



Contents lists available at ScienceDirect

Journal of Human Evolution

journal homepage: www.elsevier.com/locate/jhevol

A diminutive Pliocene guenon from Kanapoi, West Turkana, Kenya

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ARTICLE INFO

Article history:

Received 15 May 2018

Accepted 22 May 2019

Available online xxx

Keywords:

*Miopithecus**Nanopithecus**Cercopithecini*

Dwarfing

ABSTRACT

Although modern guenons are diverse and abundant in Africa, the fossil record of this group is surprisingly sparse. In 2012 the West Turkana Paleo Project team recovered two associated molar teeth of a small primate from the Pliocene site of Kanapoi, West Turkana, Kenya. The teeth are bilophodont and the third molar lacks a hypoconulid, which is diagnostic for *Cercopithecini*. The teeth are the same size as those of extant *Miopithecus*, which is thought to be a dwarfed guenon, as well as a partial mandible preserving two worn teeth, previously recovered from Koobi Fora, Kenya, which was also tentatively identified as a guenon possibly allied with *Miopithecus*. Tooth size and proportions, as well as analysis of relative cusp size and shearing crest development clearly separate the fossil from all known guenons. Based on the Kanapoi material, we erect a new genus and species, *Nanopithecus browni* gen. et sp. nov. The small size of the specimen suggests either that dwarfing occurred early in the lineage, or at least twice independently, depending on the relationship of the new species with extant *Miopithecus*. Further, the distinctive habitat and geographic separation from *Miopithecus* suggests that the origin of small body size is not uniquely linked to the current habitat of *Miopithecus*, and possibly that relatives of extant *Miopithecus* were much more widely distributed in the past. This in turn argues caution in using extant biogeography in models of the origins of at least some guenons.

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1. Introduction

The modern guenons (*Cercopithecini*) comprise a widespread radiation of African primates including up to six genera (*Erythrocebus*, *Allenopithecus*, *Chlorocebus*, *Allochocebus*, *Miopithecus* and *Cercopithecus*; Pozzi et al., 2014; Lo Bianco et al., 2017) with more than 30 species that inhabit diverse habitats throughout sub-Saharan Africa. Recent molecular studies place the origin of the guenons at approximately 10–12 Ma. Most studies recognize *Allenopithecus* as the sister taxon to the remaining guenons with the divergence at approximately at 8–10 Ma (supporting Strasser and Delson, 1987). *Miopithecus* is placed as the sister taxon to either the arboreal guenons (*Cercopithecus*), or both the arboreal and terrestrial (*Erythrocebus*, *Allochocebus*, and *Chlorocebus*) guenons, with a split at approximately 7–8 Ma (Tosi et al., 2004, 2005; Hart et al., 2012; Perelman et al., 2011; Springer et al., 2012; Pozzi et al., 2014). Though little is understood about the evolutionary history of

the radiation of modern guenons, the group is thought to be African in origin, and the modern distribution of most extant species is thought to reflect a series of vicariance events related to patterns of habitat fragmentation associated with climate change beginning in the late Miocene (Kingdon, 1971; Kamilar et al., 2009; Hart et al., 2012; Lo Bianco et al., 2017).

Though molecular studies have helped clarify the phylogenetic relationships among guenon genera and provide strong evidence of the antiquity of the group, the fossil record of guenons remains comparatively poor. Unfortunately, identification of fossil specimens to species is hampered by morphological near uniformity of cercopithecine molar teeth. Most guenon fossils are known from East African deposits dated to 0.6 Ma and younger and are attributed to *Chlorocebus* sp. indet. or *Erythrocebus patas* (see Jablonski and Frost, 2010). Specimens from Omo, dated to 2.9 Ma, have been attributed to *Cercopithecus* sp. (Eck and Howell, 1972). A single fragmentary mandible from Kanam (Kenya) and isolated teeth from Olduvai (Tanzania), and Lobo (Kenya; Szalay and Delson, 1979; Harrison and Harris, 1996; Jablonski and Frost, 2010), and a horizon of uncertain age at Taung have also been referred to this group

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(Szalay and Delson, 1979; Broadfield et al., 1994). The oldest known guenon fossil is an isolated tooth from the United Arab Emirates dated to 6.5–8.0 Ma, referred only to Cercopithecini indet. (Gilbert et al., 2014). This specimen is reported as similar in tooth size to a modern vervet or blue monkey, which falls comfortably within the size range of most living guenons (approximately 3–9 kg average adult body mass) with the exception of the largest, *Erythrocebus* (average male mass 12.4 kg) and smallest, *Miopithecus* (average female mass 1.1 kg; Smith and Jungers, 1997; Delson et al., 2000).

One fossil specimen from Koobi Fora, Kenya, has been suggested to have affinities with extant *Miopithecus* (Jablonski et al., 2008). KNM-ER 396, a mandibular fragment with worn M_2 – M_3 , has been noted as a possible relative of the modern talapoin (*Miopithecus*) on the basis of tooth size, even though Jablonski et al. (2008) only tentatively referred the specimen to *Cercopithecus* species indet. B.

Notably, *Miopithecus* is not only the smallest living catarrhine primate, but it is also thought to be phylogenetically dwarfed (Strasser and Delson, 1987; Shea, 1992). The presence of *Miopithecus* in the early Pliocene would suggest that dwarfing occurred early in this lineage (Jablonski et al., 2008; Lo Bianco et al., 2017). Further, as modern talapoin is confined to dense tropical forest in west central Africa while the Turkana Basin was characterized by dry woodlands and savannas (Bobe, 2011), the finding of a guenon closely related or ancestral to *Miopithecus* would have significant biogeographic and ecological implications for the evolution of this genus and possibly for the evolution of guenons as a group (Lo Bianco et al., 2017). Unfortunately, the KNM-ER 396 teeth are heavily worn, precluding anything other than its identification as a guenon that is similar in tooth size to modern talapoin.

Fieldwork at the Pliocene site of Kanapoi, Kenya, was renewed in 2012 by the West Turkana Paleo Project. Surface prospecting at the type locality of *Australopithecus anamensis* ('Nzube's Mandible Site'; Leakey et al., 1995) recovered two isolated mandibular teeth. The specimens are very small, and morphologically resemble the living West African talapoin, *Miopithecus*. If related to *Miopithecus*, these specimens would either confirm the presence of a close relative to modern talapoin at almost 4.2 Ma in East Africa, or imply that small body size was achieved at least twice among Cercopithecini. Here we describe these new specimens and discuss their relevance to understanding the evolution of guenons.

2. Geological context

Kanapoi was first described by Patterson (1966; see also Patterson et al., 1970), and later more comprehensively as part of a description of the geology of the Lower Kerio Valley (Powers, 1980). Kanapoi is located to the southwest of Lake Turkana (Fig. 1), and comprises a series of fluvial and lacustrine deposits and paleosols (Feibel, 2003). Deposits at Kanapoi are included in the Kanapoi Formation, and are securely dated between 4.195 and 4.108 Ma (McDougall and Brown, 2008). In addition to hominins, Nzube's Mandible Site has yielded remains of anurans, squamates, rodents, chiropterans, bovids, suids, and carnivorans (Manthi, 2006). Analysis of the site yields evidence for low-energy deposition, and sieving operations at the site consistently yield numerous micro-faunal specimens consistent with low-energy deposition. Reconstructions of the paleoenvironment suggest a seasonal, mixed savanna-woodland habitat (Wynn, 2000; Feibel, 2003; Harris et al., 2003).

KNM-KP 53150A and B were found on the surface within a few centimeters of one another. There are no younger sediments near the site, and annual rains have consistently exposed new fossil material. The color and condition of the specimens is consistent with other fossil material found at the site, suggesting that the specimens were exposed with little transportation and hence

derive from the paleosol upon which they were recovered. The proximity of the specimens, the preservation, and the morphology all strongly suggest that the teeth came from a single individual. Subsequent dry sieving of the surrounding matrix failed to recover additional material.

3. Materials and methods

Comparative dental metric data (Table 1; complete data in Supplemental Online Material [SOM] Table S1) comprising standard mesiodistal and buccolingual tooth dimensions for extant primates were taken from Plavcan (1990). These include data from extant species of *Miopithecus*: *Miopithecus talapoin* (Schreber, 1774) from Angola, and *Miopithecus ogouensis* (Kingdon, 1997) from Cameroon and Gabon. Tooth size measurements of KNM-KP 53150 and KNM-ER 396 were taken using a microscope with calibrated measurement software at the National Museums of Kenya. Tooth size data for NME L621-4A, the smallest guenon from Omo Shungura, Ethiopia, dated to 2.9 Ma (Eck and Howell, 1972), were taken using calipers on the original specimen. Tooth size data were ln-transformed before analysis. Ln-transformed tooth dimensions were compared graphically to those of extant guenons, and a principal components analysis (PCA) of the ln-transformed tooth dimension data was run in SYSTAT v. 13 (Systat Software, San Jose, CA) using a variance-covariance matrix.

Shearing crest data for KNM-KP 53150 were measured by R.F.K. using high fidelity epoxy casts of the specimens. Shearing crest data were not taken for KNM-ER 396 because the specimen is too worn. Eight crest lengths and two cusp heights were measured on the M_2 of samples of *M. talapoin* ($n = 4$), *M. ogouensis* ($n = 19$) and the new taxon erected here (Table 2). A description of the measurements is found in Kay (1978). Because the specimens being compared are similar in size, we expressed each shearing crest length and cusp height as a ratio of the measurement to mesiodistal molar length, following Kay (1978). We employ PCA to compare *M. talapoin*, *M. ogouensis*, and the described specimen on the basis of these measurements. Additionally, species means of size-adjusted shearing data from Kay (1978) for a series of guenons as well as *Lophocebus albigena* were compared to that for KNM-KP 53150 using PCA (Table 3). These analyses were conducted in SYSTAT 13 v. 13.

To assess the phylogenetic position of the new taxon, we employed the morphological character-taxon matrix of Gilbert et al. (2014) with the addition of the extant guenon *Miopithecus* and the newly described taxon. The revised character/taxon matrix under consideration consists of 13 characters and 11 taxa, including 6 living cercopithecine genera and 5 fossil taxa. A Nexus-formatted file is presented in SOM File S1. All multistate characters were considered ordered. In analysis 1, the characters were not scaled. In analysis 2, multistate characters were scaled by the number of character states, such that the sum of the steps in the morphocline equals 1.0. Character descriptions and weights are provided in Gilbert et al. (2014). Both phylogenetic analyses were performed with PAUP 4.0a (Build 163; 2018) for Macintosh (Swofford, 2002), 1000 replications, using a heuristic search with random taxon input, tree-bisection-reconnection option for branch swapping options.

Mandibular dental data were taken by J.M.P. for 738 specimens representing 26 species and subspecies of extant guenons, as well as KNM-ER 396 (SOM Table S2) using digital slide calipers. Many of these are the same specimens for which dental data were collected. Jaw depth was taken as the maximum dimension below the alveolar margin between M_1 and M_2 , while jaw breadth was the minimum breadth dimension in the same plane.

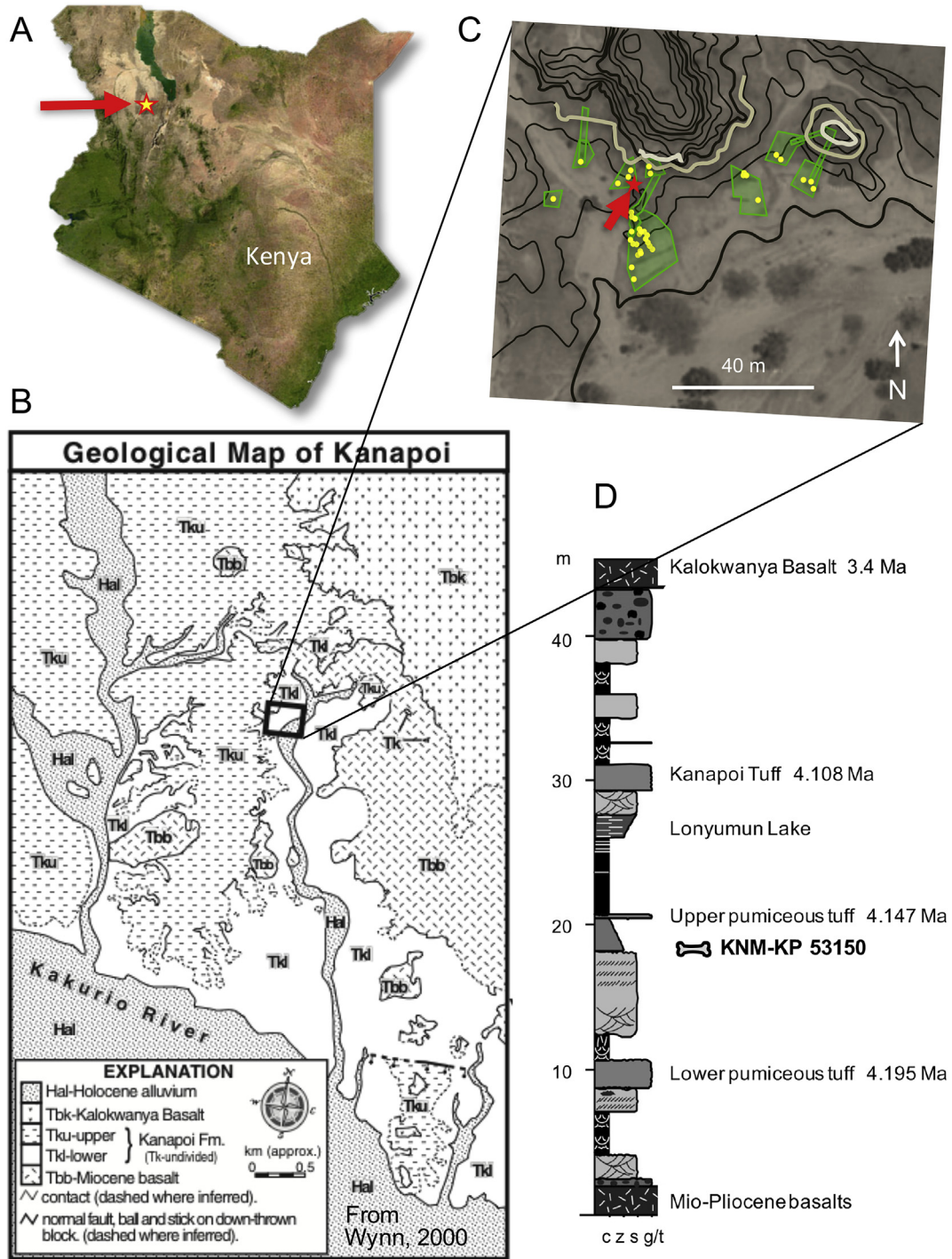


Figure 1. Map showing the location of Kanapoi (A), the geological map of the area (B), the location of the fossil at the site (C), and the stratigraphic location of the specimen based on Feibel (2003) (D).

4. Systematic paleontology

Order Primates Linnaeus, 1758
 Suborder Anthropoidea Mivart, 1864
 Superfamily Cercopithecoidea Gray, 1821
 Family Cercopithecidae Gray, 1821
 Subfamily Cercopithecinae Gray, 1821
 Tribe Cercopithecini Gray, 1821
 Subtribe Cercopithecina Gray, 1821
 Genus *Nanopithecus* gen. nov.

Type species *Nanopithecus browni* gen. et sp. nov.

Diagnosis As for the type species.

Nanopithecus browni gen. et sp. nov.

Holotype KNM-KP 53150 A and B, associated right M₃ and M₂, respectively, attributed to a single individual (Fig. 2) housed in the National Museums of Kenya.

Paratype KNM-ER 396, left mandibular fragment with M₂–M₃ (Fig. 3; see also Jablonski et al., 2008: Fig. IV.6).

Table 1Sample sizes and means for extant species and individual values for extant *Miopithecus* and fossils used in this analysis.^a

Species	Sex ^b	n	M ₂ MD	M ₂ BLtal	M ₂ BLtri	M ₃ MD	M ₃ BLtri	M ₃ BLtal
<i>Allenopithecus nigroviridis</i>	F/M	4/10	6.36/6.71	5.50/5.76	5.22/5.50	6.01/6.59	5.25/5.60	4.30/4.73
<i>Allochocebus lhoesti</i>	F/M	11/14	6.80/6.75	5.37/5.37	5.41/5.39	6.56/6.68	5.23/5.20	4.64/4.69
<i>Allochocebus preussi</i>	F/M	7/7	6.28/6.66	4.87/5.19	5.08/5.30	6.16/6.41	4.84/5.09	4.34/4.44
<i>Chlorocebus aethiops</i>	F/M	16/12	6.27/6.69	5.24/5.54	4.99/5.33	6.09/6.43	5.05/5.24	4.19/4.38
<i>Cercopithecus albogularis</i>	F/M	8/12	6.44/6.95	5.20/5.51	5.00/5.39	6.11/6.67	5.05/5.27	4.39/4.68
<i>Cercopithecus ascanius</i>	F/M	18/21	5.61/5.79	4.74/4.82	4.72/4.78	5.49/5.65	4.56/4.62	3.87/4.01
<i>Cercopithecus cephus</i>	F/M	15/24	5.85/6.07	4.70/4.89	4.64/4.89	5.54/5.71	4.52/4.61	3.93/4.07
<i>Cercopithecus diana</i>	F/M	18/7	6.53/6.68	5.04/5.15	4.85/4.94	6.30/6.43	4.80/4.81	4.15/4.22
<i>Cercopithecus mona</i>	F/M	10/17	5.93/6.21	4.85/5.27	4.88/5.30	5.68/6.13	4.66/5.19	4.09/4.54
<i>Cercopithecus neglectus</i>	F/M	15/24	6.47/6.89	5.25/5.65	5.12/5.47	6.36/6.95	5.01/5.43	4.45/4.87
<i>Cercopithecus nictitans</i>	F/M	20/23	6.47/6.87	5.03/5.32	4.96/5.23	6.15/6.61	4.78/5.13	4.32/4.59
<i>Cercopithecus petaurista</i>	F/M	4/11	6.06/6.28	4.75/5.06	4.78/5.01	5.81/6.07	4.59/4.84	3.93/4.08
<i>Cercopithecus pogonius</i>	F/M	17/18	5.87/5.95	5.02/5.20	4.96/5.32	5.55/5.75	4.69/4.97	3.92/4.20
<i>Cercopithecus wolffi</i>	F/M	8/8	5.57/5.91	4.85/5.18	4.64/5.11	5.41/5.85	4.72/4.96	3.97/4.24
<i>Erythrocebus patas</i>	F/M	9/26	7.71/8.11	6.18/6.40	5.96/6.22	7.35/7.91	5.94/6.18	5.30/5.45
<i>Miopithecus talapoin</i>	F	—	4.31	3.87	3.75	4.12	3.87	3.31
<i>Miopithecus talapoin</i>	M	—	4.44	4.06	4.13	4.31	3.69	3.25
<i>Miopithecus talapoin</i>	M	—	4.69	4.38	4.19	4.63	4.13	3.31
<i>Miopithecus talapoin</i>	M	—	4.75	4.31	4.13	4.44	4.13	3.38
<i>Miopithecus talapoin</i>	M	—	4.75	4.38	4.19	4.75	4.25	3.44
<i>Miopithecus ogouensis</i>	F	—	4.75	4.31	4.12	4.56	4.06	3.25
<i>Miopithecus ogouensis</i>	F	—	4.75	4.56	4.31	4.62	4.25	3.37
<i>Miopithecus ogouensis</i>	F	—	4.06	3.50	3.31	3.87	3.12	2.75
<i>Miopithecus ogouensis</i>	F	—	4.06	3.56	3.43	3.75	3.37	3.06
<i>Miopithecus ogouensis</i>	F	—	3.68	3.31	3.25	3.43	3.06	2.68
<i>Miopithecus ogouensis</i>	F	—	4.00	3.62	3.25	3.81	3.31	2.93
<i>Miopithecus ogouensis</i>	F	—	3.75	3.31	3.19	3.69	3.06	2.75
<i>Miopithecus ogouensis</i>	F	—	3.88	3.56	3.44	3.75	3.38	2.94
<i>Miopithecus ogouensis</i>	F	—	4.31	3.63	3.50	—	—	—
<i>Miopithecus ogouensis</i>	F	—	3.87	3.31	3.25	3.68	3.12	2.68
<i>Miopithecus ogouensis</i>	M	—	4.06	3.62	3.56	3.93	3.50	3.06
<i>Miopithecus ogouensis</i>	M	—	4.12	3.62	3.37	3.87	3.37	2.87
<i>Miopithecus ogouensis</i>	M	—	4.00	3.50	3.31	3.81	3.06	3.00
<i>Miopithecus ogouensis</i>	M	—	4.18	3.56	3.56	4.06	3.25	3.00
<i>Miopithecus ogouensis</i>	M	—	4.12	3.68	3.62	4.06	3.43	3.06
<i>Miopithecus ogouensis</i>	M	—	4.18	3.68	3.56	4.00	3.37	3.00
<i>Miopithecus ogouensis</i>	M	—	4.25	3.75	3.62	3.87	3.43	2.81
<i>Miopithecus ogouensis</i>	M	—	4.25	3.81	3.62	3.93	3.43	3.00
<i>Miopithecus ogouensis</i>	M	—	4.37	3.81	3.62	4.18	3.62	3.18
<i>Miopithecus ogouensis</i>	M	—	4.25	3.68	3.68	4.06	3.37	2.93
<i>Miopithecus ogouensis</i>	M	—	4.18	3.62	3.56	4.12	3.43	3.12
<i>Miopithecus ogouensis</i>	M	—	4.19	3.63	3.44	4.19	3.50	3.13
<i>Miopithecus ogouensis</i>	M	—	4.00	3.44	3.25	3.75	3.00	2.69
<i>Miopithecus ogouensis</i>	M	—	4.25	3.63	3.38	4.13	3.31	3.00
<i>Miopithecus ogouensis</i>	M	—	4.31	3.44	3.38	4.00	3.19	2.75
<i>Miopithecus ogouensis</i>	M	—	4.00	3.38	3.31	4.00	—	3.00
<i>Miopithecus ogouensis</i>	M	—	3.94	3.50	3.31	3.94	3.13	2.88
<i>Miopithecus ogouensis</i>	M	—	3.94	3.44	3.25	3.81	3.25	2.94
<i>Miopithecus ogouensis</i>	M	—	4.44	4.00	3.69	4.31	3.56	3.25
<i>Miopithecus ogouensis</i>	M	—	3.93	3.56	3.37	3.81	3.18	3.06
<i>Miopithecus ogouensis</i>	M	—	4.56	4.06	3.93	4.31	3.75	3.43
<i>Miopithecus ogouensis</i>	M	—	4.18	3.62	3.37	4.00	3.43	2.93
<i>Miopithecus ogouensis</i>	M	—	3.81	3.37	3.25	3.75	3.25	3.00
KNM-KP 53150A	?	—	—	—	—	4.03	3.01	2.89
KNM-KP 53150B	?	—	4.16	3.24	3.02	—	—	—
KNM-ER 396	?	—	4.16	3.14	3.22	3.99	2.86	2.78
L621-4a	?	—	5.60	5.10	4.70	5.30	4.60	3.80

Abbreviations: M = Male; F = Female; MD = mesiodistal length; BLtri = buccolingual breadth across the trigonid; BLtal = buccolingual breadth across the talonid.

^a These data were applied to the tooth size analysis, and were measured by J.M.P. Tooth size data for the analysis of shearing quotients were gathered separately by R.F.K. on a different set of individual species. All measurements in mm.^b Sample sizes and means for females and males for each dimension of all extant taxa except *Miopithecus* are presented separated by a slash ("/"). Complete data for species other than *Miopithecus* can be found in the [SOM Table S1](#).

Diagnosis A diminutive cercopithecoid (dental size comparable to *Miopithecus*) with fully developed bilophodont mandibular molars. M₃ lacks a hypoconulid, as typical for Cercopithecini. Tooth size is comparable to that of extant *Miopithecus* and smaller than all other known fossil and extant guenons. Molar teeth are

narrower relative to their breadth than for extant guenons, including *Miopithecus*. Molar tooth shearing crests are relatively poorly developed by comparison to extant *Miopithecus* and other extant guenons.

Type locality Nzube's Mandible Site, Kanapoi Fm., Kenya.

Table 2Shearing crest data for specimens of *Nanopithecus* and extant *Miopithecus*.

Species	Museum ID ^a	Sex	M ₂ ln	Crt 1	Crt 2	Crt 3	Crt 4	Crt 5	Crt 6	Crt 7	Crt 8	c hgt hypc'd	c hgt metc'd
<i>M. talapoin</i>	BRM 1855122675	male	5.00	1.38	1.69	1.50	1.69	1.88	1.06	1.94	1.81	2.94	3.06
<i>M. talapoin</i>	BRM 4491	male	4.44	1.00	1.69	1.31	1.06	1.31	1.19	1.44	1.56	3.00	2.63
<i>M. talapoin</i>	FMN 84147	male	4.69	1.00	1.75	1.56	1.25	1.56	0.94	1.56	1.50	3.13	3.19
<i>M. talapoin</i>	PCA A3863	?	4.69	1.44	1.94	1.50	1.38	1.63	1.19	1.94	1.56	3.50	3.38
<i>M. ogouensis</i>	BRM 1939 1131	?	4.38	1.06	1.50	1.25	1.25	1.56	1.06	1.31	1.50	2.94	2.50
<i>M. ogouensis</i>	BRM 1977 3099	female	4.25	1.06	1.63	1.25	1.06	1.38	1.31	1.38	1.38	2.69	2.75
<i>M. ogouensis</i>	BRM 1977863	male	4.00	1.06	1.69	1.19	1.25	1.31	1.00	1.75	1.38	2.94	2.88
<i>M. ogouensis</i>	BRM 5 5 23	male	4.06	1.00	1.81	1.31	1.31	1.56	1.19	1.63	1.25	2.63	2.50
<i>M. ogouensis</i>	BRM 5 5 23 8	male	4.25	1.19	1.88	1.31	1.38	1.75	1.13	1.63	1.56	2.88	2.69
<i>M. ogouensis</i>	BRM 8 6 14 1	male	3.88	1.00	1.75	1.31	1.19	1.31	0.94	1.44	1.63	2.69	2.31
<i>M. ogouensis</i>	BRM 97 7 1 1	female	3.81	0.94	1.63	1.31	1.31	1.31	1.25	1.38	1.63	3.06	2.69
<i>M. ogouensis</i>	CAM 51	female	4.00	0.94	1.81	1.38	1.38	1.38	1.06	1.44	1.13	3.00	2.63
<i>M. ogouensis</i>	FMN 95273	male	3.94	1.00	1.56	1.19	1.19	1.19	1.19	1.38	1.31	2.56	2.69
<i>M. ogouensis</i>	MER 346	male	4.25	1.06	1.69	1.38	1.31	1.31	1.25	1.56	1.63	2.63	2.69
<i>M. ogouensis</i>	PMC 15672	?	4.38	1.25	1.81	1.38	1.31	1.75	0.94	1.56	1.25	3.44	2.88
<i>M. ogouensis</i>	PMC 17361	?	4.38	1.19	1.63	1.38	1.25	1.44	1.38	1.63	1.25	3.63	2.50
<i>M. ogouensis</i>	PMC 34251	?	4.06	0.94	1.69	1.44	1.06	1.63	1.00	1.63	1.06	2.94	3.00
<i>M. ogouensis</i>	USN 220349	?	3.95	1.06	1.56	1.42	1.19	1.42	0.97	1.38	1.38	2.98	2.39
<i>M. ogouensis</i>	USN 395343	?	3.81	1.13	1.63	1.19	1.25	1.44	1.19	1.75	1.50	2.44	2.75
<i>M. ogouensis</i>	USN 396195	female	4.00	1.06	1.75	1.50	1.25	1.50	1.13	1.63	1.19	2.94	2.63
<i>M. ogouensis</i>	USN 397614	?	3.94	1.06	1.56	1.31	1.06	1.25	0.81	1.56	1.19	2.56	2.63
<i>M. ogouensis</i>	USN 397625	?	3.88	0.94	1.69	1.31	1.19	1.25	1.13	1.19	1.25	3.00	2.50
<i>M. ogouensis</i>	USN 397649	?	3.63	1.13	1.50	1.19	1.19	1.25	1.25	1.44	1.19	2.31	2.81
<i>N. browni</i>	KNM KP 53150	?	4.24	1.12	1.44	1.21	1.37	1.40	1.21	1.21	0.99	2.23	2.30

Abbreviations: m2 ln = mesiodistal length of M₂; Crt = shearing crest; c hgt hypc'd = crown height at the hypoconid; c hgt metac'd = crown height at the metaconid.^a Institutional abbreviations: BRM = Natural History Museum, London, UK; FMN = Field Museum of Natural History, Chicago, USA; PCA, PMC, CAM, MER = Powel Cotton Museum, Burchington, Kent, UK; USN = Smithsonian Institution, Natural History, Washington DC, USA; KNM = Kenya National Museums, Kenya.**Table 3**Species means of ratio of crest lengths and cusp heights to second molar length in samples of extant African Cercopithecidae and *Nanopithecus*.

Species	Taxon	n	C1/M ₂	C2/M ₂	C3/M ₂	C4/M ₂	C5/M ₂	C6/M ₂	C7/M ₂	C8/M ₂	Hh/M ₂	Mh/M ₂
<i>Colobus guereza</i>	Colobinae	20	0.34	0.38	0.34	0.39	0.44	0.38	0.36	0.39	0.72	0.65
<i>Allenopithecus nigroviridis</i>	Cercopithecini	16	0.31	0.43	0.29	0.31	0.39	0.28	0.38	0.3	0.84	0.69
<i>Cercopithecus mitis</i>	Cercopithecini	33	0.27	0.41	0.33	0.31	0.35	0.28	0.34	0.31	0.64	0.58
<i>Chlorocebus spp.</i> ^a	Cercopithecini	11	0.31	0.37	0.3	0.32	0.37	0.28	0.34	0.31	0.71	0.64
<i>Erythrocebus patas</i>	Cercopithecini	17	0.3	0.4	0.32	0.32	0.37	0.32	0.4	0.35	0.7	0.63
<i>Miopithecus ogouensis</i>	Cercopithecini	19	0.26	0.41	0.33	0.3	0.35	0.28	0.37	0.33	0.71	0.66
<i>Miopithecus talapoin</i>	Cercopithecini	4	0.26	0.38	0.31	0.28	0.34	0.23	0.36	0.34	0.67	0.65
<i>Lophocebus albigena</i>	Papionini	36	0.26	0.38	0.28	0.27	0.33	0.25	0.33	0.25	0.67	0.63
<i>Nanopithecus browni</i> (KNM KP 53150, holotype)		1	0.26	0.34	0.29	0.32	0.33	0.29	0.33	0.23	0.53	0.54

Abbreviations: C1/M₂ = crest 1/M₂ mesiodistal length (repeated for crests 2–8); Hh/M₂ = hypoconulid crown height/M₂ mesiodistal length.^a *Chlorocebus* spp. includes *Chlorocebus aethiops* and *Chlorocebus pygerythrus*.

Age and distribution Known from the type locality, 4.195–4.108 Ma (Early Pliocene). KNM-ER 396 was reported from Koobi Fora, Kenya, presumed from Allia Bay below the Tula Bor Tuff,¹ giving a minimum age of 3.4 Ma (Jablonski et al., 2008; McDougall and Brown, 2008).

Etymology The genus name refers to diminutive size of the specimen, dentally as small as the smallest extant cercopithecoid monkey, *Miopithecus*. The species is named for the late Francis H. Brown (1943–2017), in recognition of his enormous contributions to understanding the geology of the Omo-Turkana Basin within which the specimens were recovered.

4.1. Anatomical descriptions

KNM-KP 53150A This specimen is a right M₃ that preserves the entire crown, but no root (Fig. 2). The crown is complete and shows relatively light wear. Enamel is missing around the dentine horn of

the metaconid. The metaconid tip is slightly damaged. Some slight pitting of the enamel surface around the outside of the crown suggests the damage occurred postmortem. The tooth roots are broken off just inferior to the cemento-enamel junction of the crown, exposing a single bilobate cross-sectional shape for the root cavity.

KNM-KP 53150A is bilophodont with a rectangular outline and lacking a hypoconulid. It shows the distinctive narrowing of the distal cusps characteristic of guenon third molars. There is no evidence of an interproximal facet on the distal face of the crown, again consistent with the identification of the tooth as a third molar. The entoconid is the smallest cusp. The lingual walls of the lingual cusps are steep and bulge slightly from occlusal surface to cemento-enamel junction. The lingual surface of the entoconid is slightly more convex than that of the metaconid, so that the tip of the entoconid is placed slightly closer to the mesiodistal axis of the tooth than that of the metaconid. There is a deep median lingual notch between metaconid and hypoconid. The preprotocristid is thicker than the premetacristid and angled about 45° to the mesiodistal axis of the tooth in occlusal view. The trigonid is slightly elevated above the talonid, which is large and deeply excavated. The distal fovea is slightly smaller than the trigonid basin, and more rounded in outline and somewhat deeper.

The buccal cusps are more worn than the lingual cusps, as is typical of cercopithecoid lower molars in general. There is slight

¹ Jablonski et al. (2008: 108) stated: "Unfortunately, because KNM-ER 396 was collected in 1969, before aerial photographs were available, the provenance cannot be accurately checked, but it is certainly from the Allia Bay region and must be older than the Tulu Bor Tuff." The accession card lists the collecting site as Area 203, photo 1695, "below '3–9' tuff" and on the back of the card "same site as KNM-ER 127."

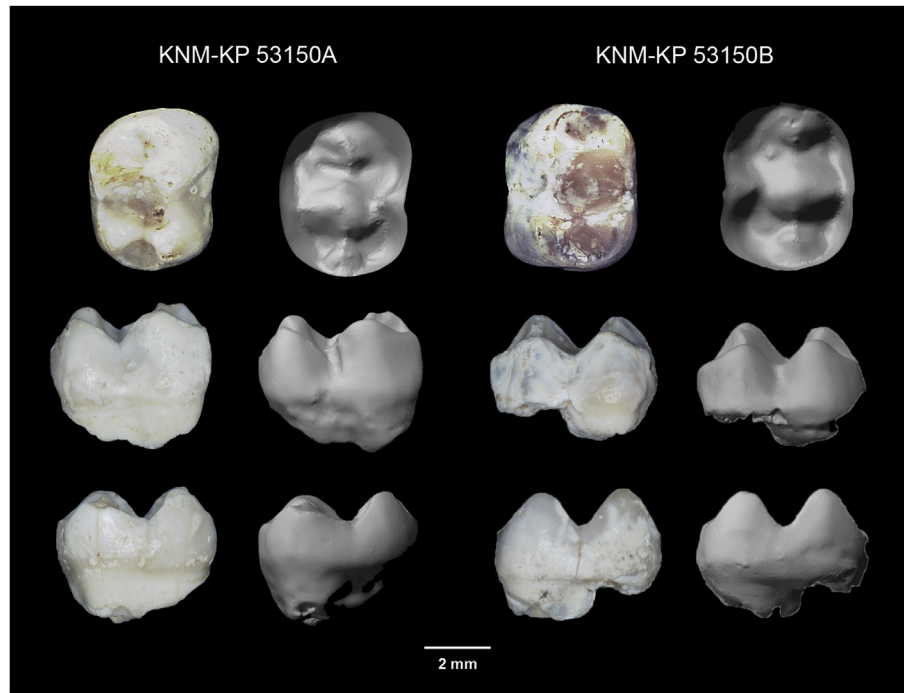


Figure 2. KNM-KP 53150, holotype of *Nanopithecus browni* gen. et sp. nov. molars in occlusal (top), lingual (center), and buccal (bottom) views. KNM-KP 53150A, mandibular right third molar is illustrated on the left, and KNM-KP 53150B, a mandibular left second molar is illustrated on the right. For each, a photograph of the discolored original is shown alongside a rendered surface scan for clarity.

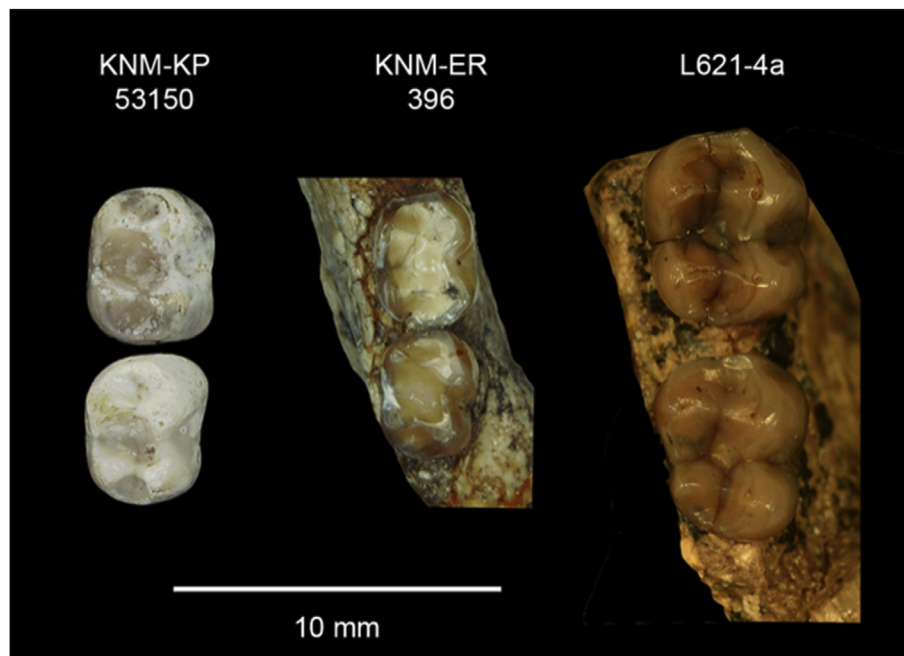


Figure 3. The holotype of *Nanopithecus browni* gen. et sp. nov. (KNM-KP 53150A and B; bottom and top, respectively) compared to M_2 and M_3 of KNM-ER 396 (paratype of *Nanopithecus browni* gen. et sp. nov.) and NME L621-4a (*Cercopithecus* sp.), which is the smallest *Cercopithecus* known in the fossil record apart from *Nanopithecus*.

dentine exposure on the protoconid, visible despite minor damage, indicating that the tooth was in occlusion, and that the individual was dentally an adult. The hypoconid cusp tip shows slight wear on its mesial face, but none on the distal face. There is a distinct interproximal contact facet for M_2 on the mesial face of the tooth. **KNM-KP 53150B** This specimen is a complete left M_2 with relatively light wear (Fig. 2). The crown is broken off of the root just inferior to

the cemento-enamel junction. The root is missing just at the cemento-enamel junction on the mesial side, with damage to the enamel at the junction on the lingual and buccal sides from excavation of the dentine cavity into the crown. On the distal side of the tooth, the root is broken off below the cemento-enamel junction, with a small oval pulp cavity preserved. This breakage makes an estimate of the cusp height unreliable.



Figure 4. The holotype of *Nanopithecus browni* gen. et sp. nov. compared to M₂ and M₃ of extant guenons: A) *N. browni* (KNM-KP 53150A and B, the former reversed for comparison); B) *Miopithecus ogouensis* (USNM 598521); C) *Miopithecus talapoin* (USNM 397649); D) *Cercopithecus pogonias* (USNM 598511); E) *Cercopithecus cephus* (USNM 218840); F) *Cercopithecus nictitans* (USNM 480890); G) *Cercopithecus mitis* (USNM 452553); H) *Chlorocebus aethiops ngamiensis* (USNM 367915).

The identification of KNM-KP 53150B as a second molar is based on tooth proportions and size. KNM-KP 53150B is larger than KNM-KP 53150A, especially in buccolingual dimensions, and thus is relatively broader buccolingually, as typically seen for a second, not a first, mandibular molar.

The tooth is bilophodont and nearly rectangular in outline. The four cusps are approximately equal in size in occlusal view. The lingual walls of the lingual cusps are vertically steep and slightly superoinferiorly convex. The protoconid and hypoconid display a noticeable buccal flare when viewed in the occlusal plane. The median buccal cleft (between protoconid and hypoconid) extends almost to the cervix. The preprotocristid is thickened and extends to a slight swelling at the mesiobuccal corner of the trigonid at an acute angle to the mesiodistal axis of the tooth in occlusal view. The talonid is deep, with steep walls defined by the transverse lophids. The trigonid is shallower and slightly smaller than the distal fovea.

The buccal cusps are moderately worn, with small dentine lakes exposed at the tips. The lingual cusps are nearly unworn, showing only very slight blunting at their apices. There are well-defined mesial and distal interproximal contact facets.

The KNM-KP 53150 teeth are clearly those of an adult, showing typical permanent crown morphology. Guenon mandibular deciduous premolars normally show distinct waisting of the crown, relatively thin enamel, and are notably buccolingually narrow relative to mesiodistal breadth. While KNM-KP 53150A and B both show relative buccolingual narrowing compared to the teeth of most extant guenons, tooth shape is not comparable to the degree seen in deciduous premolars. Furthermore, KNM-KP 53150A shows distinctive morphology of a permanent third molar, particularly with reference to cusp proportions and crown shape. Because the two teeth differ from one another in a manner consistent with distinctions between permanent molars, and KNM-KP 53150B is buccolingually wider than KNM-KP 53150A, there is no morphological evidence consistent with these teeth being deciduous premolars.

KNM-ER 396 This specimen (Fig. 3) is a small left mandibular fragment with heavily worn M₂–M₃, described and figured by Jablonski et al. (2008), who referred the specimen to *Cercopithecus* sp. B, and suggested that it may represent a close relative of *Miopithecus*. The M₃ lacks a hypoconulid. The mandible is broken just behind M₃ posteriorly, and just in front of M₁ anteriorly, preserving the roots of this tooth, although the M₁ alveolar margin is damaged. The root of the oblique crest is preserved, terminating approximately at the distal

edge of the M₃. The inferior border of the mandibular corpus is slightly concave, and appears to flare posteriorly where it would continue to the gonial region. The medial wall of the corpus beneath M₁ is crushed inwards. The distal end of the M₃ is angled medially relative to the MD axis of M₂, whereas the roots of M₁ suggest that the mesial end of this tooth swung medially relative to the MD axis of M₂. The impression is that in the occlusal view the molar arcade was bowed rather than straight. Jablonski et al. (2008) reported that the mandible is 9.2 mm in height between M₂ and the alveolus of M₁, and 4.9 mm in breadth below M₂. Measurements taken by J.M.P. with standard sliding calipers yield a jaw depth of 10.3 mm at the point between M₁ alveolus and M₂, and a jaw breadth of 5.0 mm at the same level.² This compares to average jaw depth of 9.2 mm ($n = 12$, $SD = 1.04$) for female and 9.82 mm ($n = 17$, $SD = 0.54$) for male extant *Miopithecus* and an average jaw breadth of 4.01 mm ($n = 12$, $SD = 0.52$) for female and 4.14 mm ($n = 17$, $SD = 0.27$) for males (unpublished data measured by J.M.P.). Metrically, KNM-KP 53150A and B are nearly identical in size and tooth proportions to those of KNM-ER 396 (Fig. 5), supporting Jablonski et al.'s (2008) assessment and suggesting that this specimen can be referred to *Nanopithecus*. Unfortunately the crowns are heavily worn, so a direct comparison of crest morphology cannot be made to the holotype specimen. The similarity in size and proportions to the KNM-KP 53150 teeth supports the identification of the *N. browni* holotype teeth as M₂ and M₃.

4.2. Comparative anatomy

Together, the two diminutive Kenyan specimens are slightly smaller in tooth area than the average of extant *Miopithecus*, though they fall within the range of the sample available here for tooth area (Figs. 4 and 5). They are much smaller than teeth of other extant guenons (Fig. 4). The smallest guenon fossil from Ethiopia, NME L621–4A from Cycle 4 of Member G of the Shungura Member

² Differences in the jaw depth measurement probably reflect a difference in the way the calipers were held against the specimen. The measurement taken here is directly comparable to the comparative data for guenons presented here, all measured by the same individual using the same calipers. The jaw depth measured here is taken as the maximum dimension from the alveolar border between M₁ and M₂ and the inferior border of the corpus. Jaw breadth is the minimum dimension in the same plane, and appears to have been measured the same way here and in Jablonski et al. (2008).

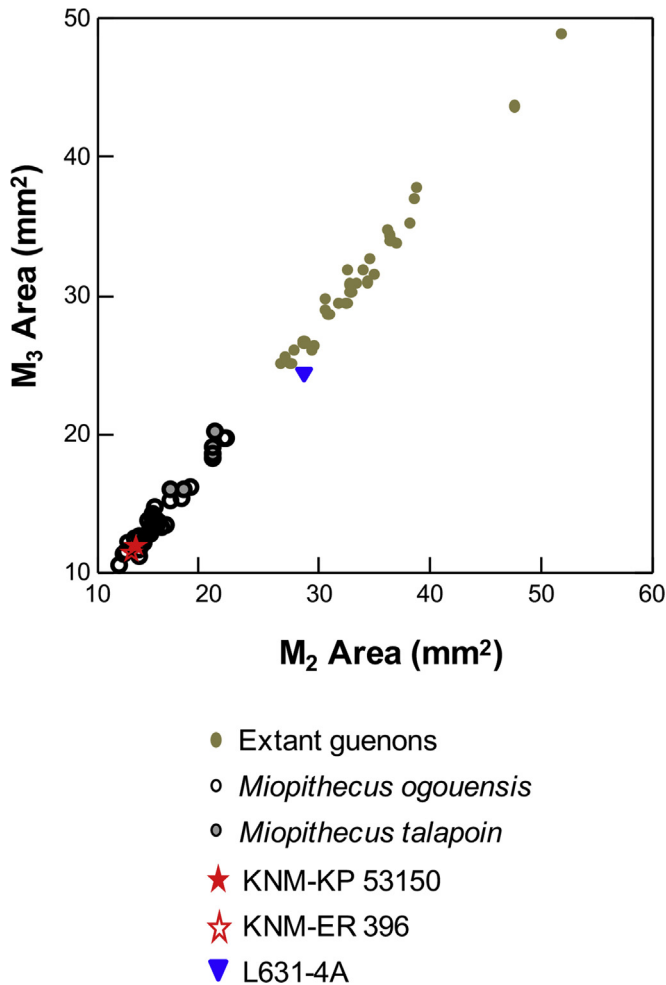


Figure 5. Plot of tooth area (mm²) of KNM-KP 53150 and KNM-ER 396, holotype and paratype, respectively, of *Nanopithecus browni* gen. et sp. nov., and NME L621-4a *Cercopithecus* sp., versus other extant guenons. Values for the extant guenons are species means. Tooth area calculated as the product of mesiodistal length times buccolingual breadth across the trigonid basin. Using the breadth across the talonid basin yields nearly identical results.

(1.9 Ma; Eck and Howell, 1972) falls at the small end of the extant guenon tooth size range but is still considerably larger than *Miopithecus* and the two Kenyan specimens (Figs. 3 and 5).

The *Nanopithecus browni* second molars are narrower buccolingually relative to mesiodistal length than those of any living guenon, including *Miopithecus* (Fig. 6). Plotting the buccolingual dimensions against each other (Fig. 7) reveals that the Kenyan specimens are unremarkable compared to extant guenons for M₂, corroborating that the primary difference between the Kenyan fossils and other guenons (including NME L621-4a) involves a proportionally narrow crown.

For the M₃, both KNM-KP 53150A and KNM-ER 396 show trigonid breadths that differ relative to mesiodistal length from those seen in extant *Miopithecus*, falling outside of the extant *Miopithecus* distribution (Fig. 7). However, the proportion of the talonid breadth versus mesiodistal tooth length falls within the extant *Miopithecus* distribution. The bivariate comparisons for both teeth are confirmed using a PCA that includes all six tooth dimensions (Table 4). The first principal component (PC1) explains 92% of the variance, with loadings all positive and even indicating that this axis reflects overall size. PC2 explains 3.5% of the variance, with mesiodistal dimensions loading negatively and buccolingual dimensions showing positive loadings, indicating that this axis

separates specimens by length and breadth proportions. PC1 separates the Kenyan fossils and *Miopithecus* from all other extant cercopithecines on the basis of overall tooth size (Fig. 8). PC2 separates the Kenyan fossils, which cluster tightly together, from *Miopithecus*, reflecting the buccolingual narrowing of the teeth as compared to *Miopithecus*.

Analysis of shearing crests again corroborates the distinctiveness of the fossils from any other cercopithecine. A PCA of size-adjusted M₂ crest lengths and cusp heights for individuals and species of *Miopithecus* and *Nanopithecus* suggests that *Nanopithecus* is distinct from living *Miopithecus* (Table 5; Fig. 9). PC1 explains 36.2% of the variance. The loadings are all positive, but the strongest are for the heights of the hypoconid and metaconid and shearing crests 2, 3, and 7, suggesting that PC1 is not a simple size component, but instead is dominated by the development of these shearing crests. The second principal component explains 23.1% of the variance, and the loadings show a distinction between hypoconid height versus metaconid height. *Nanopithecus* is separated from extant *Miopithecus* only on the first axis, emphasizing that the fossil species has proportionally lower shearing crest lengths and cusps heights than extant *Miopithecus*. Given the light wear on the fossils, the results are not attributable to differences in tooth wear.

The PCA of species means of the size-adjusted shearing crest lengths and cusp heights in a broader sample of extant cercopithecines (including six species of Cercopithecini) again illustrates the wide differences that exist between *Nanopithecus* and other Cercopithecidae (Fig. 10; Table 6). Loadings on the PC1 are all positive and relatively uniform, with the first axis explaining 62.5% of the variance, and thus separating taxa with better-developed shearing crests and higher cusps from those that have less well-developed crests and lower cusp heights. *Nanopithecus* is well-separated from other taxa along this axis. This separation may represent a combination of factors related to more folivory (*Colobus*) and semiterrestrial or terrestrial foraging (*Allenopithecus* and *Erythrocebus*; Kingdon, 1971; Gautier, 1985) that separates these taxa from those that eat proportionately more fruit and are more arboreally adapted (Williams and Kay, 2001; Kay et al., 2002). From this limited data it is reasonable to speculate that the weak development of shearing crests and low crowns suggest that *Nanopithecus* was quite frugivorous, though the results may also suggest it was arboreal, or of course both.

Comparison of the jaw dimensions off KNM-ER 396 to those of extant guenons suggests proportional differences in jaw shape of *N. browni*. Figure 11 illustrates a comparison of jaw dimensions for extant guenons, including *Miopithecus*. Dimensions measured here fall just outside the range of extant *Miopithecus*, with a proportionally shallower and broader jaw. Given that the jaw breadth is only slightly greater than molar breadth, the analysis suggests that *Nanopithecus* had a proportionally shallower jaw than extant *Miopithecus*. The jaw dimensions themselves place this specimen at the large end of the *Miopithecus* range. Considering that tooth size for *Nanopithecus* falls at the small end of the range of extant *Miopithecus*, this suggests a proportional difference between tooth size and jaw size in *Nanopithecus*. Notably, there is a horizontal crack measuring 0.3 mm extending horizontally across the external face of the corpus of KNM-ER 396. Subtracting 0.3 mm from the mandibular depth of KNM-ER 396 would make the jaw depth appear even shallower as compared to extant *Miopithecus*.

4.3. Phylogenetic analysis

Majority consensus findings of the phylogenetic analyses agree in placing *Nanopithecus* in the clade of non-*Allenopithecus* guenons. Analysis 1 (Fig. 12A) yields 8 most parsimonious trees with

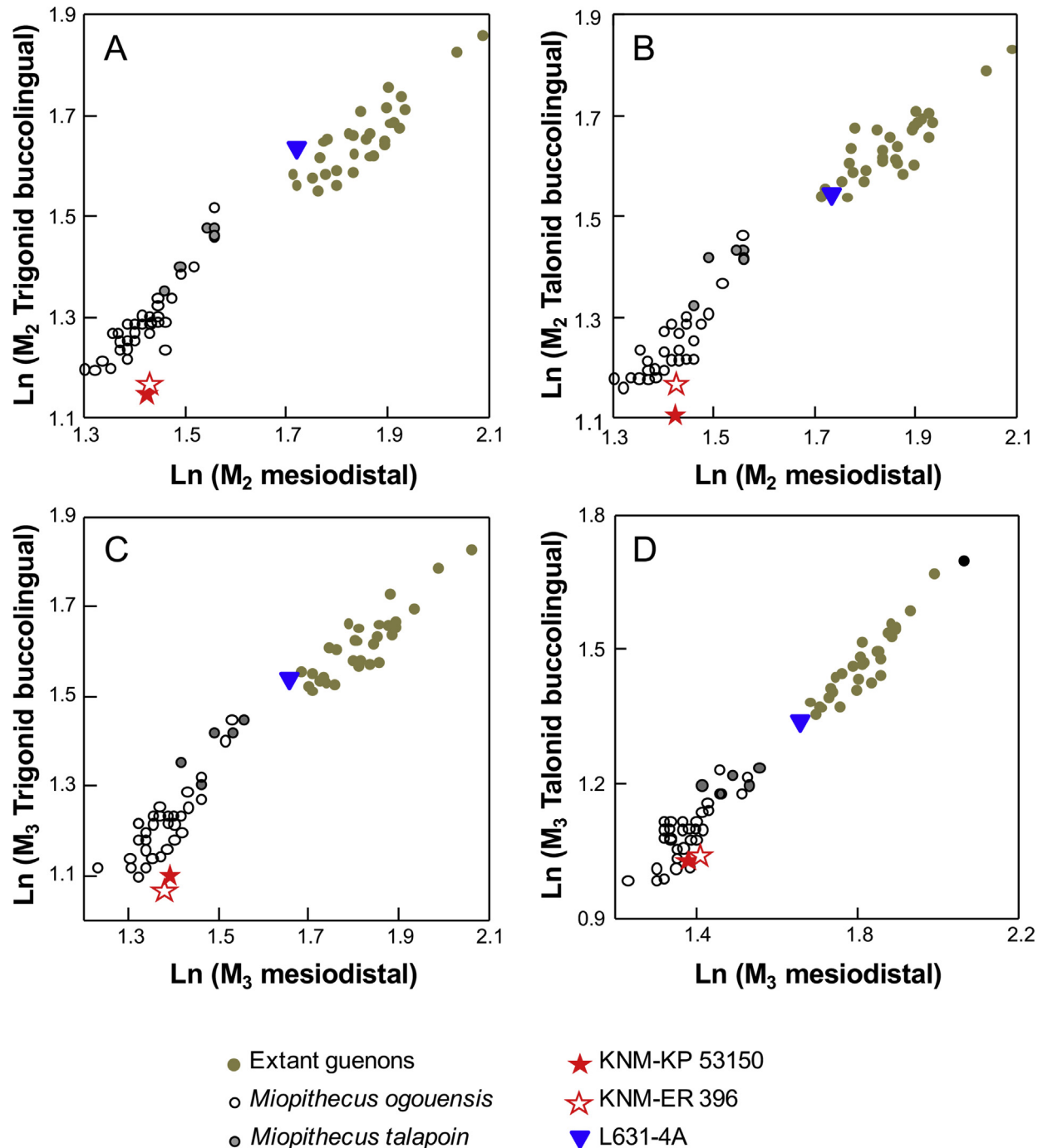


Figure 6. Plots of tooth crown proportions of *Miopithecus talapoin*, *M. ogouensis*, and other extant guenons versus *Nanopithecus* and *Cercopithecus* specimen NME L621-4a: A–B) dimensions of M₂; C–D) dimensions of M₃. All measurements in millimeters. Data for average values of males and females in each guenon species are plotted in green (Table 1), while specimens of each *Miopithecus* species are shown individually. All data are ln-transformed.

branch lengths of 29 steps, a consistency index of 0.655, a retention index of 0.730 and a rescaled consistency index of 0.478. The majority consensus of the recovered trees again resembles that reported in Gilbert et al. (2014: Fig. S4). *Miopithecus* and the unnamed taxon represented by AUH 1321, described by Gilbert et al. (2014), link with *Cercopithecus* and those three taxa form an unresolved trichotomy that links with *Nanopithecus* and extant *Chlorocebus*. The strict consensus of the various trees in analysis 1 yields the same result. Analysis 2 (Fig. 12B) yields 5 most parsimonious trees with branch lengths of 20.5 steps, a consistency

index of 0.634, a retention index of 0.694 and a rescaled consistency index of 0.448. The majority consensus of the recovered trees resembles that reported by Gilbert et al. (Gilbert et al., 2014: Fig. S4). *Miopithecus*, *Nanopithecus*, *Chlorocebus*, *Cercopithecus*, and AUH 1321 form an unresolved polytomy. *Allenopithecus* usually, but not always falls as the outgroup of this cluster. For the strict consensus of the various trees resulting from analysis 2, the linkage with *Allenopithecus* with any other cluster (*Macaca* plus *Cercopithecus*, or the non-*Allenopithecus* guenons) becomes a trichotomy.

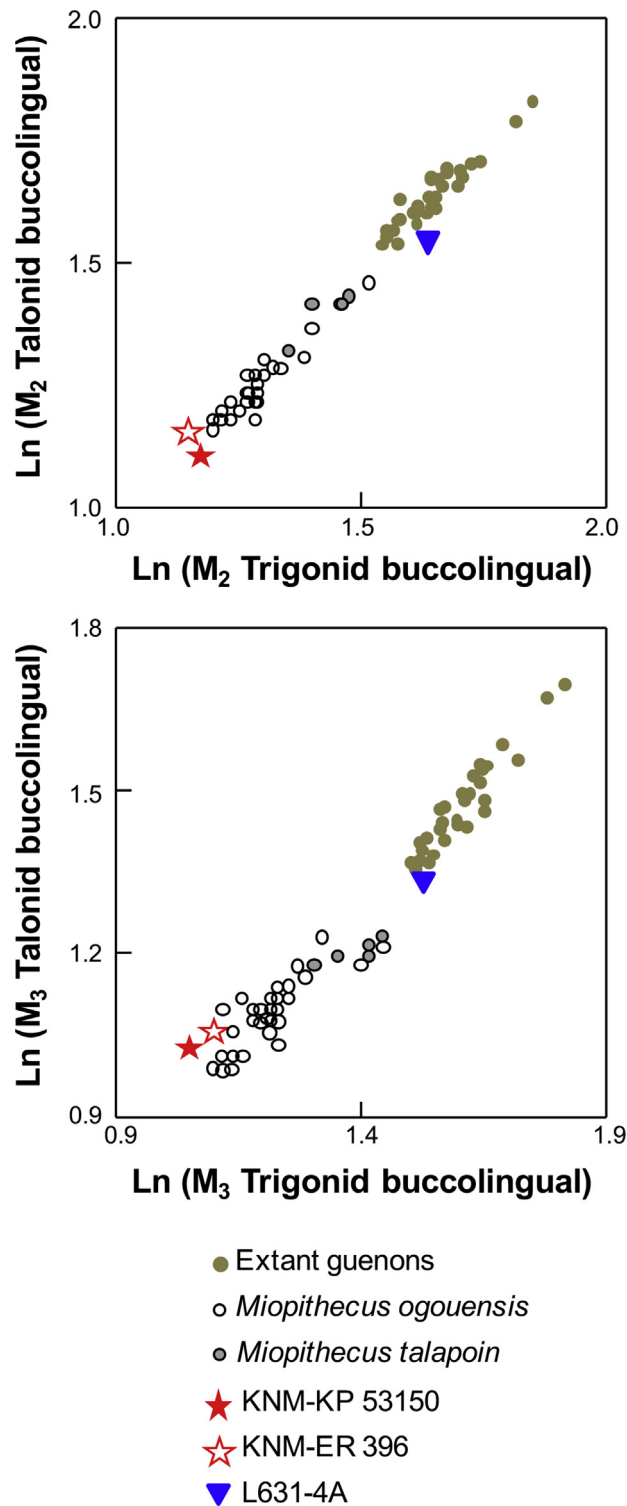


Figure 7. Plots of molar breadth dimensions across the talonid and trigonid basins for M_2 and M_3 of extant and fossil guenons. All data are ln-transformed. All extant guenons except *Miopithecus* and the fossils are represented by separate mean values of males and females in each species.

5. Discussion

The fossil record of guenons remains very poor, in spite of the diversity and abundance of the living species in Africa. This deficiency has been attributed to three factors. First, the radiation of modern 'arboreal' guenon taxa (genus *Cercopithecus* sensu Hart

Table 4

Factor loadings for PCA of tooth dimensions of extant and fossil guenons illustrated in Figure 8.

	Principal Component					
	1	2	3	4	5	6
M_2 MD	0.137	-0.033	0.017	0.010	0.017	-0.005
M_3 MD	0.145	-0.040	-0.006	-0.009	-0.017	0.004
M_2 BL _{tri}	0.128	0.023	0.022	-0.007	0.003	0.017
M_2 BL _{tal}	0.128	0.022	0.008	0.026	-0.013	-0.006
M_3 BL _{tri}	0.139	0.023	0.004	-0.023	0.001	-0.014
M_3 BL _{tal}	0.143	0.011	-0.041	0.005	0.009	0.004
% Variance explained	92.0	3.5	2.1	1.2	0.69	0.45

Abbreviations: MD = mesiodistal; BL_{tri} = buccolingual breadth across the trigonid basin; BL_{tal} = buccolingual breadth across the talonid basin.

et al., 2012) is relatively recent according to molecular analyses (Tosi et al., 2004, 2005; Hart et al., 2012; Perelman et al., 2011; Springer et al., 2012; Pozzi et al., 2014), suggesting that in spite of the antiquity of the basal splits within the group, cercopithecins were not common or diverse before approximately 600 ka. Second, most guenons are relatively small, and so their rarity in the fossil record might be explained by either a bias against preservation of small specimens (Jablonski and Frost, 2010), or a bias against collecting small specimens. Third, apart from *Chlorocebus* species and *E. patas*, most guenons, including *Miopithecus*, live in dense forests, where preservation is not favored, and where today exposures that

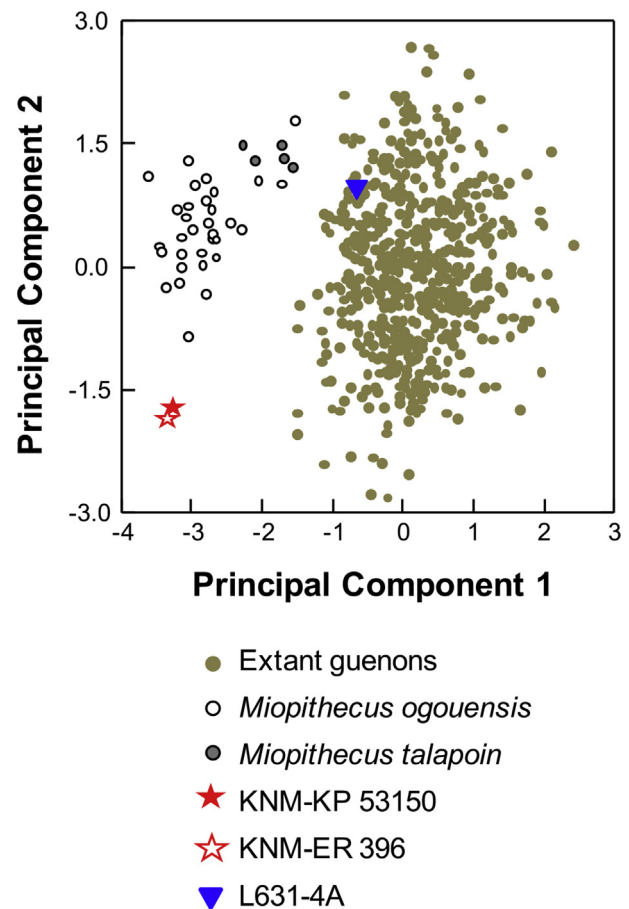


Figure 8. Results of a principal components analysis (PCA) of ln-transformed tooth size dimensions of all guenon specimens used in this study. 92% of the variance is explained by PC1, and 3.5% of the variance by PC2. Individuals of all but *Miopithecus* and the fossils are marked in green.

Table 5

Factor loadings for principal components analysis of size-adjusted shearing crest lengths and cusp heights of extant *Miopithecus* and KNM-KP 53150 illustrated in Figure 9.

M ₂ Measurement	PC1	PC2	PC3	PC4	PC5
Crest 1/M ₂ length	0.005	0.011	0.003	0.002	0.009
Crest 2/M ₂ length	0.024	0.006	0.008	-0.001	0.007
crest 3/M ₂ length	0.014	-0.002	-0.002	0.002	0.002
Crest 4/M ₂ length	0.005	0.009	0.010	-0.001	0.018
Crest 5/M ₂ length	0.009	0.005	-0.003	0.018	0.018
Crest 6/M ₂ length	0.005	0.008	0.010	-0.034	0.012
Crest 7/M ₂ length	0.024	0.027	0.004	0.013	0.006
Crest 8/M ₂ length	0.003	0.013	0.036	0.006	-0.016
Hypoconid height/M ₂ length	0.060	-0.040	0.004	-0.001	-0.002
Metaconid height/M ₂ length	0.038	0.037	-0.018	-0.007	-0.014
% Variance explained	36.2	23.1	10.8	9.6	7.9

might yield fossils are still rare. Leakey (1988) suggested that the absence of guenons in the fossil record of East African sites, in spite of the relative abundance of other primates and smaller mammals, indicates that guenons may have been rare at the time, at least in these habitats, and that collection and preservation bias alone cannot explain the paucity of guenon fossils.

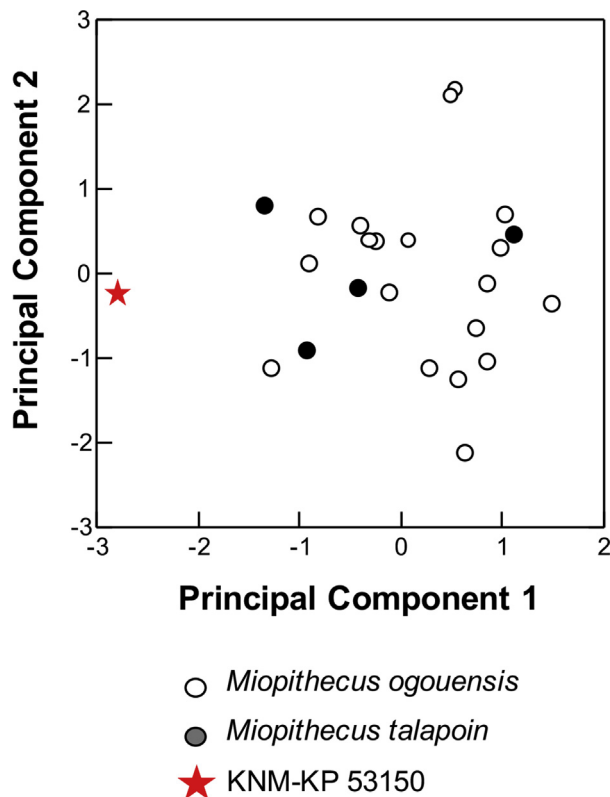


Figure 9. Results of a principal components analysis (PCA) based on eight M₂ shearing crest ratios and two cusp height ratios, as shown by a plot of the second versus the first PCAs. 36.2% of variance is accounted for by PC1 and 23.1% by PC2.

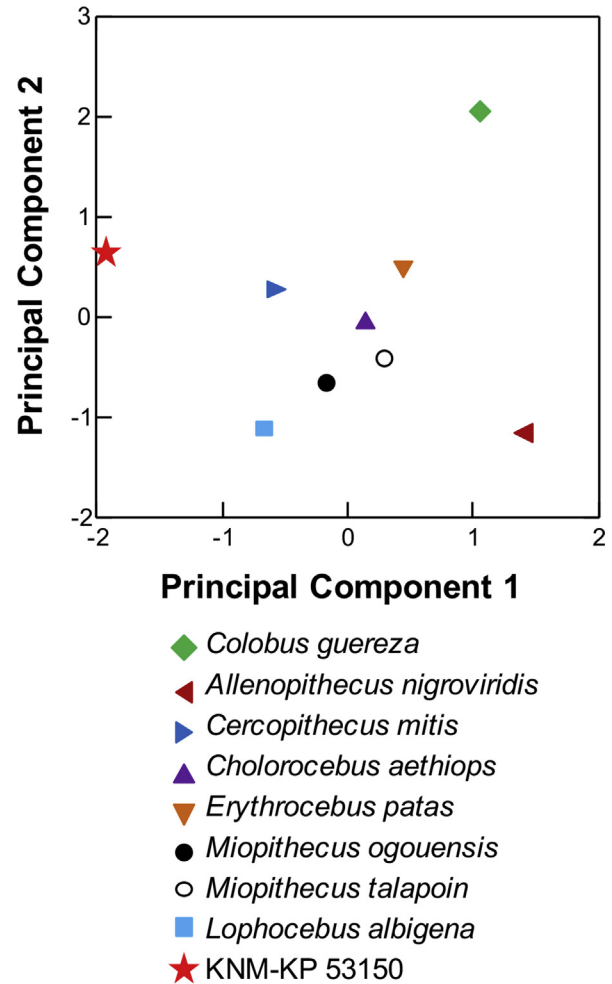


Figure 10. Results of a principal components analysis (PCA) of mean shearing quotients of selected extant cercopithecoid taxa and *Nanopithecus* as shown by a plot of the second versus the first principal components. PC1 accounts for 62.5% of the variance; PC2 accounts for 24.8%.

Genetic evidence suggests that although cercopithecins likely diverged from papionins at 10–12 Ma, the present diversity of guenons is a relatively recent phenomenon. Although phylogenetic studies are still not in complete agreement, and therefore divergence dates are not well established, genetic studies nevertheless place the origin of most of the major groups between about 8 Ma and 5 Ma, with diversification of species within most major groups after about 3 Ma (e.g., Tosi et al., 2005; Guschanski et al., 2013; Lo Bianco et al., 2017), so many of the living taxa may have existed well before 0.6 Ma. It may be more reasonable to expect that many taxa could have originated earlier and then later gone extinct, so we cannot say how diverse guenons were at any time since their last common ancestor. Complicating this is the fact that, apart from *Allenopithecus*, modern guenons are relatively uniform in their dental anatomy. As a result, identifying fossil species for which we have only teeth and unraveling their relationships to one another and to extant taxa is fraught with uncertainty. *Nanopithecus* is unusual in this regard, as the dental proportions and crest morphology are distinct from all extant guenons.

KNM-KP 53150, though presenting only two teeth, confirms the presence of a *Miopithecus*-sized guenon in East Africa almost 4.2 Ma (as originally noted by Jablonski et al., 2008). The preserved crown morphology of these specimens demonstrate unambiguously that *Nanopithecus* is distinct from all living guenons. Jaw dimensions of

Table 6
Factor loadings for the principal components analysis (PCA) illustrated in Figure 10.

M ₂ measurement	PC1	PC2	PC3
Crest 1/M ₂ length	0.022	0.016	−0.011
Crest 2/M ₂ length	0.019	−0.010	0.005
Crest 3/M ₂ length	0.007	0.013	0.013
Crest 4/M ₂ length	0.012	0.030	−0.008
Crest 5/M ₂ length	0.027	0.020	−0.008
Crest 6/M ₂ length	0.016	0.037	−0.008
Crest 7/M ₂ length	0.027	−0.003	0.013
Crest 8/M ₂ length	0.035	0.022	0.025
Hypoconid height/M ₂ length	0.077	−0.024	−0.011
Metaconid height/M ₂ length	0.040	−0.016	0.003
% Variance explained	62.5	24.8	7.8

KNM-ER 396 likewise suggest a proportionally shallow mandible with relatively small teeth.

The exact phylogenetic relationships of *Nanopithecus* cannot at the moment be ascertained given that it is only known from these few teeth. The phylogenetic analysis reported here links *Nanopithecus* with extant guenons to the exclusion of other cercopithecoids. However, beyond including *Nanopithecus* with other

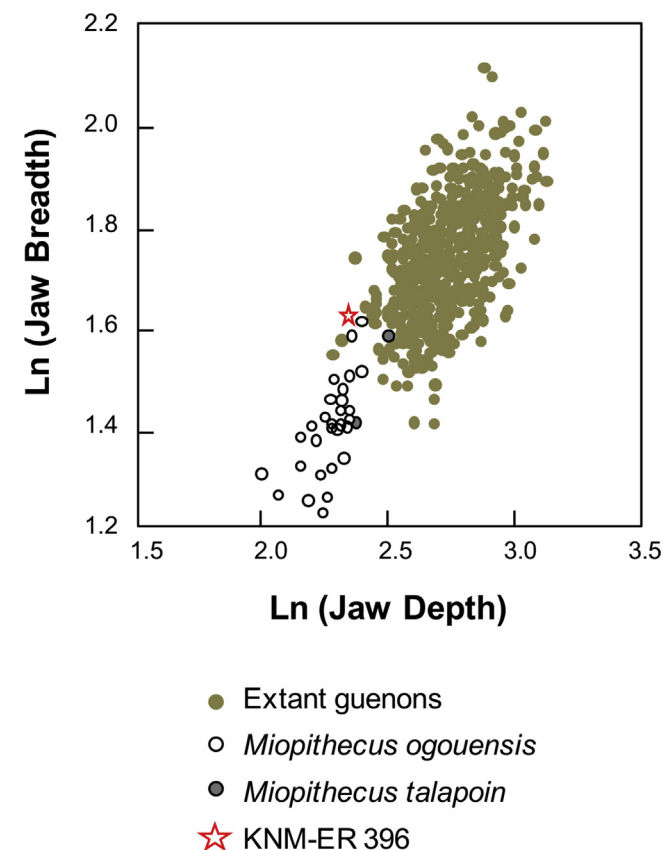


Figure 11. Bivariate plot of Ln-transformed mandibular dimensions of extant guenons and KNM-ER 396.

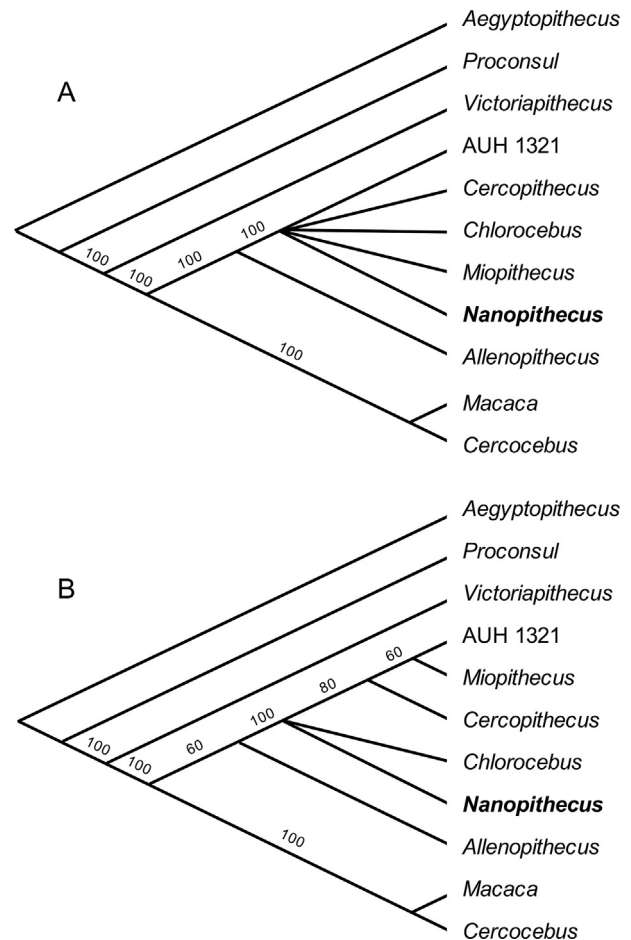


Figure 12. 50% majority consensus cladograms for the phylogenetic position of *Nanopithecus*. A) Multistate characters scaled by the number of steps (7 characters have weight 1; 6 characters have weight 0.5). B) All steps in the morphocline have weight equal to 1, so two state characters are 0 > 1, equals one step, whereas 3-state characters are 0 > 1 > 2 equals two steps. In A and B, the numbers on the branches correspond to the percentage of trees that have the arrangement illustrated.

guenons to the exclusion of *Allenopithecus* no further resolution of the place of *Nanopithecus* can be determined. Clearly the small size links it with *Miopithecus*, although its morphology is distinct from species of that genus. If *Nanopithecus* is allied with *Miopithecus*, then the dwarfing event for this taxon must have occurred prior to 4.2 Ma, and small body size has been retained in *Miopithecus*. If *Nanopithecus* is not closely related to *Miopithecus*, dwarfing may have occurred at least twice within the guenons. An alternative possibility is that small body size is primitive for guenons, but the presence of a vervet-sized specimen from Arabia at 8.0–6.5 Ma (Gilbert et al., 2014) argues against this. At the moment, it is impossible to choose between these two hypotheses, but given the larger size of all other known guenons compared to *Nanopithecus* or *Miopithecus* it seems more probable that *Nanopithecus* and *Miopithecus* are related and, therefore, that *Nanopithecus* serves as potential evidence that small body size was derived for this lineage by at least 4 Ma.

Biogeographically, the discovery of a dwarf guenon in East Africa is important. Until this time, most fossils appear to suggest that the modern biogeographic distribution of guenons broadly reflects the evolutionary history of the group, at least in the sense that identifiable East African guenon fossils are limited to *Chlorocebus* and *Erythrocebus* (Frost and Alemseged, 2007; Jablonski and Frost, 2010). The current distribution of guenons in Africa is thought to

reflect allopatric speciation through Plio-Pleistocene fragmentation of forest blocks (Gautier-Hion et al., 1988; Hamilton, 1988; Kamilar et al., 2009; Lo Bianco et al., 2017). Extant *Miopithecus* is found only in lowland forest and swamps in Angola, Cameroon, and Gabon. *Nanopithecus* is found on the other side of the continent along with *A. anamensis* in an environment that is reconstructed as mixed savanna and woodland (Bohe, 2011). While it seems most reasonable to assume, without further evidence, that *Nanopithecus* probably was arboreal, if this species is in fact related to *Miopithecus*, then the current distribution of *Miopithecus* provides no certain indication of the extent of the past distribution. Regardless of whether the taxa are related, the presence of two apparently dwarfed guenons in disparate habitats suggests that, at the very least, dwarfing is not associated with a single habitat or ecological circumstance. In broader terms, this throws up a caution that the evolutionary history of modern guenon groups may not be associated with the current distribution of species, and in fact there could be significant ecological variation in extinct taxa that is not anticipated by modern biogeography or habitat distribution.

Acknowledgements

We thank the curators of the museums for permission to examine the specimens in their care, especially Yonas Yilma of the Ethiopian National Museums. We thank Steve Frost, Meave Leakey, Chris Gilbert, Eric Delson, and David Alba for helpful discussions, comments, and advice. We thank the crew of the West Turkana Paleo Project, whose hard work and dedication yielded these fossils, the Government of Kenya, Turkana County, the people of Kanapoi, and the staff of the National Museums of Kenya for their support and assistance. We thank Claire Terhune and the University of Arkansas MicroCT Imaging Consortium for Research and Outreach (MICRO), funded by NSF instrumentation grant BCS-1725925 for assistance creating dental surface scans. This work was funded by NSF Grants BCS-1231749 (to C.V.W. and F.K.M.), and BCS-1231675 (to J.M.P. and P.S.Ungar), the Wenner Gren Foundation, the University of Missouri Research Board, and PAST of South Africa.

Supplementary Online Material

Supplementary online material to this article can be found online at <https://doi.org/10.1016/j.jhevol.2019.05.011>.

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