NMNH)	x	x
	Colobus polykomos	x	x
	Colobus vellerosus	x	x
	Erythrocebus patas	xx	xx
	Papio anubis	xx	xx
	Piliocolobus badius	x	x
	Procolobus verus (NMNH)		
Ethiopia (acacia woodland, afro-alpine, semi-desert, other woodland)	*Cercopithecus mitis*	xx	xx
	Cercopithecus neglectus	xx	xx
	Chlorocebus aethiops (NMNH)	x	x
	Chlorocebus djamdjamensis	x	x
	Colobus guereza	xx	xx
	Erythrocebus patas	xx	xx
	Papio anubis	xx	xx
	Papio hamadryas	x	x
	Theropithecus gelada (ANSP, NME)	xx	xx
Gabon (forest mosaics, tropical rainforest)	*Allochrocebus solatus*	x	x
	Cercocebus torquatus	xx	xx
	Cercopithecus cephus	xx	xx
	Cercopithecus mona	x	xx
	Cercopithecus nictitans	xx	xx
	Cercopithecus pogonias (CMNH, NMNH)	xx	xx

	Colobus satanas	x	x
	Lophocebus albigena	xx	xx
	Mandrillus sphinx	xx	xx
	Miopithecus ogouensis	xx	xx
Kenya (acacia woodland, afro-alpine, forest mosaics, montane grassland, tropical rainforest)	*Cercopithecus ascanius*	x	xx
	Cercopithecus mitis	xx	xx
	Cercopithecus neglectus	xx	xx
	Chlorocebus aethiops	x	x
	Chlorocebus pygerythrus (ANSP, NMNH)	xx	xx
	Chlorocebus tantalus	xx	xx
	Colobus angolensis	x	x
	Colobus guereza	xx	xx
	Colobus polykomos (ANSP, NMNH)	x	x
	Erythrocebus patas	xx	xx
	Papio anubis	xx	xx
	Papio cynocephalus	x	x
Malawi (swamp, miombo woodland, montane grassland, mopane woodland, other woodland)	*Cercopithecus mitis*	xx	xx
	Chlorocebus pygerythrus	xx	xx
	Papio cynocephalus	x	x
	Piliocolobus tephrosceles (CMNH, NMNH)	xx	xx
Niger (acacia woodland, semi-desert, other woodland)	*Chlorocebus tantalus*	xx	xx
	Erythrocebus patas	xx	xx
	Papio anubis	xx	xx
Senegal (forest mosaics, other woodland)	*Cercopithecus campbelli* (NMNH)	x	x
	Chlorocebus sabaeus	x	x
	Colobus polykomos	x	x
	Erythrocebus patas	xx	xx
	Papio papio (NMNH)	x	x
	Piliocolobus badius	x	x
	Piliocolobus temminckii (NMNH)	x	xx
South Africa (montane grassland, semi-desert, other woodland)	*Cercopithecus mitis*	xx	xx
	Chlorocebus pygerythrus	xx	xx
	Papio ursinus	xx	xx
South Sudan (other woodland)	*Cercopithecus mitis*	xx	xx
	Chlorocebus tantalus	xx	xx
	Colobus guereza	xx	xx
	Erythrocebus patas	xx	xx
	Papio anubis	xx	xx
Uganda (tropical rainforest, other woodland)	*Allochrocebus lhoesti* (CMNH, NMNH)	xx	xx
	Cercopithecus ascanius	x	xx
	Cercopithecus denti	x	x
	Cercopithecus mitis	xx	xx
	Cercopithecus neglectus	xx	xx

	Chlorocebus pygerythrus	xx	xx
	Chlorocebus tantalus	xx	xx
	Colobus guereza	xx	xx
	Erythrocebus patas	xx	xx
	Lophocebus albigena	xx	xx
	Papio anubis	xx	xx
	Piliocolobus badius	x	x
	Piliocolobus tephrosceles	xx	xx
Zambia (edaphic grassland, swamp, miombo woodland, *dry evergreen forest*)	*Cercopithecus mitis*	xx	xx
	Chlorocebus cynosuros	x	x
	Colobus angolensis	x	x
	Papio cynocephalus	x	x
	Papio ursinus	xx	xx
<u>Habitats</u>			
Acacia Woodland	*Allochrocebus lhoesti*	xx	xx
	Cercopithecus ascanius	x	xx
	Cercopithecus denti	x	x
	Cercopithecus mitis	xx	xx
	Cercopithecus neglectus	xx	xx
	Chlorocebus aethiops	x	x
	Chlorocebus cynosuros	x	x
	Chlorocebus pygerythrus	xx	xx
	Chlorocebus sabaeus	x	x
	Chlorocebus tantalus	xx	xx
	Colobus angolensis	x	x
	Colobus guereza	xx	xx
	Colobus polykomos	x	x
	Erythrocebus patas	xx	xx
	Lophocebus albigena	xx	xx
	Papio anubis	xx	xx
	Papio cynocephalus	x	x
	Papio hamadryas	x	x
	Papio papio	x	x
	Papio ursinus	xx	xx
	Piliocolobus badius	x	x
	Piliocolobus pennantii	x	x
	Piliocolobus tephrosceles	xx	xx
Afro-Alpine	*Allochrocebus lhoesti*	xx	xx
	Cercopithecus ascanius	x	xx
	Cercopithecus hamlyni	x	x
	Cercopithecus mitis	xx	xx
	Cercopithecus mona	x	xx
	Cercopithecus neglectus	xx	xx

	Cercopithecus nictitans	xx	xx
	Chlorocebus djamdjamensis	x	x
	Chlorocebus pygerythrus	xx	xx
	Chlorocebus tantalus	xx	xx
	Colobus guereza	xx	xx
	Lophocebus albigena	xx	xx
	Papio anubis	xx	xx
	Papio hamadryas	x	x
	Piliocolobus tephrosceles	xx	xx
	Theropithecus gelada	xx	xx
Desert	*Chlorocebus pygerythrus*	xx	xx
	Papio hamadryas	x	x
	Papio ursinus	xx	xx
Edaphic Grassland	*Chlorocebus cynosuros*	x	x
	Chlorocebus tantalus	xx	xx
	Colobus angolensis	x	x
	Erythrocebus patas	xx	xx
	Papio anubis	xx	xx
	Papio cynocephalus	x	x
	Papio ursinus	xx	xx
Forest Mosaics	*Cercocebus agilis*	xx	xx
	Cercocebus atys	x	x
	Cercocebus torquatus	xx	xx
	Cercopithecus ascanius	x	xx
	Cercopithecus campbelli	x	x
	Cercopithecus cephus	xx	xx
	Cercopithecus mitis	xx	xx
	Cercopithecus mona	x	xx
	Cercopithecus neglectus	xx	xx
	Cercopithecus nictitans	xx	xx
	Cercopithecus petaurista	x	x
	Cercopithecus pogonias	xx	xx
	Chlorocebus cynosuros	x	x
	Chlorocebus pygerythrus	xx	xx
	Chlorocebus sabaeus	x	x
	Chlorocebus tantalus	xx	xx
	Colobus angolensis	x	x
	Colobus guereza	xx	xx
	Colobus polykomos	x	x
	Colobus satanas	x	x
	Erythrocebus patas	xx	xx
	Lophocebus albigena	xx	xx
	Mandrillus sphinx	xx	xx
	Miopithecus ogouensis	xx	xx

	Papio anubis	xx	xx
	Papio cynocephalus	x	x
	Papio papio	x	x
	Papio ursinus	xx	xx
	Piliocolobus bouvieri	x	x
	Piliocolobus oustaleti	x	x
	Piliocolobus temminckii	x	xx
Miombo Woodland	*Cercocebus galeritus*	x	x
	Cercopithecus ascanius	x	xx
	Cercopithecus mitis	xx	xx
	Chlorocebus cynosuros	x	x
	Chlorocebus pygerythrus	xx	xx
	Colobus angolensis	x	x
	Papio anubis	xx	xx
	Papio cynocephalus	x	x
	Papio ursinus	xx	xx
	Piliocolobus gordonorum	x	x
	Piliocolobus tephrosceles	xx	xx
Montane (secondary) grassland	*Allochrocebus lhoesti*	xx	xx
	Cercocebus torquatus	xx	xx
	Cercopithecus ascanius	x	xx
	Cercopithecus campbelli	x	x
	Cercopithecus denti	x	x
	Cercopithecus diana	x	x
	Cercopithecus hamlyni	x	x
	Cercopithecus mitis	xx	xx
	Cercopithecus neglectus	xx	xx
	Cercopithecus nictitans	xx	xx
	Cercopithecus petaurista	x	x
	Chlorocebus pygerythrus	xx	xx
	Chlorocebus sabaeus	x	x
	Chlorocebus tantalus	xx	xx
	Colobus angolensis	x	x
	Colobus guereza	xx	xx
	Colobus polykomos	x	x
	Erythrocebus patas	xx	xx
	Lophocebus albigena	xx	xx
	Papio anubis	xx	xx
	Papio cynocephalus	x	x
	Papio ursinus	xx	xx
	Piliocolobus badius	x	x
	Piliocolobus tephrosceles	xx	xx
	Procolobus verus		
Mopane Woodland	*Cercopithecus mitis*	xx	xx

	Chlorocebus aethiops	x	x
	Chlorocebus pygerythrus	xx	xx
	Papio anubis	xx	xx
	Papio cynocephalus	x	x
	Papio ursinus	xx	xx
Sedge and Reed Swamp	*Cercopithecus mitis*	xx	xx
	Chlorocebus cynosuros	x	x
	Chlorocebus pygerythrus	xx	xx
	Papio cynocephalus	x	x
	Papio ursinus	xx	xx
Shrubland and Grassy Semi-desert	*Cercopithecus mitis*	xx	xx
	Chlorocebus aethiops	x	x
	Chlorocebus cynosuros	x	x
	Erythrocebus patas	xx	xx
	Papio anubis	xx	xx
	Papio cynocephalus	x	x
	Papio hamadryas	x	x
	Papio ursinus	xx	xx
Tropical Lowland Rainforest	*Allenopithecus nigroviridis*		xx
	Allochrocebus preussi	x	x
	Allochrocebus solatus	x	x
	Cercocebus agilis	xx	xx
	Cercocebus atys	x	x
	Cercocebus chrysogaster	x	x
	Cercocebus lunulatus	x	x
	Cercocebus torquatus	xx	xx
	Cercopithecus ascanius	x	xx
	Cercopithecus campbelli	x	x
	Cercopithecus cephus	xx	xx
	Cercopithecus diana	x	x
	Cercopithecus dryas	x	x
	Cercopithecus erythrotis	x	x
	Cercopithecus lowei	x	x
	Cercopithecus mitis	xx	xx
	Cercopithecus mona	x	xx
	Cercopithecus neglectus	xx	xx
	Cercopithecus nictitans	xx	xx
	Cercopithecus petaurista	x	x
	Cercopithecus pogonias	xx	xx
	Cercopithecus roloway	x	x
	Chlorocebus sabaeus	x	x
	Chlorocebus tantalus	xx	xx
	Colobus angolensis	x	x
	Colobus guereza	xx	xx

	Colobus polykomos	x	x
	Colobus satanas	x	x
	Colobus vellerosus	x	x
	Lophocebus albigena	xx	xx
	Lophocebus aterrimus	x	x
	Mandrillus leucophaeus	x	x
	Mandrillus sphinx	xx	xx
	Miopithecus ogouensis	xx	xx
	Papio anubis	xx	xx
	Piliocolobus badius	x	x
	Piliocolobus oustaleti	x	x
	Piliocolobus preussi	x	x
	Piliocolobus tholloni	x	x
	Piliocolobus waldroni	x	x
	Procolobus verus		
Woodland (other)	*Cercocebus galeritus*	x	x
	Cercocebus lunulatus	x	x
	Cercopithecus campbelli	x	x
	Cercopithecus diana	x	x
	Cercopithecus lowei	x	x
	Cercopithecus mitis	xx	xx
	Cercopithecus mona	x	xx
	Cercopithecus neglectus	xx	xx
	Cercopithecus nictitans	xx	xx
	Cercopithecus petaurista	x	x
	Chlorocebus aethiops	x	x
	Chlorocebus cynosuros	x	x
	Chlorocebus pygerythrus	xx	xx
	Chlorocebus sabaeus	x	x
	Chlorocebus tantalus	xx	xx
	Colobus guereza	xx	xx
	Colobus polykomos	x	x
	Colobus vellerosus	x	x
	Erythrocebus patas	xx	xx
	Papio anubis	xx	xx
	Papio cynocephalus	x	x
	Papio papio	x	x
	Papio ursinus	xx	xx
	Piliocolobus badius	x	x
	Piliocolobus temminckii	x	xx
	Piliocolobus tephrosceles	xx	xx
	Procolobus verus		

Sites			
Aberdare National Park (montane grassland)	*Cercopithecus mitis*	xx	xx
	Chlorocebus pygerythrus	xx	xx
	Colobus guereza	xx	xx
	Papio anubis	xx	xx
Abijatta-Shalla Lakes National Park (acacia woodland)	*Chlorocebus aethiops*	x	x
	Colobus guereza	xx	xx
	Papio anubis	xx	xx
Akagera National Park (acacia woodland)	*Cercopithecus ascanius*	x	xx
	Cercopithecus mitis	xx	xx
	Chlorocebus pygerythrus	xx	xx
	Colobus angolensis	x	x
	Colobus guereza	xx	xx
	Papio anubis	xx	xx
	Piliocolobus badius	x	x
Badiar National Park (forest mosaics)	*Chlorocebus sabaeus*	x	x
	Colobus polykomos	x	x
	Erythrocebus patas	xx	xx
	Papio papio	x	x
	Piliocolobus temminckii	x	xx
Campo Maan National Park (tropical lowland rainforest)	*Cercocebus torquatus*	xx	xx
	Cercopithecus cephus	xx	xx
	Cercopithecus mona	x	xx
	Cercopithecus neglectus	xx	xx
	Cercopithecus nictitans	xx	xx
	Colobus satanas	x	x
	Lophocebus albigena	xx	xx
	Mandrillus sphinx	xx	xx
	Miopithecus ogouensis	xx	xx
Deux Bales National Park (other woodland)	*Chlorocebus sabaeus*	x	x
	Erythrocebus patas	xx	xx
	Papio anubis	xx	xx
Equatoria region (Lotti Forest[2]) (other woodland)	*Cercopithecus mitis*	xx	xx
	Chlorocebus tantalus	xx	xx
	Colobus guereza	xx	xx
	Erythrocebus patas	xx	xx
	Papio anubis	xx	xx
Fernan Vaz Lagoon[2] (forest mosaics)	*Cercocebus torquatus*	xx	xx
	Cercopithecus cephus	xx	xx
	Cercopithecus nictitans	xx	xx
	Cercopithecus pogonias	xx	xx
	Colobus satanas	x	x
	Lophocebus albigena	xx	xx
	Miopithecus ogouensis	xx	xx

Gombe National Park (miombo woodland)	*Cercopithecus ascanius*	x	xx
	Cercopithecus mitis	xx	xx
	Chlorocebus pygerythrus	xx	xx
	Colobus angolensis	x	x
	Papio anubis	xx	xx
	Piliocolobus tephrosceles	xx	xx
Kakamega National Reserve (tropical lowland rainforest)	*Cercopithecus ascanius*	x	xx
	Cercopithecus mitis	xx	xx
	Cercopithecus neglectus	xx	xx
	Chlorocebus tantalus	xx	xx
	Colobus guereza	xx	xx
	Papio anubis	xx	xx
Kibira National Park (montane grassland)	*Allochrocebus lhoesti*	xx	xx
	Cercopithecus ascanius	x	xx
	Cercopithecus mitis	xx	xx
	Chlorocebus pygerythrus	xx	xx
	Colobus guereza	xx	xx
	Lophocebus albigena	xx	xx
	Papio anubis	xx	xx
	Piliocolobus badius	x	x
Kidepo Valley National Park (other woodland)	*Chlorocebus pygerythrus*	xx	xx
	Erythrocebus patas	xx	xx
	Papio anubis	xx	xx
Knysna National Lake Area	*Cercopithecus mitis*	xx	xx
	Chlorocebus pygerythrus	xx	xx
	Papio ursinus	xx	xx
Lac Fitri (edaphic grassland)	*Chlorocebus tantalus*	xx	xx
	Erythrocebus patas	xx	xx
	Papio anubis	xx	xx
Lake Manyara National Park	*Cercopithecus mitis*	xx	xx
	Chlorocebus pygerythrus	xx	xx
	Lophocebus albigena	xx	xx
	Papio anubis	xx	xx
Lengwe National Park (mopane woodland)	*Cercopithecus mitis*	xx	xx
	Chlorocebus pygerythrus	xx	xx
	Papio cynocephalus	x	x
Liwonde National Park (other woodland)	*Cercopithecus mitis*	xx	xx
	Chlorocebus pygerythrus	xx	xx
	Papio cynocephalus	x	x
	Piliocolobus tephrosceles	xx	xx
Mahale Mountains National Park (montane grassland)	*Cercopithecus ascanius*	x	xx
	Cercopithecus mitis	xx	xx
	Chlorocebus pygerythrus	xx	xx
	Colobus angolensis	x	x

	Papio anubis	xx	xx
	Papio cynocephalus	x	x
	Piliocolobus tephrosceles	xx	xx
Mana Pools National Park (mopane woodland)	*Cercopithecus mitis*	xx	xx
	Chlorocebus pygerythrus	xx	xx
	Papio ursinus	xx	xx
Massif du Ziama Classified Forest (tropical rainforest)	*Cercocebus atys*	x	x
	Cercopithecus campbelli	x	x
	Cercopithecus diana	x	x
	Cercopithecus nictitans	xx	xx
	Cercopithecus petaurista	x	x
	Chlorocebus sabaeus	x	x
	Colobus polykomos	x	x
	Papio anubis	xx	xx
	Piliocolobus badius	x	x
	Procolobus verus		
Mbam et Djerem National Park (forest mosaics)	*Cercopithecus mona*	x	xx
	Cercopithecus neglectus	xx	xx
	Cercopithecus nictitans	xx	xx
	Chlorocebus tantalus	xx	xx
	Colobus guereza	xx	xx
	Lophocebus albigena	xx	xx
	Miopithecus ogouensis	xx	xx
	Papio anubis	xx	xx
Mont Fouari Faunal Reserve (tropical rainforest)	*Cercopithecus cephus*	xx	xx
	Cercopithecus mona	x	xx
	Cercopithecus nictitans	xx	xx
	Miopithecus ogouensis	xx	xx
Mount Assirik (other woodland)	*Chlorocebus sabaeus*	x	x
	Colobus polykomos	x	x
	Erythrocebus patas	xx	xx
	Papio papio	x	x
	Piliocolobus badius	x	x
Mount Nimba Strict Nature Reserve (montane grassland)	*Cercocebus torquatus*	xx	xx
	Cercopithecus campbelli	x	x
	Cercopithecus diana	x	x
	Cercopithecus nictitans	xx	xx
	Cercopithecus petaurista	x	x
	Chlorocebus sabaeus	x	x
	Colobus polykomos	x	x
	Piliocolobus badius	x	x
	Procolobus verus		
Murchison Falls National Park	*Cercopithecus ascanius*	x	xx
	Cercopithecus mitis	xx	xx

(forest mosaics)	*Chlorocebus tantalus*	xx	xx
	Colobus guereza	xx	xx
	Erythrocebus patas	xx	xx
	Papio anubis	xx	xx
Nairobi National Park (acacia woodland)	*Colobus polykomos*	x	x
	Cercopithecus mitis	xx	xx
	Chlorocebus pygerythrus	xx	xx
	Papio anubis	xx	xx
Ngorongoro Conservation Area (acacia woodland)	*Chlorocebus pygerythrus*	xx	xx
	Colobus guereza	xx	xx
	Papio anubis	xx	xx
Omo National Park (other woodland)	*Cercopithecus mitis*	xx	xx
	Cercopithecus neglectus	xx	xx
	Chlorocebus aethiops	x	x
	Colobus guereza	xx	xx
	Erythrocebus patas	xx	xx
	Papio anubis	xx	xx
Parc W Niger National Park (other woodland)	*Chlorocebus tantalus*	xx	xx
	Erythrocebus patas	xx	xx
	Papio anubis	xx	xx
Rio Muni[2] (tropical rainforest)	*Cercocebus torquatus*	xx	xx
	Cercopithecus cephus	xx	xx
	Cercopithecus neglectus	xx	xx
	Cercopithecus nictitans	xx	xx
	Cercopithecus pogonias	xx	xx
	Colobus satanas	x	x
	Lophocebus albigena	xx	xx
	Mandrillus sphinx	xx	xx
	Miopithecus ogouensis	xx	xx
Shimba Hills Nature Reserve (forest mosaics)	*Cercopithecus mitis*	xx	xx
	Chlorocebus pygerythrus	xx	xx
	Colobus angolensis	x	x
	Papio cynocephalus	x	x
Tsoulou Faunal Reserve (forest mosaics)	*Cercopithecus mona*	x	xx
	Cercopithecus nictitans	xx	xx
	Miopithecus ogouensis	xx	xx
Zemongo Faunal Reserve (other woodland)	*Chlorocebus tantalus*	xx	xx
	Colobus guereza	xx	xx
	Erythrocebus patas	xx	xx
	Papio anubis	xx	xx
Zinave National Park (mopane woodland)	*Cercopithecus mitis*	xx	xx
	Chlorocebus aethiops	x	x
	Papio anubis	xx	xx

Modern cercopithecid taxa included in analyses at the country, habitat, and site level, with notes on sample completeness. See Figure S1 for a map of modern countries and localities. Habitats were based on mapping units of White's (1983) vegetation units, and are described in more detail in Table 1. Habitats for modern countries and sites are listed in parentheses; some countries included habitats (italics) not analyzed separately. The first occurrence for each taxon lists the collections where specimens were measured for this study: American Museum of Natural History (AMNH), Academy of Natural Sciences of Philadelphia at Drexel University (ANSP), Carnegie Museum of Natural History (CMNH), National Museum of Ethiopia (NME), and Smithsonian National Museum of Natural History (NMNH). A full specimen list is available from the author on request.

1. "xx" = complete at species level, "x" = complete at genus level.
2. Museum-based taxocene. All other species lists taken from Rowan et al. (2020).

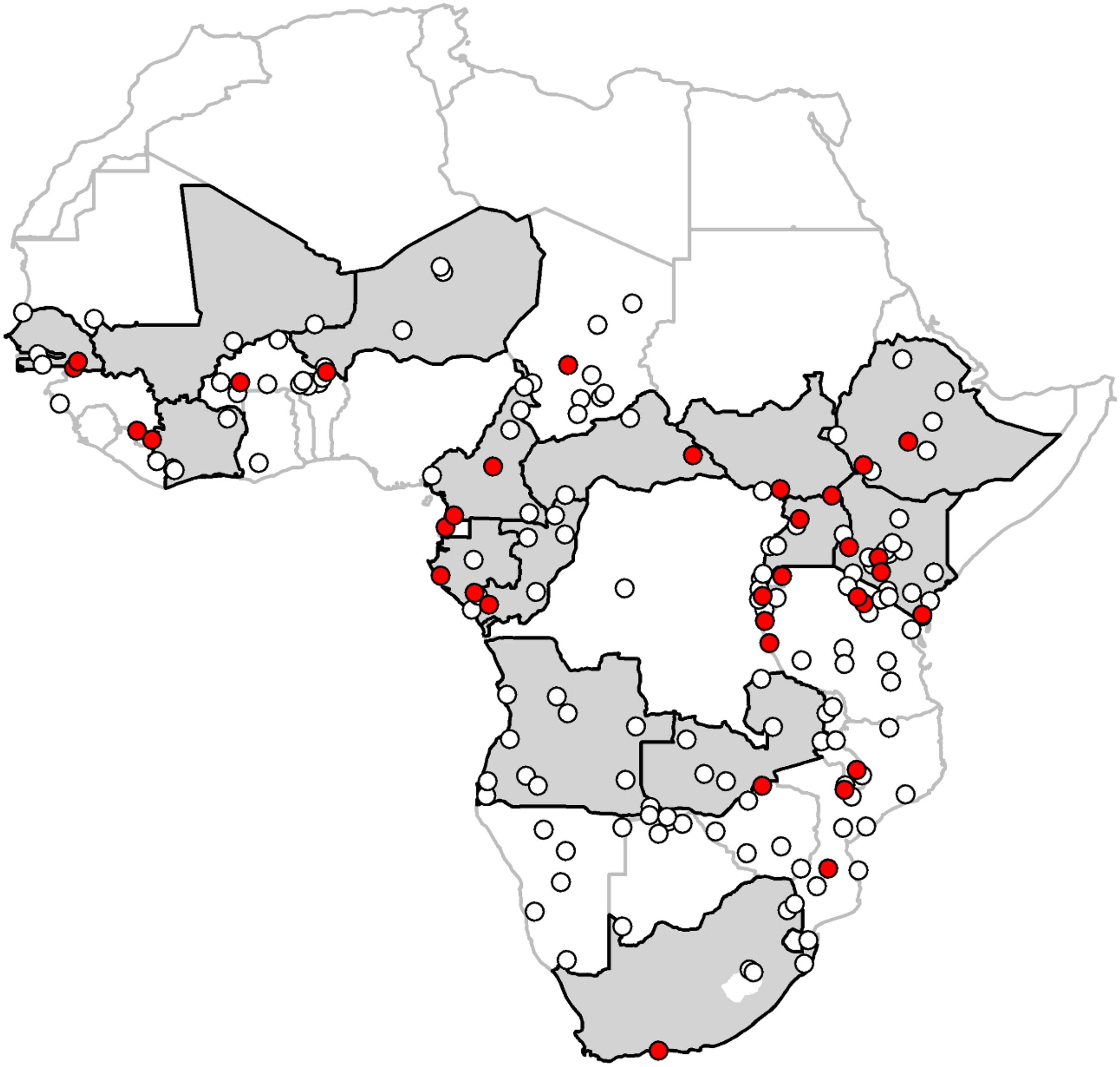

Figure S1. Modern localities (circles) used to generate country- (grey) and habitat-level (not pictured) taxocenes, and from which representative sites (red) were selected.

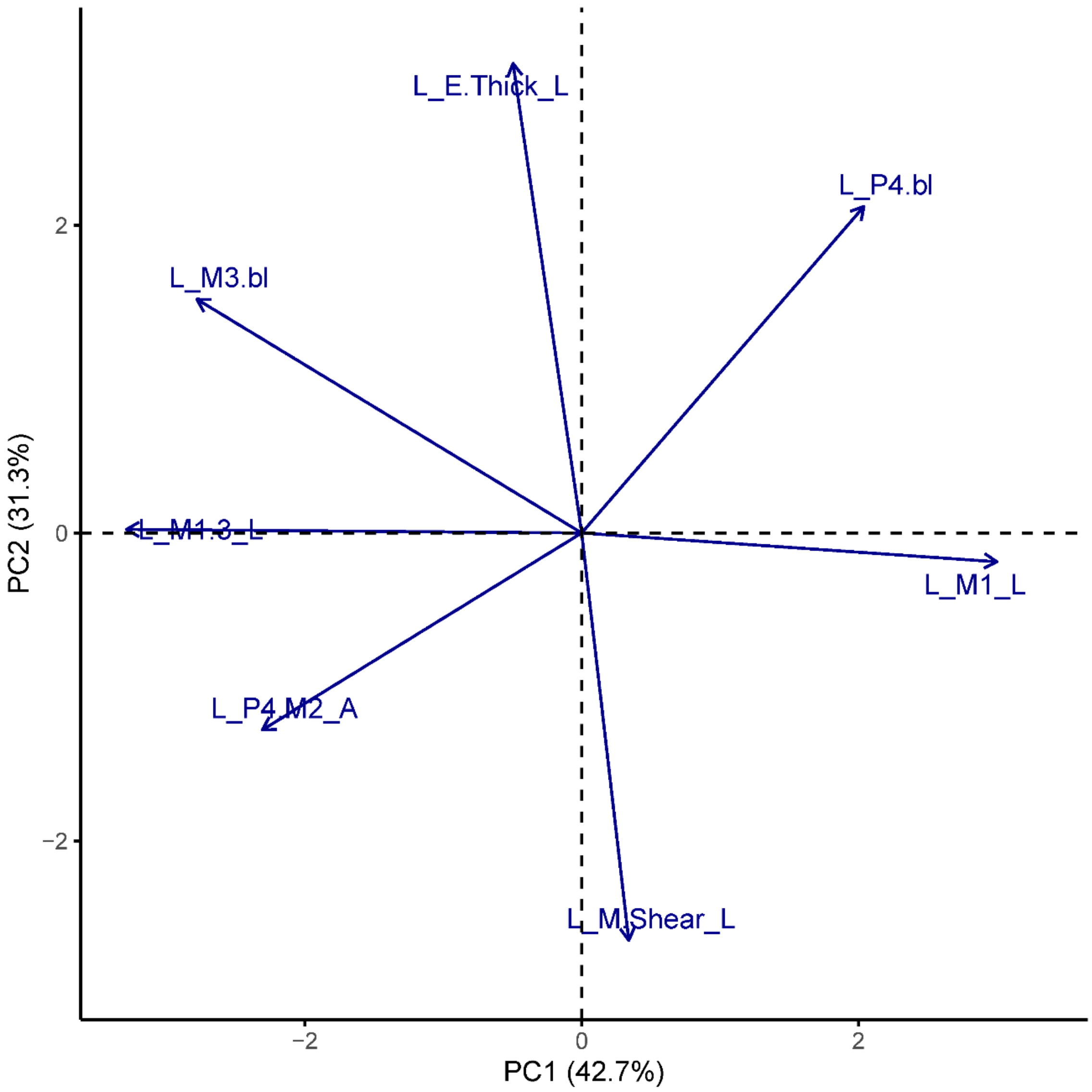

Figure S2. Biplot of mandibular variables in principal component space, based on species averaged dental ratios.

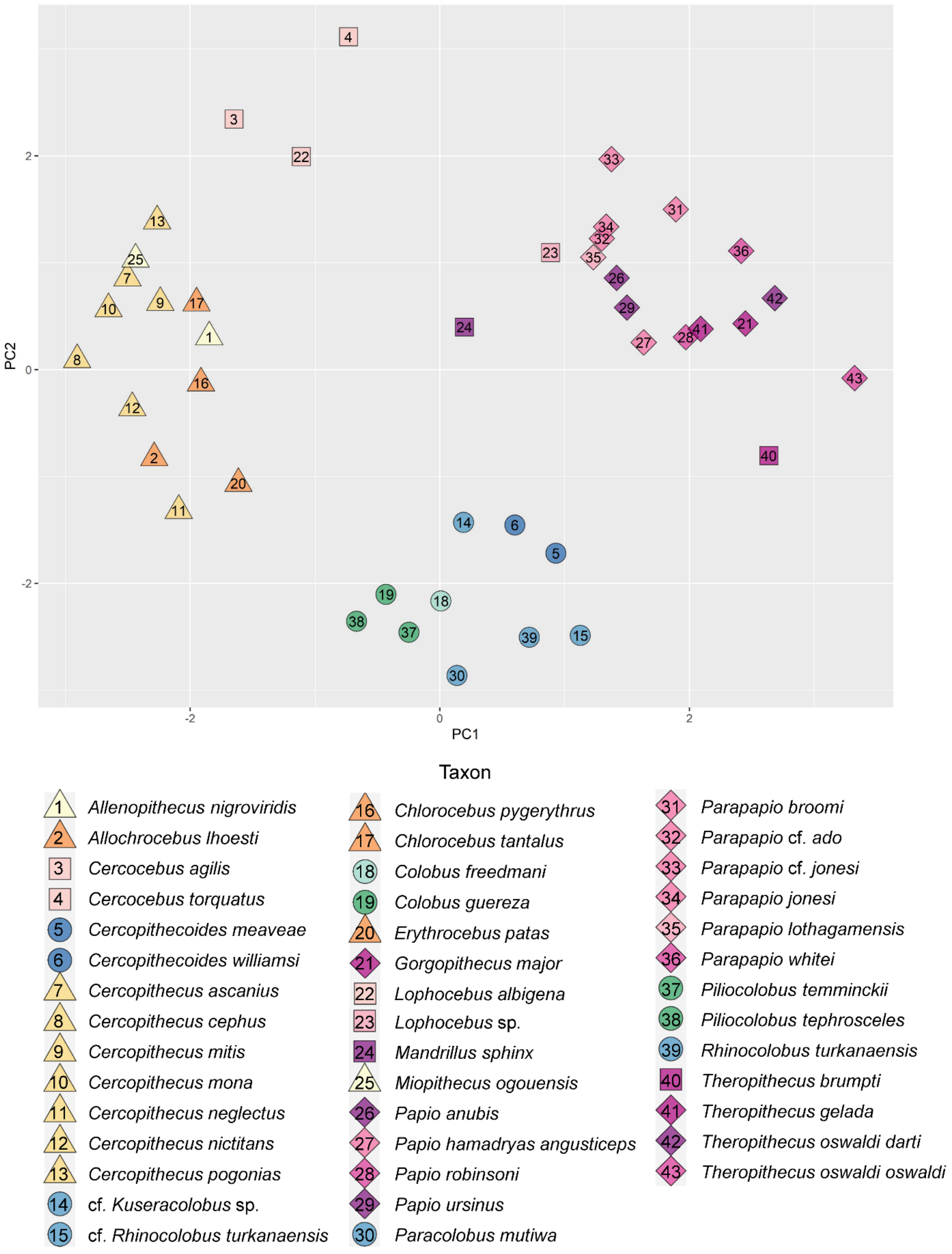

Figure S3. Species positioning within the principal component niche space based on averaged maxillary dental variables.

TABLE S3. COMPLETE RESAMPLED MAXILLARY AND MANDIBULAR NICHE METRICS FROM ALL MODERN TAXOCENES.

	Maxillary				Mandibular			
Taxocene (# of Species)	Volume	Disp.	PC1	PC2	Volume	Disp.	PC1	PC2
Countries								
Angola (6)	12.20	2.25	-1.24	-0.16	10.61	2.02	-0.80	0.26
Cameroon (20)	23.41	1.98	-1.66	-0.39	23.04	1.97	-1.23	-0.11
Central African Republic (13)	19.64	1.85	-1.98	0.00	18.65	1.87	-1.42	0.35
Congo (16)	17.55	1.79	-2.04	-0.24	16.90	1.85	-1.46	0.17
Ivory Coast (13)	21.51	2.03	-1.69	-0.63	21.57	2.00	-1.54	-0.55
Ethiopia (9)	17.63	2.24	-0.74	-0.33	14.45	2.05	-0.61	-0.05
Gabon (10)	17.02	1.82	-2.24	0.27	11.10	1.59	-1.78	0.50
Kenya (13)	16.25	1.81	-1.42	-0.43	13.10	1.69	-1.09	-0.19
Malawi (4)	8.38	1.97	-1.20	-0.35	9.93	2.08	-0.84	-0.28
Niger (3)	5.61	1.83	-0.63	-0.15	5.78	1.93	-0.72	0.04
Senegal (7)	15.09	1.93	-1.18	-1.14	13.78	2.00	-1.01	-1.01
South Africa (3)	6.45	2.52	-1.53	-0.24	6.75	2.14	-1.04	0.11
South Sudan (5)	12.50	1.95	-1.09	-0.75	11.85	1.90	-1.07	-0.36
Uganda (13)	18.83	1.78	-1.97	-0.54	16.41	1.78	-1.44	-0.30
Zambia (5)	11.38	2.40	-0.76	-0.24	9.87	2.03	-0.42	0.11
Habitats								
Acacia woodland (23)	21.60	1.98	-1.26	-0.46	19.52	1.97	-0.87	-0.27
Afro-alpine (16)	21.91	1.96	-1.62	-0.19	19.25	1.89	-1.22	0.08
Desert (3)	3.38	1.83	0.20	0.40	4.15	1.82	0.34	0.49
Edaphic grassland (7)	10.52	1.97	-0.43	-0.20	9.71	1.93	-0.30	0.01
Forest mosaics (31)	27.83	2.03	-1.68	-0.21	23.86	1.96	-1.22	0.08
Miombo woodland (11)	19.13	2.15	-1.13	-0.21	17.62	2.13	-0.66	-0.04
Montane grassland (25)	22.62	1.87	-1.78	-0.52	24.91	1.94	-1.40	-0.27
Mopane woodland (6)	8.01	2.04	-0.45	0.31	7.51	1.92	-0.28	0.52
Sedge and reed swamp (5)	6.94	2.12	-0.93	0.14	7.25	1.93	-0.67	0.43
Shrubland and grassy semi-desert (8)	10.82	1.98	-0.33	0.14	10.18	1.95	-0.28	0.38
Tropical lowland rainforest (41)	27.49	1.88	-2.02	-0.34	26.85	1.95	-1.52	-0.05
Woodland (27)	25.1	1.96	-1.52	-0.50	26.35	2.04	-1.28	-0.27
Sites								
Aberdare (4)	11.04	2.18	-1.26	-0.38	9.90	2.07	-0.82	-0.10
Abijatta Shalla (3)	7.83	2.22	-0.47	-0.50	7.29	2.06	-0.29	-0.35
Akagera (7)	15.12	2.00	-1.42	-0.89	13.03	1.94	-0.81	-0.53
Badiar (5)	10.51	1.83	-0.85	-1.14	9.64	1.90	-0.68	-0.86
Campo Maan (9)	13.80	1.73	-2.17	0.19	13.26	1.69	-1.61	0.59

Deux Bales (3)	5.89	1.95	-0.80	-0.28	4.95	1.97	-0.88	-0.19
Equatoria (5)	12.52	1.95	-1.10	-0.74	11.85	1.90	-1.07	-0.36
Fernan Vaz (7)	13.99	1.83	-2.48	0.48	8.59	1.57	-1.87	0.72
Gombe (6)	12.99	1.98	-1.78	-0.54	12.87	2.03	-1.02	-0.24
Kakamega (6)	13.95	1.94	-1.80	-0.23	11.32	1.79	-1.27	0.18
Kibira (8)	17.54	2.07	-1.77	-0.47	15.47	2.02	-1.12	-0.15
Kidepo Valley (3)	6.66	1.95	-0.79	-0.04	6.62	1.84	-0.88	0.00
Knysna (3)	6.35	2.50	-1.54	-0.24	6.83	2.14	-1.03	0.11
Lac Fitri (3)	5.77	1.84	-0.64	-0.13	5.81	1.93	-0.73	0.05
Lake Manyara (4)	9.63	2.12	-1.71	0.28	8.04	1.82	-0.85	0.93
Lengwe (3)	5.12	2.15	-1.29	0.05	4.88	1.86	-0.92	0.46
Liwonde (4)	8.37	1.95	-1.19	-0.35	10.03	2.09	-0.85	-0.27
Mahale Mountains (7)	13.99	2.18	-1.34	-0.45	13.14	2.11	-0.68	-0.14
Mana Pools (3)	5.59	2.31	-1.46	0.06	4.87	1.90	-0.86	0.43
Massif du Ziama (10)	19.99	2.03	-1.82	-0.64	20.00	2.07	-1.63	-0.56
Mbam et Djerem (8)	18.45	1.91	-1.86	0.00	16.24	1.83	-1.41	0.22
Mont Fouari (4)	3.19	1.09	-3.10	0.07	2.36	0.99	-2.55	0.43
Mount Assirik (5)	9.14	1.74	-0.79	-0.92	9.71	1.89	-0.62	-0.89
Mount Nimba Strict (9)	13.48	1.77	-2.13	-0.84	17.35	2.01	-1.85	-0.60
Murchison Falls (6)	15.30	2.06	-1.74	-0.53	11.88	1.80	-1.28	-0.09
Nairobi (4)	9.96	2.04	-1.26	-0.25	9.75	2.05	-0.89	-0.11
Ngorongoro (3)	10.70	2.55	-0.90	-0.54	9.78	2.27	-0.15	-0.23
Omo (6)	12.81	1.89	-1.43	-0.59	11.59	1.74	-1.19	-0.26
Parc W Niger (3)	5.77	1.84	-0.64	-0.13	5.69	1.92	-0.74	0.04
Rio Muni (9)	16.91	1.92	-2.50	0.34	13.69	1.87	-1.83	0.70
Shimba Hills (4)	9.76	2.08	-1.35	-0.32	7.96	1.86	-0.96	0.09
Tsoulou (3)	2.44	1.11	-3.02	0.04	1.81	1.04	-2.42	0.55
Zemongo (4)	8.64	1.87	-0.72	-0.79	8.86	1.90	-0.63	-0.53
Zinave (3)	5.56	2.00	-1.13	0.27	4.49	1.83	-0.89	0.60

TABLE S4. AVERAGE RESAMPLED MANDIBULAR NICHE METRICS FROM FOSSIL SITE MEMBERS AND *BASINS*.

	Number of Taxa	Volume	Dispersion	PC1 Centroid	PC2 Centroid
Sidi Hakoma	4	5.27	1.83	1.68	-0.38
Kada Hadar	3	6.54	2.35	1.34	0.41
Pliocene Hadar Formation	*4*	*6.93*	*2.06*	*1.49*	*-0.41*
Shungura Mb. C	6	16.15	2.15	0.89	-0.96
Pliocene Omo Valley	*7*	*16.10*	*1.98*	*1.06*	*-0.99*
Shungura Mb. E	5	4.78	1.81	1.62	-1.23
Shungura Mb. G	7	17.23	2.20	1.25	-1.04
Gelasian Omo Valley	*8*	*16.17*	*1.96*	*1.14*	*-1.02*
Tulu Bor	6	17.17	2.20	0.83	-0.37
Pliocene East Turkana	*6*	*15.44*	*1.96*	*1.19*	*-0.12*
Upper Burgi	6	6.95	1.74	1.40	-1.63
Gelasian East Turkana	*6*	*5.50*	*1.65*	*1.32*	*-1.43*
KBS	9	19.80	2.21	1.07	-0.76
Okote	6	17.08	2.23	1.17	-0.01
Calabrian East Turkana	*9*	*19.63*	*2.17*	*1.06*	*-0.77*
Makapansgat Mb. 3	7	9.35	1.72	1.64	0.53
Makapansgat Mb. 4	5	8.27	1.58	2.11	0.88
Sterkfontein Mb. 4	6	5.20	1.35	1.62	0.63
Gelasian South Africa	*9*	*8.95*	*1.45*	*1.62*	*0.40*
Swartkrans Mb. 1	5	4.12	1.18	2.22	-0.19
Kromdraai A	3	2.57	1.19	1.78	0.53
Calabrian South Africa	*7*	*7.34*	*1.30*	*1.96*	*-0.35*