

Fossil Cercopithecoidea from the Middle Pleistocene Kapthurin Formation, Kenya

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ABSTRACT

The modern monkeys of eastern Africa are mostly absent from the fossil record until their likely direct ancestors appear in the later Middle Pleistocene. In this report, we describe a large collection of fossil cercopithecoids from the Kapthurin Formation of Kenya, the Middle Pleistocene sedimentary sequence best known for its fossil hominins, Acheulean and Middle Stone Age stone tools, and fossil chimpanzee. The collection of fossil Cercopithecoidea from the Kapthurin Formation comprises four taxa—cf. *Chlorocebus* sp., *Theropithecus oswaldi leakeyi*, cf. *Papio* sp., and cf. *Colobus* sp. Of these, only *T. o. leakeyi* is extinct. A likely representative of the modern vervets represented by a partial cranium, KNM-BK 42140, and fragmentary craniodental and postcranial remains, and is here referred to cf. *Chlorocebus* sp.. *Theropithecus o. leakeyi*, the dominant papionin of Plio-Pleistocene Africa, is represented by a robust male partial cranium (KNM-BK45609) and mandible (KNM-BK 22638). A likely representative of the modern common baboon, cf. *Papio* sp. is represented by three isolated teeth. The largest number of cercopithecoid fossils from the Kapthurin Formation represent a small morph of *Colobus*; the assemblage includes a well-preserved partial cranium (KNM-BK 42141), a partially dentate maxilla (KNM-BK 62), and two partial mandibles (KNM-BK 56 and KNM-TH-46347) and are here referred to cf. *Colobus* sp.. This collection greatly increases the known fossil record for *Colobus*.

Most of the fossil Cercopithecoidea from the Kapthurin Formation derive from within the Middle Silts and Gravels Member (K3), below the Grey Tuff, and are bracketed between ⁴⁰Ar/³⁹Ar dates of ~545 ka and ~509 ka. The fossils are significant because, with the exception of *T. o. leakeyi*, they together approach a modern monkey fauna typical of an ecotonal habitat, with one dedicated gallery forest arborealist (cf. *Colobus* sp.), two habitat generalists considered mostly terrestrial (cf. *Chlorocebus* sp.. and cf. *Papio* sp.), and one probable terrestrialist (*T. o. leakeyi*). Today, modern vervets, baboons, and colobus monkeys are sympatric with chimpanzees at Kibale, Budongo, and Mahale, and these situations may shed light on paleoenvironments during deposition of sediments of the Kapthurin Formation.

INTRODUCTION

Vervets (*Chlorocebus pygerythrus*), common baboons (*Papio hamadryas* subspp.), and black-and-white colobus monkeys (*Colobus guereza* subspp.) are among the most common species of monkeys living today in eastern Africa. These species are rare in the fossil record, however, even at

Late Pleistocene sites. The recently improved fossil record for these modern species is helping to illuminate their phyletic relationships to other cercopithecoids, but much still remains to be learned about the morphological diversity of the groups in the past, especially in relation to other mammalian herbivores, during the rapidly changing environ-

ments of the Pleistocene (Arenson et al. 2022; Brasil et al. 2023a; b; Frost and Alemseged 2007; Jablonski 2002; Jablonski and Leakey 2008c; Leakey and Leakey 1976). Ironically, Cercopithecoidea are common elements of the Plio-Pleistocene fossil record, but most of the species known from this period are medium- and large-bodied colobines, extinct species of *Theropithecus* that have no clear descendants among modern species, as well as other papionins more closely related to modern mangabeys and mandrills (Delson 1993; Eck and Jablonski 1984; Gilbert 2013; Jablonski 2002; Jablonski and Frost 2010; Jablonski and Leakey 2008b; Leakey, M.G. 1982, 1993; Leakey, R.E.F. 1969). Thus, paleoprimatologists face the challenge of figuring out how, when, and why the “old guard” species of the Plio-Pleistocene became extinct and how and when the modern communities of monkeys in eastern Africa were established. Some insight into the nature of this succession came from study of the cercopithecoid assemblage at Koobi Fora in the Lake Turkana Basin. There, the transition from typical Pliocene monkey fauna—dominated by a large, probably mostly arboreal colobine (*Rhinocolobus turkanaensis*) and the terrestrial giant *Theropithecus oswaldi*—to a more modern one including a mangabey (classified as *Lophocebus albigena*) and a highly arboreal early colobus (*Colobus freedmani*) is glimpsed in the fossil record of the Early Pleistocene-aged Okote Member (Frost and Delson 2002; Jablonski and Leakey 2008a; Leakey et al. 2008).

The fossil monkeys from the Kapthurin Formation (frequently hereafter, the Formation) are noteworthy because they represent a large, diverse, and well-dated Middle Pleistocene collection, which includes some of the earliest and most complete examples of likely close relatives of modern and familiar eastern African species like the vervet and black-and-white colobus. The modern character of the monkey fossils of the Formation was noted previously (Cornelissen et al. 1990), but the fossils have not been described in detail before. Cornelissen and colleagues noted that, “The primate fossils consist of bones belonging to *Cercopithecus* sp. (among others a fairly complete mandible, maxilla, skull-fragments, tibia and fibula), *Colobus* sp. and *Theropithecus* cf. *oswaldi*” (Cornelissen et al. 1990: 64). Their report included a photograph of one *T. oswaldi* specimen, now numbered KNM-BK 22638, and briefly compared the find to *Theropithecus jonathani*, a morph now included in *T. oswaldi leakeyi* (Getahun et al. 2023) and referred to as the giant “gorilla-sized gelada baboon” known from Olduvai Gorge (Cornelissen et al. 1990). Since the 1990 publication by Cornelissen and colleagues, many new and relatively complete cercopithecoid fossils have been recovered, and a more detailed descriptive account of the Formation’s monkey fauna is long overdue.

BACKGROUND

The geology, archaeology, and vertebrate paleontology of the Kapthurin Formation of Kenya has recently been reviewed (Tryon 2023). The Kapthurin Formation forms the ~125-m-thick Middle Pleistocene portion of the Miocene-Holocene sedimentary sequence that crops out over an area

of ~150km² west of Lake Baringo, in Kenya’s Rift Valley. The formation is divided into a sequence of numbered and named members, from K1 (Lower Silts and Gravels Member) at the base to K5 (Upper Silts and Gravels Member) at the top. We focus here primarily on sediments attributed to K3 (Middle Silts and Gravels Member), which is bounded by K2 (Pumice Tuff Member), and K4 (Bedded Tuff Member). Within K3 are two additional tephra deposits that serve as locally important stratigraphic markers—the Grey Tuff and the Lebus Tuff (Tallon 1976, 1978). All Kapthurin Formation sediments are normally magnetized, suggesting that they postdate the Brunhes-Matuyama reversal, with additional chronological control provided by ⁴⁰Ar/³⁹Ar age estimates on multiple volcanic deposits and an extensive tephrostratigraphic framework (Blegen et al. 2018; Deino and McBrearty 2002; Tryon and McBrearty 2006). Most of the sediments are >198 ka, although the age of the uppermost portion of the Formation remains poorly defined.

The Kapthurin Formation is perhaps best known for its extensive Acheulean and Middle Stone Age lithic industries (Blegen 2017; Johnson and McBrearty 2010; McBrearty et al. 1996; Tryon et al. 2005) as well as fossil hominin mandibular and postcranial remains (Leakey et al. 1969; Solan and Day 1992; Wood and Van Noten 1986) and chimpanzee teeth (McBrearty and Jablonski 2005). Almost all fossils from the Kapthurin Formation derive from K3 (Middle Silts and Gravels Member) sediments, with an age range of ~545–395 ka, with the majority underlying the Grey Tuff and thus constrained in age to ~545–509 ka. Most of the monkey fossils reported here derive from this ~545–509 ka interval. The nature of the sediments, taxonomy of the recovered fossils, and isotopic analyses of bovid teeth and pedogenic carbonates all suggest that the K3 Member sediments preserve a range of wooded-to-grassy environments crossed by ephemeral streams, marshes, and a variably fresh-to-alkaline lake. The fossils reported here were initially collected from three major campaigns in the Kapthurin Formation, directed in succession by then Margaret Leakey (now Avery), Richard Leakey, Francis Van Noten, and Sally McBrearty (Cornelissen et al. 1990; Johnson and McBrearty 2012; Leslie et al. 2016; McBrearty 1999; O’Brien et al. 2021; Tallon 1978). Fossils from the Kapthurin Formation were also collected in the late 1960s and 1970s by Walter William “Bill” Bishop, who worked in the Tugen Hills, including the Kapthurin Formation, with the Leakeys and later with his students. Because work in the Kapthurin Formation preceded the more geographically extensive investigations in the Tugen Hills more broadly, specimens derived from older expeditions generally bear the KNM-BK label, whereas those collected later bear the more geographically inclusive KNM-TH designation.

MATERIALS AND METHODS

The Cercopithecoidea fossils from the Kapthurin Formation documented here comprise 57 specimens attributable to the genera of modern vervet (seven specimens) and colobus monkey (26 specimens), six specimens referable to *Colobinae* gen. et sp. indet., three specimens probably referable

to the genus of common baboon (*Papio*), nine specimens of *Theropithecus oswaldi leakeyi* and five specimens that could be classified only as Cercopitheidae indet. These specimens are listed in Table 1, which includes all currently available information on specimen provenience and estimated age as gathered from primary sources. The specimens are stored in the National Museums of Kenya (KNM) in Nairobi, Kenya, and bear specimen numbers with the designation KNM-BK or KNM-TH, depending on exactly when and where they were collected.

The specimens described here were originally studied in the Palaeontology Section of the National Museums of Kenya in 2003 and 2004, and again briefly in 2008 and 2009. At the time, they were compared to other collections of fossil Cercopithecoidea roughly contemporaneous to the Kaphthurin Formation materials at the Museum. Comparative samples of extant monkeys were measured in the skeletal collections stored in the Osteology section of the Museum. Specimens were measured using digital calipers, and specimen data maintained in spreadsheets. Simple summary statistics only (means and ranges) were performed on the data.

In this paper, we have been guided by the most recent taxonomies available for the specimens at hand, specifically, those of Turner and colleagues for *Chlorocebus* (Turner et al. 2018), Getahun and colleagues for *Theropithecus* (Getahun et al. 2023), Brasil and colleagues for *Papio* (Brasil et al. 2023b) and Matsuda and colleagues for colobines (Matsuda et al. 2022).

SYSTEMATIC PALEONTOLOGY

The assemblage of 57 Cercopithecoidea fossils from the Kaphthurin Formation includes some relatively complete crania, which make possible sound taxonomic assignments to the genus level and suggestions for identifications at the species level. The modern genus of black-and-white colobus monkeys, *Colobus* is represented by 27 specimens, 11 of which preserve anatomy suggesting the modern guereza and a further 16 lack strongly diagnostic anatomy. We here err on the side of taxonomic caution and assign all specimens to *Colobus* sp. indet.. *Theropithecus oswaldi* or *T. cf. oswaldi* are represented by nine specimens. Six specimens can be assigned to *Chlorocebus* sp. indet. and one to cf. *Chlorocebus*. Three specimens, all isolated teeth, represent what is thought to be the modern common baboon, and are assigned here to cf. *Papio*. Six specimens have been assigned to Colobinae gen. et sp. indet., and a further five specimens representing fragmentary or juvenile cranial and dental remains cannot be classified beyond the family level.

Order Primates (Linnaeus, 1758)
Family Cercopithecidae (Gray, 1821)
Subfamily Cercopithecinae (Gray, 1821)
Tribe Cercopithecini (Gray, 1821)
Genus *Chlorocebus* (Gray, 1870)

CHLOROCEBUS SP. INDET.

Kaphthurin Formation Material

The guenon fossils from the Formation that preserve highly diagnostic morphology can be assigned to the genus *Chlorocebus*. The extant species of *Chlorocebus* are distinguished morphologically mostly by differences in pelage, and secondarily by differences in body size and sexual dimorphism (Turner et al. 2018). In the absence of information about pelage, differential diagnosis of *Chlorocebus* species, especially between *Chlorocebus pygerythrus* and *Ch. aethiops*, on the basis of dental and skeletal evidence is difficult (Taylor et al. 2023). The male specimens of *Chlorocebus* from the Kaphthurin Formation exhibit a bell-shaped maxillary dental arcade and palate characteristic of larger male representatives of *Ch. pygerythrus*, but this is not a sufficiently unambiguous diagnostic characteristic to warrant assignment of the specimens to that species. *Chlorocebus pygerythrus*, it must be noted, is the largest, most strongly sexually dimorphic, and most geographically widespread guenon species today, with its distribution covering the Tugen Hills region of eastern Africa, within which the Kaphthurin Formation is located. We thus feel that it is more likely that the *Chlorocebus* from the Kaphthurin Formation represents *Ch. pygerythrus* than *Ch. aethiops*, the smaller, less sexually dimorphic species distributed today mostly within Ethiopia and Sudan (Haus et al. 2013). The species identity of the Kaphthurin Formation *Chlorocebus* specimens clearly warrants more careful comparative study, especially in light of the considerable overlap in size between *Chlorocebus* morphs recently described from Late Pleistocene Middle Awash sites (Taylor et al. 2023). Differentiating the Kaphthurin Formation *Chlorocebus* from other *Chlorocebus* species and from the talapoin is somewhat more straightforward. The Kaphthurin Formation *Chlorocebus* is larger than the talapoin, *Miopithecus*, and smaller than the patas monkey, *Ch. patas*. Its rostrum is shorter and less squared than *Ch. patas*. The molar cusps are also not as tall and sharp as are those of L'Hoest's monkey, *Ch. lhoesti* (Jablonski and Frost 2010). In the postcranium, the *Chlorocebus* from the Kaphthurin Formation is distinguished from other guenons by its anteriorly flattened humeral head (Nakatsukasa 1994; Rose 1989).

The most remarkable and important specimens of *Chlorocebus* sp. indet. from the Kaphthurin Formation are the nearly complete male cranium, KNM-BK42140, and a maxilla fragment from a male containing the C¹ (KNM-BK 97). All of the other specimens are much more fragmentary.

Craniodental Material

KNM-BK 42140 (Figure 1): The specimen is a partial cranium of a male that preserves most of the upper facial skeleton and rostral portion of the calvaria. On the right side of the dentition, the incisors have been lost and the C¹ and P³ have been broken at the cervix; most of the P⁴ and all three molars are preserved. On the left side, I¹-I² have also been lost, but the base of the C¹, and the P³ through the M² are preserved; the M³ has been lost. The upper face of the speci-

TABLE 1. SITE LOCATIONS AND ESTIMATED AGES SUMMARIZED
 (from Blegen et al. 2018; Cornelissen et al. 1990; McBrearty et al. 1996; Tryon 2003. ND = no data).

Genus and species	KNM specimen number	Site	Stratigraphic position	Estimated age (ka)	Element(s)	Comments
<i>Chlorocebus</i> sp. indet.	KNM-BK 42140	Loc. 38	K3 above Lebus & Grey Tuffs	465–395	Cranium, male, nearly complete	Dentition lacking only the incisors
<i>Chlorocebus</i> sp. indet.	KNM-BK 97	ND	"Middle Kapth"	545–395	Maxilla fragment, male, left, with C ¹ , alveolus of P ³ , and P ⁴ roots	
<i>Chlorocebus</i> sp. indet.	KNM-TH 47130	JKS (GnJh20)	K3 below Grey Tuff	545–509	Mandible fragment with M ₂ and partial alveolus of M ₃ , right	Lingual aspect of M ₂ eroded
<i>Chlorocebus</i> sp. indet.	KNM-TH 47023	LS (GnJh23)	K3	545–395	M ² , right	
<i>Chlorocebus</i> sp. indet.	KNM-TH 47131	GnJh15	K3 immediately below K4	509–395, closer to 395	Proximal humerus, left	Weathered with small expansion cracks
<i>Chlorocebus</i> sp. indet.	KNM-TH 45978	Loc. 3C	K3 below Grey Tuff	545–509	Femur, nearly complete, left	Greater trochanter eroded; condyles missing
<i>cf. Chlorocebus</i>	KNM-TH 47026	LS (GnJh23)	K3 below Grey Tuff	545–509	2nd caudal vertebra	
<i>Theropithecus oswaldi leakeyi</i>	KNM-BK 45609	BKS	K3 above Grey Tuff	509–395	Cranium, male, partial	Neurocranium and partial face; robust muscular attachments
<i>Theropithecus oswaldi leakeyi</i>	KNM-BK 47049	MAS (GnJh19)	K3 below Grey Tuff	545–509	Frontal bone, partial	

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 (from Blegen et al. 2018; Cornelissen et al. 1990; McBrearty et al. 1996; Tryon 2003. ND = no data) (continued).

Genus and species	KNM specimen number	Site	Stratigraphic position	Estimated age (ka)	Element(s)	Comments
<i>Theropithecus oswaldi leakeyi</i>	KNM-TH 22638	HMS (GnJh21)	Probably K3 below Grey Tuff	545–509	Mandible, male, complete, in three pieces	Heavily worn anterior teeth
<i>Theropithecus oswaldi leakeyi</i>	KNM-TH 47030	LS (GnJh23)	K3 below Grey Tuff	545–509	C ¹ , partial, right	Cusp tip broken postmortem; probable male, but small
<i>Theropithecus oswaldi leakeyi</i>	KNM-TH 46357	Loc. 10 (GnJh45)	K3'	545–395	P ⁴ , right	
<i>Theropithecus oswaldi leakeyi</i>	KNM-TH 47029	LS (GnJh23)	K3 below Grey Tuff	545–509	C ₁ , male, right	
<i>Theropithecus oswaldi leakeyi</i>	KNM-TH 46353	ND	ND	<790	P ₄ , right	
<i>Theropithecus oswaldi leakeyi</i>	KNM-TH 47028	Loc. 18 (GnJh53)	K3 1.15m above K2	545–509, closer to 545	M ₁ , left	
<i>Theropithecus oswaldi leakeyi</i>	KNM-TH 47132	GnJh17	K3	545–395	Femur, proximal, right	Badly cracked and partially repaired; missing trochanters
cf. <i>Papio</i>	KNM-TH 47036	ND	"Middle Kapth"	545–395	I ¹ , crown, right	
cf. <i>Papio</i>	KNM-TH 47046	Loc. 25 (GnJh58)	K3 below Grey Tuff	545–509	I ¹ , crown, left	Root not fully formed; probably associated with KNM-TH 47051
cf. <i>Papio</i>	KNM-TH 47051	JKS (GnJh20)	K3 below Grey Tuff	545–509	M ₁ , right	Unerupted molar probably associated with KNM-TH 47046

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(from Blegen et al. 2018; Cornelissen et al. 1990; McBrearty et al. 1996; Tryon 2003. ND = no data) (continued).

Genus and species	KNM specimen number	Site	Stratigraphic position	Estimated age (ka)	Element(s)	Comments
<i>Colobus</i> sp. indet.	KNM-BK 42141	Loc. 3 (GnJh39)	K3 Below Grey tuff	545–509	Cranium, nearly complete, male	Complete dentition
<i>Colobus</i> sp. indet.	KNM-BK 62	ND	K3 below Grey Tuff	545–509	Maxilla, right, with C ¹ -M ² present, and associated mandible	Mandibular rami broken
<i>Colobus</i> sp. indet.	KNM-TH 46347	MS (GnJh31)	K3 below Grey Tuff	545–509	Maxilla, partial, with P ³ -M ³ present bilaterally	
<i>Colobus</i> sp. indet.	KNM-TH 47127	JKS (GnJh20)	K3 below Grey Tuff	545–509	Mandible, partial, female, right, with P ₃ -P ₄ and partial M ₁	
<i>Colobus</i> sp. indet.	KNM-BK 56	EKG (GnJh1)	Probably K3 above Grey Tuff	509–395	Mandible, partial, male, C ₁ -P ₄ , M ₂ -M ₃ present	Teeth heavily worn; very old individual
<i>Colobus</i> sp. indet.	KNM-TH 46355	Loc. 2 (GnJh38)	K3 above Grey Tuff	509–395	Mandible, partial, and associated teeth	With small bone fragments
<i>Colobus</i> sp. indet.	KNM-TH 46356	BKS	K3	545–395	Mandible, partial, left, with M ₂	Ramus and condyle preserved

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 (from Blegen et al. 2018; Cornelissen et al. 1990; McBrearty et al. 1996; Tryon 2003. ND = no data) (continued).

Genus and species	KNM specimen number	Site	Stratigraphic position	Estimated age (ka)	Element(s)	Comments
<i>Colobus</i> sp. indet.	KNM-TH 47048	MAS (GnJh19)	K3 below Grey Tuff	545–509	Mandible (juvenile), partial, right, dM ₁ -M ₁ present	M ₂ in crypt
<i>Colobus</i> sp. indet.	KNM-TH 47128	Loc. 38	K3 below Grey Tuff	545–509	Mandible, partial, juvenile, right, dI ₁ -dI ₂ present	dC ₁ broken at cervix
<i>Colobus</i> sp. indet.	KNM-TH 47126	JKS (GnJh20)	K3 below Grey Tuff	545–509	M ₂ , crown, right	
<i>Colobus</i> sp. indet.	KNM-TH 47129	MAS (GnJh19)	K3 below Grey Tuff	545–509	dM ₂ , crown, left	With partial roots
<i>Colobus</i> sp. indet.	KNM-BK 57	ND	ND	<790	Mandible, partial, right, with M ₁ -M ₃	
<i>Colobus</i> sp. indet.	KNM-TH 47036	LS (GnJh23)	K3 below Grey Tuff	545–509	Mandible, fragments, left, with M ₂ -M ₃ in main fragment	
<i>Colobus</i> sp. indet.	KNM-TH 47031	LS (GnJh23)	K3 below Grey Tuff	545–509	C ¹ , tip, right	
<i>Colobus</i> sp. indet.	KNM-TH 47055	Loc. 2 (GnJh38)	K3 Below grey tuff	545–509	P ⁴ , left	
<i>Colobus</i> sp. indet.	KNM-BK 58	ND	ND	<790	M ₃ , right	
<i>Colobus</i> sp. indet.	KNM-TH 47043	LS (GnJh23)	K3 below Grey Tuff	545–509	P ₄ , left, male	Heavily worn
<i>Colobus</i> sp. indet.	KNM-TH 46354	Loc. 3 (GnJh39)	K3 Below grey tuff	545–509	P ₄ , crown, left	

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(from Blegen et al. 2018; Cornelissen et al. 1990; McBrearty et al. 1996; Tryon 2003. ND = no data) (continued).

Genus and species	KNM specimen number	Site	Stratigraphic position	Estimated age (ka)	Element(s)	Comments
<i>Colobus</i> sp. indet.	KNM-BK 61	ND	ND	<790	M ₂ , right	
<i>Colobus</i> sp. indet.	KNM-TH 47035	Loc. 25 (GnJh58)	K3	545–395	M ₂ , crown, left	
<i>Colobus</i> sp. indet.	KNM-TH 47042	LS (GnJh23)	K3 below Grey Tuff	545–509	M ₂ , partial, left	Protolophid only
<i>Colobus</i> sp. indet.	KNM-TH 46358	JKS (GnJh20)	K3 Below grey tuff	545–509	M ₃ , crown, left	
<i>Colobus</i> sp. indet.	KNM-TH 47040	LS (GnJh23)	K3 below Grey Tuff	545–509	dM ² , right	
<i>Colobus</i> sp. indet.	KNM-TH 47032	Loc. 4	K3 below Grey Tuff	545–509	Humerus, proximal, left	
<i>Colobus</i> sp. indet.	KNM-TH 46346	LS (GnJh23)	K3 below Grey Tuff	545–509	Metacarpal III	
<i>Colobus</i> sp. indet.	KNM-TH 47037	LS (GnJh23)	K3 below Grey Tuff	545–509	Proximal manual phalanx IV, left	
<i>Colobus</i> sp. indet.	KNM-TH 47033	LS (GnJh23)	K3 below Grey Tuff	545–509	Proximal manual phalanx V, left	
Colobinae gen. et sp. indet.	KNM-TH 47041	LS (GnJh23)	K3 below Grey Tuff	545–509	I ¹ , left	Heavily worn
Colobinae gen. et sp. indet.	KNM-TH 47044	LS (GnJh23)	K3 below Grey Tuff	545–509	C ₁ , female, right	Very small
Colobinae gen. et sp. indet.	KNM-TH 47045	LS (GnJh23)	K3 below Grey Tuff	545–509	M ³ , left	Possibly associated with KNM-TH 47044
Colobinae gen. et sp. indet.	KNM-TH 46351	Loc. 55	K3 Below grey tuff	545–509	Humerus, distal, left	In three pieces

TABLE 1. SITE LOCATIONS AND ESTIMATED AGES SUMMARIZED

(from Blegen et al. 2018; Cornelissen et al. 1990; McBrearty et al. 1996; Tryon 2003. ND = no data) (continued).

Genus and species	KNM specimen number	Site	Stratigraphic position	Estimated age (ka)	Element(s)	Comments
Colobinae gen. et sp. indet.	KNM-TH 46359	Loc. 2 (GnJh38)	K3 Below grey tuff	545–509	Femur, proximal shaft, left	In two pieces
Colobinae gen. et sp. indet.	KNM-BK 55	EKG (GnJh1)	Probably K3 above Grey Tuff	509–395	Femur, shaft, left	
Cercopithecidae indet.	KNM-BK 59	ND	ND	<790	Calvaria, fragment	
Cercopithecidae indet.	KNM-BK 60	ND	ND	<790	Cranial fragment	
Cercopithecidae indet.	KNM-TH 47025	MS (GnJh31)	K3 below Grey Tuff	545–509	Cranial fragments, juvenile	Parial left temporal; pieces of parietal and occipital squama
Cercopithecidae indet.	KNM-TH 47050	Loc. 39	K4	395–198	Calvaria fragment	
Cercopithecidae indet.	KNM-TH 47047	Loc. 25 (GnJh58)	K3 below Grey Tuff	545–509	Molar fragment	

men is mostly complete, but slight crushing of the frontal bone during fossilization has resulted in the orbits of the specimens being compressed inferiorly and expanded laterally, especially on the right side. On both sides, the bodies of the zygomatics are preserved. On the left, the zygomatic root of the zygomatic arch is intact, but neither arch has been preserved. The palate is mostly complete and undistorted, save for the rostral margin of the incisive foramina, which has been lost. On the cranial base, the body of the sphenoid has been slightly crushed and displaced to the left. The sphenoccipital synchondrosis appears to have been not completely fused, but its connection to the basilar portion of the occipital is intact. The rostral portion of the calvaria only is preserved; all of the parietal and occipital bones are missing. The small portion of the frontoparietal suture that is preserved on the right is slightly open. This evidence, the absence of a sagittal crest, and the absence of complete fusion of the sphenoccipital synchondrosis support the status of KNM-BK 42140 as a younger full adult.

The male status of KNM-BK 42140 is clearly indicated by the large size of the bases of the C's and the fairly prominent canine pillars on the rostral surface of the muzzle and the prominent temporal lines. Despite the slight deformation the specimen has suffered, the morphology of its facial skeleton mark it as a probable vervet, complete with a short, narrow muzzle, a moderately deep posterior maxilla, a narrow interorbital region composed of long, evenly sloping nasal bones, inverted trapezoidal orbits, and a lightly built supraorbital torus. The nasal aperture is small and faintly heart-shaped. The superior surface of the frontal bone is smooth, and exhibits virtually no postglabellar sulcus. The temporal lines are slightly raised, but do not meet to form a sagittal crest. The bodies of the zygomatics are deep and flat, and bear two large infraorbital foramina bilaterally. Large zygomaticofacial foramina are observed on both sides. The palate is very deep with a flattened arch; on its posterior aspect, deeply excavated greater palatine foramina are observed. The cranial distinctions of *Chlorocebus* and

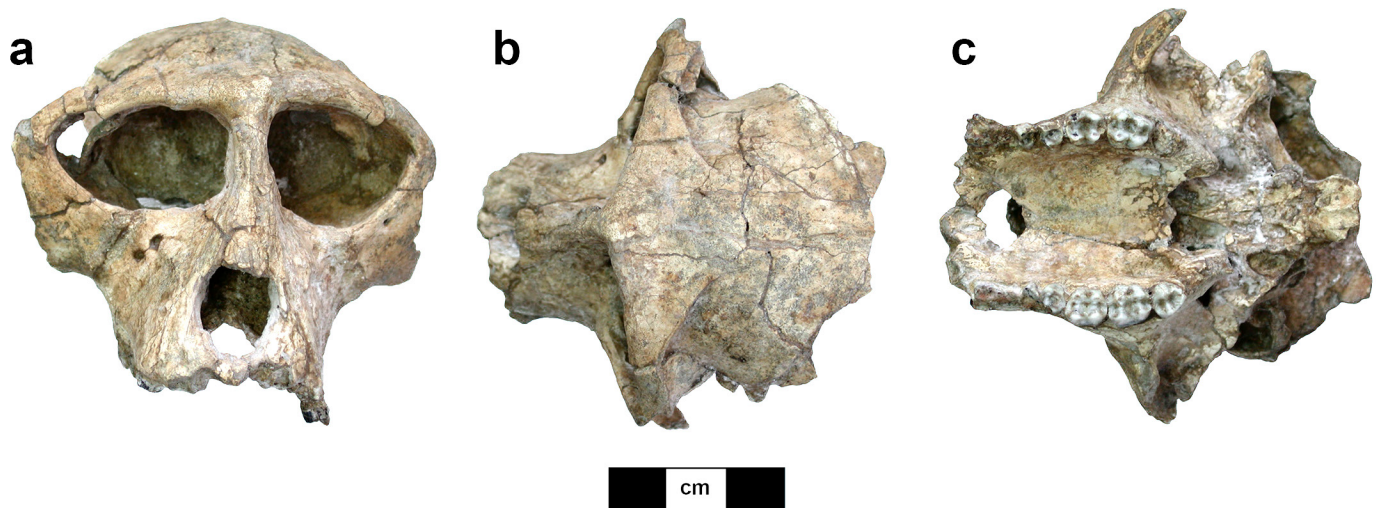


Figure 1. KNM-BK 42140. *Chlorocebus* sp. indet. *pygerythrus* male cranium. a) frontal view; b) vertical view; and, c) basal (occlusal) view.

a complete discussion of the diagnostic cranial features of *Chlorocebus* species have been provided by a recent review written to support the description of a new species of *Chlorocebus* from Tanzania (Arenson et al. 2022). The specimen is assigned to *Chlorocebus* sp. indet.. Its similarities to the modern vervet, *Ch. pygerythrus*, warrant further comparative study. The morphology of its individual teeth and the bell shape of its upper dental arcade closely resemble those of the vervet. The bell shape of the palate and maxillary dental arcade is seen in larger male vervet individuals because of the large size of the canine and its alveolus; behind this feature the maxilla is constricted around the diminutive P^3 , narrowing the palate before it broadens at the level of the molars. This morphology is illustrated in the comparative illustrations provided in two recent works on fossil *Chlorocebus* from Ethiopia and Tanzania (Arenson et al. 2022; Taylor et al. 2023). The molars KNM-BK 42140 are typical of those of most guenons in being small and bunodont, with low cusps and relatively large crushing basins. The molars display an even mesial to distal wear gradient, and the third molars—especially the distal loph/ids—in both the maxilla and mandible are reduced in size. Measurements of KNM-BK 42140 are provided in Table 2.

KNM-BK 97 (Figure 2): The specimen consists of a nearly complete left C^1 of a male and an adjacent fragment of maxilla bearing the buccal wall of the alveolus of the P^3 and the nearly complete alveolus and root of the P^4 . The C^1 is closely comparable in morphology to that of modern *Ch. pygerythrus*, being very slender and only slightly mesially curved, but a definitive species assignment cannot be made in the absence of more detailed comparative study. The tooth exhibits a deep but narrow developmental groove on its mesial surface. The tip of the C^1 appears to have been broken after fossilization. The measurements of the C^1 are given in Table 3.

KNM-TH 47130: The specimen is a fragment of the right side of the mandible with a complete M_2 and the alveolus of the proximal root of the M_3 . The body of the mandible is shallow. The lingual aspect of the mandibular corpus at the level of the roots of the M_1 is thickened superiorly, as in modern *Ch. pygerythrus*. The enamel of the preserved tooth has been eroded and pock-marked as a result of heavy surface weathering. Portions of the protoconid and hypoconid cusps were also broken *post mortem*. The specimen is larger than the modern species in all dimensions, but is otherwise identical. The measurements of M_2 are provided given in Table 3. The depth of the mandibular corpus at M_2 = 15.13 mm; and the thickness of the mandibular corpus at M_2 = 6.85 mm.

KNM-TH 47023: The specimen is an isolated right M^2 . The moderate wear of the lingual cusps indicates that the animal was a mature adult at death. The measurements of the specimen are provided given in Table 3.

Postcranial Material

KNM-TH 47131 (Figure 3a-c): The specimen is a proximal left humerus of a large guenon that is irregularly broken at the level of the superior portion of the deltoid crest. The surface of the bone displays numerous expansion cracks and erosion of the cortex due to surface weathering. These features precluded measurement. The morphology of the specimen is consistent with that of the modern vervet and it is classified here as *Chlorocebus* sp. indet.. In posterior view, the articular surface of the humeral head of KHM-TH 47131 has a flattened ovoid shape like *Ch. pygerythrus* and unlike the round shape seen in *Cercopithecus* guenons. The greater tuberosity is large and anteriorly located. Its superior surface is eroded, but it appears to have extended slightly above the level of the head during life, suggesting a condition as described for *Cercopithecus lomamiensis* and *C.*

TABLE 2. MEASUREMENTS (in mm) OF THE MALE CRANIUM OF *CHLOROCEBUS* SP. INDET., KNM-BK 42140.*

Variable	Measurement
C ¹ MDL	6.84
C ¹ BLL	4.35
P ³ MDL	4.04
P ³ BLL	3.99
P ⁴ MDL	4.09
P ⁴ BLL	4.45
M ¹ MDL	6.25
M ¹ BLL (mesial loph)	5.72
M ¹ BLL (distal loph)	5.37
M ² MDL	6.70
M ² BLL (mesial loph)	6.45
M ² BLL (distal loph)	5.62
M ³ MDL	5.14
M ₃ BLL (mesial loph)	5.42
M ³ BLL (distal loph)	3.84
Palatal width	23.16
Upper bicanine breadth	33.51
Upper incisive alveoli breadth	19.57
Piriform aperture height	13.34
Piriform aperture width	12.54
Upper face height	47.03
Maxillary height	23.16
Interorbital width	7.22

*The following conventions have been followed to describe linear measurements of the teeth: MDL denotes mesiodistal length and BLL denotes buccolingual length. All measurements are defined fully elsewhere (Jablonski and Leakey 2008b).

hamlyni in which the shoulder joint is relatively mobile, but slightly restricted (Arenson et al. 2020). The surface of the greater tuberosity is marked with an indentation for the attachment of *m. supraspinatus*. These features, along with the slightly flattened neck, are characteristic of *Ch. pygerythrus* (Nakatsukasa 1994). The intertubercular groove is small, and the lesser tuberosity diminutive.

KNM-TH 45978 (Figure 3d, e): The specimen is a nearly complete left femur, missing only the greater tuberosity and the condyles. The intertrochanteric groove is shallow and indistinct. The shaft is slender and straight, and a thin linea aspera marks the posterior midshaft. The specimen is closely comparable to *Ch. pygerythrus* in morphology, with its short, thick neck, a large elliptical fossa of the head of

the femur, and a nearly round, slightly convexly curved shaft. It is classified here as *Chlorocebus* sp. indet.. It differs from the modern vervet only in its larger size. The diameter of the head is 16.83mm. This is as compared to average for extant *Ch. pygerythrus* as reported by Nakatsukasa of 13.2mm for males (range 11.2–15.0mm) and 11.1mm (range 9.6–12.7mm) for females. The estimated dorsoventral mid-shaft diameter of the fossil is 12.7mm; and the estimated mediolateral mid-shaft diameter is 11.8mm. One of the most functionally diagnostic features of the femur—the greater trochanter—is not sufficiently well preserved to inform the discussion of probable locomotor preference, but the overall similarity in femoral morphology between *Chlorocebus* from the Kapthurin Formation and living *Chloroce-*

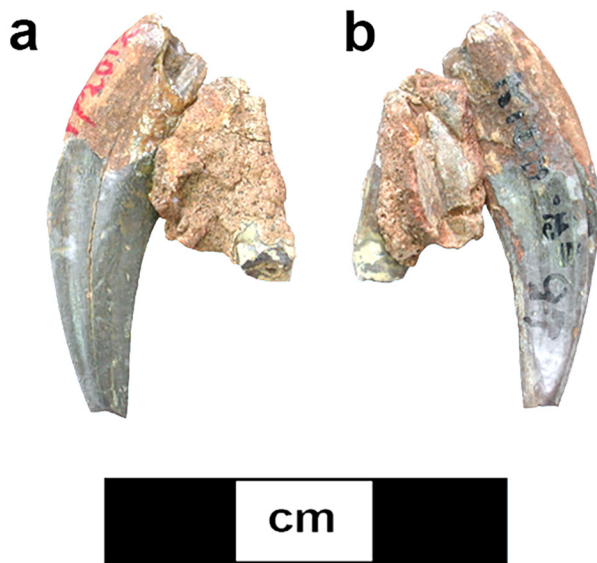


Figure 2. KNM-BK 97. *Chlorocebus* sp. indet. male left C^1 and adjacent fragment of maxilla. a) buccal view; and, b) lingual view.

bus suggests that the fossil was semiterrestrial, as discussed more expansively in the recent study by Arenson and colleagues (2020).

CF. *CHLOROCEBUS*

Kapthurin Formation Material

One specimen, a partial second caudal vertebra (KNM-TH 47026), is referred to cf. *Chlorocebus* on the basis of its morphological similarity to the comparable bone in a living vervet.

Postcranial Material

KNM-TH 47026: The specimen is a second caudal vertebra of a guenon, probably *Chlorocebus*, based on its close morphological similarity to the comparable bone in a living vervet. The rostrocaudal length of its centrum is 13.49mm.

Remarks

The Kapthurin Formation *Chlorocebus* is a slightly larger-bodied version of the modern vervet. The estimated body mass of males (based on the femoral head diameter of KNM-TH 45978) was about 6.5kg, approximately 27% larger than the mean for *Ch. pygerythrus* (Delson et al. 2000). Increases in body mass took place in many mammalian lineages during the Pleistocene, and appear to represent a physiological adaptation to increased seasonality of food resources, even among tropical species (Jablonski et al. 2000). The few postcranial fossils of the species that are available from the Kapthurin Formation are identical in morphology to those modern vervets, indicating that the fossil morph was an agile quadrupedal generalist, equally adept at arboreal climbing and terrestrial scampering. The preserved anatomy of the fossil femur (KNM-TH 45978) of *Chlorocebus* sp. indet. from the Kapthurin Formation lacks the apomorphies associated with high-speed terrestrial running seen in *Ch. patas*.

The previously recognized fossil record for *Chlorocebus* has improved, especially with the description of material from the Early Pleistocene Lower Ngaloba Beds of Laetoli in Tanzania (Arenson et al. 2022) and from the Late Pleistocene site of Halibee in the Middle Awash region of Ethiopia (Taylor et al. 2023). Prior to the publication of the Halibee material, the known fossils of *Chlorocebus* were derived from the Middle Pleistocene of the Afar, in deposits aged 0.6 Ma and younger (Jablonski and Frost 2010). Fossils of *Chlorocebus pygerythrus* very similar to those described here as *Chlorocebus* sp. indet. are known from Asbole (~0.6

TABLE 3. DENTAL MEASUREMENTS (in mm) OF SPECIMENS OF *CHLOROCEBUS* SP. INDET., WITH COMPARISONS TO SPECIES MEANS FOR MODERN *CH. PYGERTHRUS* (formerly *Ch. aethiops*) (from Swindler 2002).*

Specimen	Tooth	Sex	BLL (mesial)	BLL (distal)	MDL
KNM-BK 97	C^1	M	5.19 (m=5.2; range=4.4–6.9)		8.35 (m=7.4; range=6.0–9.2)
KNM-TH 47130	M_2	?	5.39 (male m=5.3; male range=4.8–6.1; female m=5.0; female range=4.6–5.5)	5.27 (male m=5.2; male range=4.1–6.3; female m=4.9; female range=4.6–5.3)	6.88 (male m=6.5; male range=5.8–7.4; female m=6.0; female range=5.7–6.8)
KNM-TH 47023	M^2	?	5.60 (male m=6.5; male range=5.8–7.4; female m=5.9; female range=5.2–6.8)	5.61 (male m=5.8; male range=5.1–6.9; female m=5.4; female range=4.9–5.8)	6.61 (male m=6.5; male range=5.8–7.4; female m=6.0; female range=5.7–6.8)

*Abbreviations as in Table 2.



Figure 3. cf. *Chlorocebus* postcrania. a) KNM-TH 47131. Proximal left humerus, showing expansion cracks and erosion, posterior view; b) same, medial view; c) same, lateral view; d) KNM-TH 45978, partial left femur, anterior view; and, e) same, posterior view.

Ma) and the younger site of Andalee in the Middle Awash (Frost 2007; Frost and Alemseged 2007).

Tribe Papionini (Burnett, 1828)

Genus *Theropithecus* (Geoffroy Saint-Hilaire, 1843)

Theropithecus oswaldi (Andrews, 1916)

***THEROPITHECUS OSWALDI LEAKEYI* (HOPWOOD, 1934)**

Kapthurin Formation Material

Theropithecus o. leakeyi is represented in the Kapthurin Formation by eight craniodental specimens; one more specimen, a partial femur is assigned to *T. aff. oswaldi*. These are archetypal examples of the youngest and largest morph of the species, *T. o. leakeyi*. *Theropithecus oswaldi* is distinguished from other papionins, especially *T. darti*, by its larger size, robust postglenoid processes and greater relative reduction of incisors and canines in relation to larger postcanine dental dimensions (Frost et al. 2022; Jablonski and Frost 2010). Two of the Kapthurin Formation *T. o. leakeyi* specimens are important and remarkable—the partial cranium of a large male, KNM-BK 45609, and the nearly complete mandible of a large male in three pieces, KNM-BK 22638. *Theropithecus oswaldi* presents a unique suite of craniodental morphologies and postcranial features not seen in other papionins past or present that make unequivocal diagnosis of even relatively fragmentary remains possible. These features are discussed at length elsewhere (Eck 1987; Frost et al. 2017; Jablonski et al. 2008a; Jolly 1972). The diagnosis to *T. o. leakeyi* follows that of Getahun et al. (2023).

Craniodental Material

KNM-BK 45609 (Figure 4): The specimen represents the partial cranium of an adult male *Theropithecus o. leakeyi*. Several cranial bone fragments and a portion of one unidentifiable molar tooth are also associated with the specimen. The basicranium posterior to the body of the sphenoid bone is almost completely preserved in good condition. Most of the left side of the calvaria, save for the rostral portion of the parietal and the frontal is preserved; on the right, only the posterior parietal and occipital bones are preserved. The nuchal crest is nearly completely preserved on the right, but only the lateral aspect is preserved on the left. The facial skeleton is mostly missing, except for the left zygomatic arch, which is preserved completely along with most of the body of the left zygoma. The bone is poorly mineralized.

Unequivocal diagnosis of the specimen to *T. oswaldi* is possible on the basis of its highly distinctive calvarial and basicranial morphology. The specimen represents one of the largest and most robust neurocrania of *T. o. leakeyi* to be described to date; only that from the Middle Pleistocene site of Asbole in Ethiopia is comparable (Frost and Alemseged 2007). The specimen is distinguished by its tall sagittal crest, which supported the attachment of *m. temporalis*, and its enormous circumferential nuchal crest, which supported the *m. temporalis* superiorly and the attachment of a robust nuchal musculature inferiorly. Consistent with

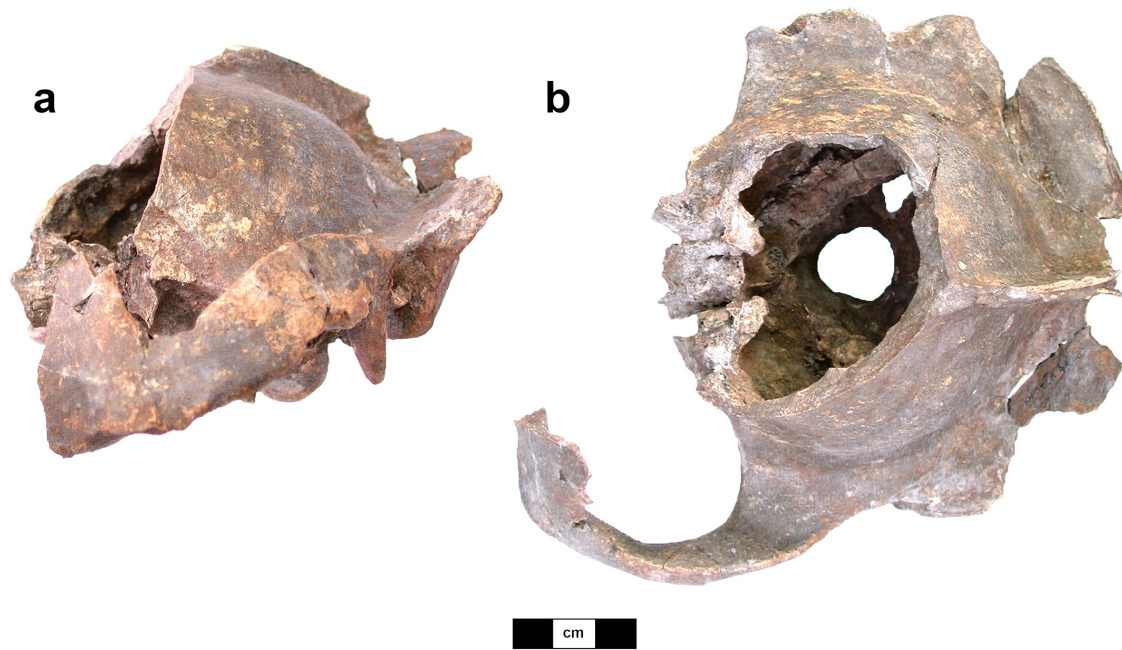


Figure 4. KNM-BK 45609. *Theropithecus o. leakeyi* male cranium. a) left lateral view; and, b) vertical view.

this is the great width and lateral projection of the temporal root of the zygomatic arch, over which the large posterior portion of *m. temporalis* passed. The zygomatic arch itself is extremely robust and exhibits a sinusoidal shape consistent with a very large *m. massetericus superficialis* having exerted considerable tension on the anterior portion of the arch during life. The inferior aspect of the anterior portion of the arch exhibits a shallow groove and a marginal ridge associated with this muscle's origin.

On the basicranium, the specimen exhibits several of the hallmark features of late *Theropithecus oswaldi*, including *T. o. leakeyi*, namely a nearly vertical nuchal plane, extremely robust postglenoid processes, and an anteroposteriorly compressed articular fossa (Jablonski 1993a; Jolly 1972). This morphology is associated with predominantly lateral jaw movements such as those produced during molar chewing, but would not have permitted strong anterior translation of the mandible such as that required in open-mouthed gape displays. Measurements of KNM-BK-45609 are provided in Table 4.

KNM-BK 47049: The specimen represents a partial frontal bone of an adult, which preserves the interorbital region, the glabella, the medial portions of the right and left supraorbital ridges, and the anteriormost portion of the temporal line on the right. This specimen exhibits the characteristic morphology of *Theropithecus oswaldi*, with its relatively broad and upright interorbital region and strong supraglabellar depression. The interorbital breadth=16.61mm.

KNM-BK 22638 (Figure 5): The specimen comprises a nearly complete mandible of a male individual in three pieces, previously figured in another work (Leakey 1993).

The right and left mandibular bodies are preserved separately, and bear the C_1 through the M_3 . The rami of both sides are lacking. A fragment of the mandibular symphysis is also preserved, containing all of the lower incisors. The specimen was temporarily reconstructed for purposes of photography.

KNM-BK 22638 represents a typical late *T. o. leakeyi*, with small, peg-like incisors, short, stubby canines, highly molarized premolars, and very large molars (especially M_3). The specimen exhibits the extremely steep mesial-to-distal molar wear gradient typical of the species, that is, a nearly functionally obsolescent M_1 coupled with a nearly unworn M_3 on both sides. The specimen does not exhibit the reversed Curve of Spee typical of the genus, probably because of the extremely heavily worn state of the M_1 . The body of the mandible is evenly deep under the premolars and molars and is very thick, especially at the level of the M_2 and M_3 .

In its size, dental proportions, and morphology, this specimen is most closely comparable to those from Bed IV and Masek Beds at Olduvai, including the holotype, NHMUK-P M14680 (Getahun et al. 2023). Measurements of KNM-BK 22638 are provided in Table 5, along with comparative data from *T. oswaldi* from the Okote Member of Koobi Fora that clearly illustrate the change in dental proportions within the species from the Early to Middle Pleistocene.

KNM-TH 47030 (Figure 6a, b): The specimen represents the complete root and the base of the crown of a right C^1 of an adult male. The specimen exhibits the hallmark features of late *T. oswaldi* canines—a thick stubby, “cigar-

TABLE 4. MEASUREMENTS (in mm) OF KNM-BK 45609, *THEROPITHECUS OSWALDI LEAKEYI* MALE PARTIAL CRANIUM.

Variable	Measurement
Biporionic width	125.86
Midparietal width	66.71
Bizygomatic width	160.00
Temporal fossa width	42.89
Zygomatic arch height	19.98
Bimastoid breadth	134.49
Occipital height	44.46
Foramen magnum length	21.57
Foramen magnum width	20.12
Posterior basicranium length	67.90
Articular fossa length	20.37
Articular fossa width	36.36
Length from the scar of <i>m. massetericus superficialis</i> to the postglenoid process	77.07

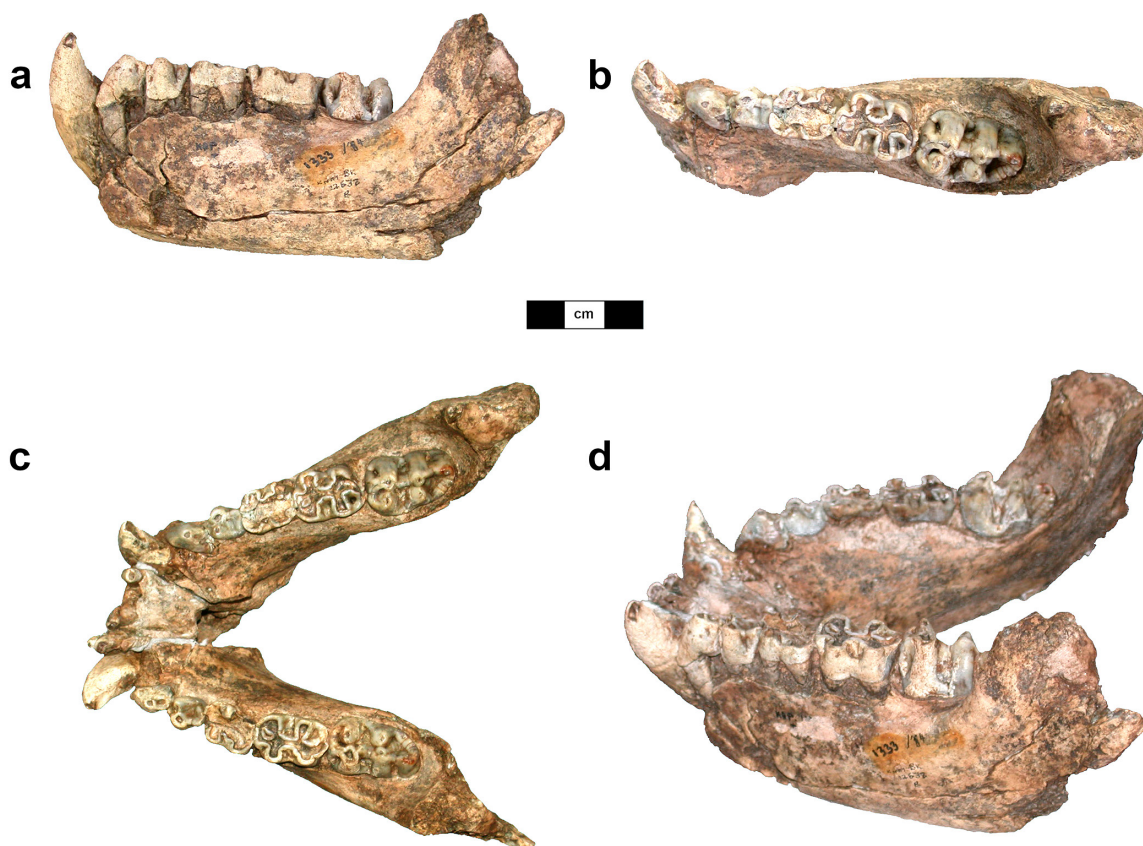


Figure 5. KNM-BK 22638. *Theropithecus o. leakeyi* male mandible. a) left hemimandible, lateral view; b) same, vertical (occlusal) view; c) whole specimen, re-assembled for photography only, vertical (occlusal) view; and, d) same, oblique view emphasizing large relative size of distal molars.

TABLE 5. MEASUREMENTS (in mm) OF KNM-TH 22638, *THEROPITHECUS OSWALDI LEAKEYI* MALE MANDIBLE, COMPARED TO MEAN MEASUREMENTS FOR *T. OSWALDI* FROM THE OKOTE MEMBER OF THE KOOBI FOR A FORMATION (based on data presented elsewhere: Jablonski et al. 2008).*

Variable	Measurement of KNM-TH 22638	<i>T. oswaldi</i> Okote Fm. Mean
I ₁ MDL	4.82	
I ₁ BLL	5.71	
I ₂ MDL	4.00	
I ₂ BLL	5.44	
C ₁ MDL	9.66	10.9 (range: 9.5–10.4; n=4)
C ₁ BLL	13.60	16.2 (range: 15.0–17.1; n=4)
P ₃ MDL	12.01	16.5 (range: 15.4–17.5; n=3)
P ₃ BLL	9.18	7.4 (range: 6.4–9.4; n=3)
P ₄ MDL	10.82	9.2 (range: 7.9–10.1; n=3)
P ₄ BLL	9.37	8.6 (range: 7.8–9.5; n=3)
M ₁ MDL	14.22	14.7 (n=1)
M ₁ BLL (mesial)	11.88	11.7 (n=1)
M ₁ BLL (distal)	12.52	11.1 (n=1)
M ₂ MDL	18.95	17.8 (range: 15.8–19.7; n=5)
M ₂ BLL (mesial)	14.15	12.9 (range: 11.8–13.9; n=5)
M ₂ BLL (distal)	13.94	12.8 (range: 11.5–14.6; n=5)
M ₃ MDL	24.27	21.2 (range: 19.8–24.0; n=3)
M ₃ BLL (mesial)	15.75	13.0 (range: 12.1–14.0; n=3)
M ₃ BLL (distal)	14.02	12.2 (range: 11.4–13.5; n=3)
C ₁ to M ₃ length	90.46	
P ₃ to M ₃ length	77.83	69.8 (n=1)
P ₄ to M ₃ length	66.07	
M ₁ to M ₃ length	57.86	47.7 (n=1)
Mandibular corpus height	39.99	39.2 (range: 36.0–45.7; n=3)
Mandibular corpus width at M ₁	20.92	15.8 (range: 13.3–17.1; n=3)
Mandibular corpus width at M ₂	23.18	18.4 (range: 14.8–20.4; n=3)

*Abbreviations as in Table 2.

butt-shaped” root supporting a diminutive crown (Jablonski 1993a, b; Jolly 1972). Measurements of the specimen are provided in Table 6.

KNM-TH 46357: The specimen is an isolated, complete right P⁴ with a highly molarized form typical of that of the species. The cusps are moderately worn, and there is little occlusal relief to describe. The roots of the tooth are embedded in medium brown sandstone matrix. Measurements of the specimen are provided in Table 6.

KNM-TH 47029 (Figure 6c-e): The specimen represents an isolated but complete right C₁ of an adult male. It is typical of *T. oswaldi* in displaying an extremely robust, non-tapering root upon which a relatively narrow and lightly

built crown is hafted. This specimen is unusual in that it exhibits evidence of probable dental caries on the enamel of its mesial surface. The crown of the tooth is lightly worn. Measurements of the specimen are provided in Table 6.

KNM-TH 46353: The specimen represents the isolated, moderately worn crown of a right P₄. Measurements of the specimen are provided in Table 6.

KNM-TH 47028: The specimen represents a moderately worn left M₁. The tooth is typical of that of a younger adult *T. oswaldi* in that it exhibits the typical “hourglass” wear figure created by deep infoldings of enamel surrounding a large irregular dumbbell-shaped lake of dentine. Measurements of the specimen are provided in Table 6.

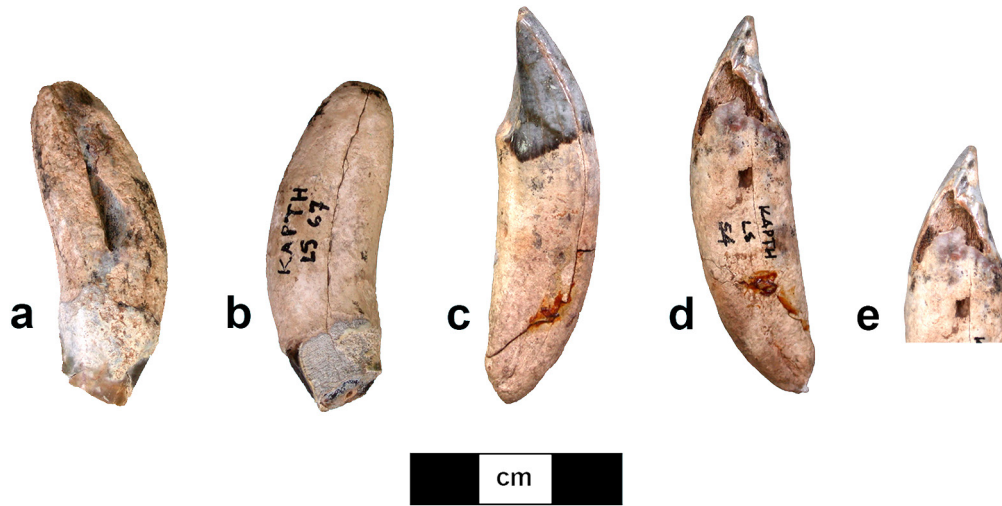


Figure 6. *Theropithecus o. leakeyi* isolated teeth. KNM-TH 47030. a) Male right C^1 , labial view; b) same, and lingual view; c) KNM-TH 47029. Male right C_1 , labial view; d) same, lingual view; and, e) same, close-up of caries on lingual aspect.

THEROPITHECUS CF. OSWALDI

Kapthurin Formation Material

Postcranial Material

KNM-TH 47132: The specimen is a partial proximal femur and proximal femoral shaft. The trochanters and a portion of the distal margin of the head are missing. The specimen was badly damaged by weathering and cracking, and required extensive gluing. Despite this, the specimen is likely that of a large *T. oswaldi*. The overall morphology of the femoral shaft and the magnitude and orientation of the *linea aspera*, in particular, are similar to those of *T. oswaldi* from the Okote Member of the Koobi Fora Formation, and to the femur of the undescribed partial skeleton of *T. o. leakeyi* (formerly referred to as *T. o. jonathani*) from Olduvai Upper Bed II (MCK II). The diameter of the head of KNM-TH 47132 can be estimated at 27.4mm.

Remarks

The partial male cranium, KNM-BK 45609, and male man-

dible, KNM-BK 22638, are among the most well-preserved specimens of late *T. o. leakeyi* known and are comparable in morphology to those described from the Daiwaitoli Formation (Frost 2007) and Asbole, Ethiopia (Frost and Alemseged 2007). The massiveness of the masticatory musculature, the size and occlusal complexity of the distal molars, and the diminutive size of the canines denote an anatomy devoted to the chewing of large amounts of fibrous and/or abrasive vegetation. The metric comparisons between the specimens of *T. o. oswaldi* from the Okote Formation and *T. o. leakeyi* from the Kapthurin Formation in Table 5 highlight the differences in dental proportions between late Early Pleistocene and the Middle Pleistocene representatives of the species. The Okote Formation *T. o. oswaldi* exhibit absolutely and relatively larger canines and P_3 s as compared to the Kapthurin Formation species (exemplified by KNM-BK 22638), but the Kapthurin Formation *Theropithecus* is absolutely and relatively larger in distal molar dimensions. The body mass of *T. o. leakeyi* from the Kapthurin Formation has been estimated at 58kg (Delson et al. 2000). *Theropithecus o. leakeyi* is now recognized from Middle Pleistocene sites

TABLE 6. MEASUREMENTS (in mm) OF ISOLATED TEETH OF *THEROPITHECUS OSWALDI LEAKEYI*.*

Specimen	Tooth	Sex	BLL (mesial)	BLL (distal)	MDL
KNM-TH 47030	C^1	M	10.42		14.00
KNM-TH 46357	P^4	?	10.00		9.07
KNM-TH 47029	C_1	M	8.23		13.47
KNM-TH 46353	P_4	?	8.83		10.29
KNM-TH 47028	M_1	?	11.64	11.09	14.60

*Abbreviations as in Table 2.

across the length and breadth of Africa, and possibly also in Spain and India, making it one of the most successful of nonhuman primate dispersal morphs (Geraads and de Bonis 2020; Getahun et al. 2023; Gibert et al. 1995). The *Theropithecus o. leakeyi* from the Kapthurin Formation is probably the geologically youngest known representative of the *T. oswaldi* lineage of “giant geladas,” the moniker coined by Clifford Jolly (1972). This makes the representatives of *T. o. leakeyi* from the Kapthurin Formation as likely contenders for the last appearance datum (LAD) of the species. This is an important biochronological watershed for the history of the genus and for the understanding of the emergence of the modern eastern African fauna (Frost et al. 2022; Getahun et al. 2023).

Tribe Papionini (Burnett, 1828)
Genus *Papio* (Müller, 1773)

CF. *PAPIO* (LINNAEUS, 1758)

Kapthurin Formation Material

Three teeth from the Kapthurin Formation—two central incisors and one lower molar—are assigned to cf. *Papio* sp. indet. because they are comparable in morphology to those of the modern common baboon. Assignment of a definite species or subspecies attribution to isolated fossil *Papio* teeth is not advisable because of the great similarities in dental morphology among living common baboons and their Late Pleistocene relatives (Brasil et al. 2023b), but the morphology of all three of the Kapthurin Formation dental specimens is consistent with that of the modern anubis baboon.

Craniodental Material

KNM-TH 47036 (Figure 7a, b): The specimen is a right I¹ crown which bears signs of etching caused by surface weathering. An assignment to modern cf. *Papio* is suggested on the basis of the large size, broad spatulate form, and V-shaped lingual tubercle of the incisor. The tooth is lightly worn. Measurements of the specimen are provided in Table 7.

KNM-TH 47046 (Figure 7c, d): The specimen comprises the crown of a right I¹, with a broken root. It is probably associated with the unerupted lower first molar crown, KNM-TH 47051, described below. The light wear stage of the tooth denotes that the individual was a juvenile at the time of death. The attribution to cf. *Papio* is likely on the basis of its large size, strongly spatulate crown morphology, and prominent lingual tubercle. The measurements of the specimen are provided in Table 7.

KNM-TH 47051 (Figure 7e): The specimen is the unworn and unerupted crown of a right M₁. The morphology and wear stage indicate that it was from the same individual as KNM-TH 47046 described above. The bunodont and puffy-sided morphology of the tooth strongly suggests its attribution to cf. *Papio*. The measurements of the specimen are provided in Table 7.



Figure 7. cf. *Papio* isolated teeth. a) KNM-TH 47036. Right I¹, labial view; b) same, lingual view; c) KNM-TH 47046. Left I¹, labial view; d) same, lingual view; e) KNM-TH 47051. Right M₁, unerupted crown, occlusal view; f) same, lingual view; and, g) same, buccal view.

Remarks

The cf. *Papio* fossils from the Kapthurin Formation are sufficient to establish presence of the genus from the Formation, but little else. Detailed comparisons of these teeth to those of modern *Papio*, particularly to the modern anubis baboon, are warranted.

Subfamily Colobinae (Jerdon, 1867)
Genus *Colobus* (Illiger, 1811)

COLOBUS SP. INDET. (RÜPPELL, 1835)

Kapthurin Formation Material

Colobus sp. indet. is represented in the Kapthurin Formation by several important specimens, the most complete of which is a male partial cranium (KNM-BK 42141), a female upper face (KNM-BK 62), and an associated male partial maxilla and mandible (KNM-TH 46347). Apart from these specimens, the collection of *Colobus* material from the Kapthurin Formation consists of fragments of jaws and isolated teeth. The Kapthurin Formation specimens of *Colobus* are morphologically closely comparable to modern *C. guereza*, but are generally smaller than any of the known species, including *C. freedmani* from Koobi Fora.

Craniodental Material

KNM-BK 42141 (Figure 8): The specimen represents the partial cranium of an adult male. The maxilla, palate, circumnasal region, and cranial base are mostly well preserved and undistorted. The maxillary premolars and molars on both sides are in pristine and virtually unworn condition. The top of the cranium was crushed before or

TABLE 7. MEASUREMENTS (in mm) OF ISOLATED TEETH OF *CF. PAPIO*, WITH COMPARISONS TO SPECIES MEANS FOR MODERN *P. CYNOCEPHALUS* (from Swindler 2002).

Specimen	Tooth	Sex	BLL (mesial)	BLL (distal)	MDL
KNM-TH 96	I ¹	?	9.35 (male m=9.3; male range=6.0–10.7; female m=8.4; female range=7.3–9.6)		10.73 (male m=10.7; male range=9.0–13.3; female m=9.8; female range=7.4–11.7)
KNM-TH 47046	I ¹	?	8.20 (comparisons same as previous specimen)		10.57 (comparisons same as previous specimen)
KNM-TH 47051	M ₁	?	8.10 (male m=8.3; male range=7.6–9.4; female m=7.7; female range=6.7–8.9)	8.16 (male m=8.8; male range=7.8–10.1; female m=8.1; female range=7.4–9.0)	10.95 (male m=10.8; male range=9.7–11.7; female m=10.1; female range=9.5–11.1)

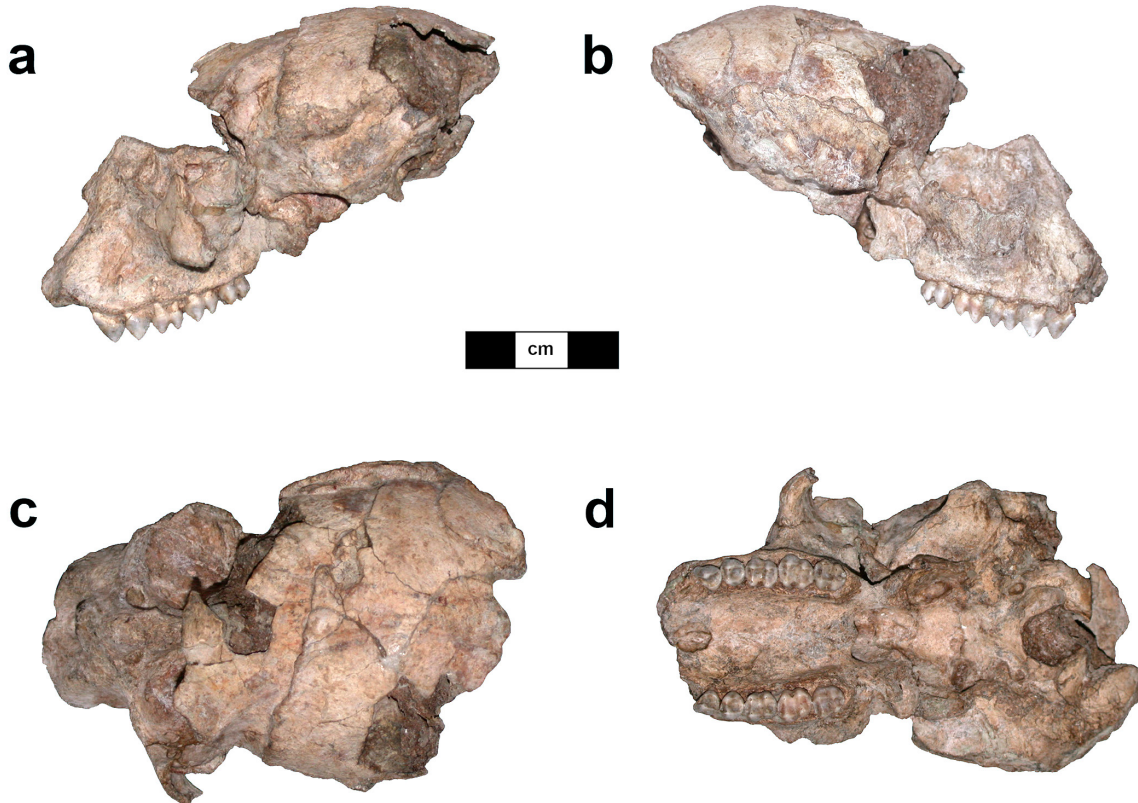


Figure 8. KNM-BK 42141. *Colobus* sp. indet., male partial cranium. a) left lateral view; b) right lateral view; c) vertical view; and, d) basal (occlusal) view.

during fossilization, resulting in the loss of the supraorbital region and flattening of the calvaria. The rostral portions of the right and left premaxillae and right maxilla are missing, resulting in a loss of the alveoli of the C¹ and I¹-I² on the right and of the I¹ on the left. On the right side of the cranium, the frontal and zygomatic bones are entirely missing, so that only the inferomedial margin of the orbit is preserved. The parietal bone has been fractured in several places, with fragments displaced inferiorly and posteriorly. On the left side of the facial skeleton, the supraorbital torus of the frontal bone and the orbital process of the zygomatic bone are missing, leaving approximately the inferior half of the orbital margin intact. On the left side of the calvaria, the posterior portion of the parietal squama is missing as is the squamous portion of the occipital bone on the left and around the inion. The basioccipital on the left and at the midline is mostly missing, resulting in the loss of most of the nuchal plane and rendering the margin of the foramen magnum deficient posteriorly. The sphenoid side of the sphenoccipital synchondrosis appears to have been thrust slightly over the occipital side during fossilization, possibly because the joint was not fully ossified at the time of death.

In all preserved portions of its anatomy, the specimen represents a colobus monkey, and is similar in its details to the modern black and white colobus monkey of Kenya, *Colobus guereza*. The large size of the C¹ alveolus preserved on the left side and the prominent canine pillar over the surface of the C¹ root clearly indicate that the specimen was a male. The craniodental anatomy of modern *Colobus guereza* and of KNM-BK 42141 differ from that of the red colobus, *Piliocolobus badius*, and the green colobus, *Procolobus verus*, in the absence of a median sagittal mental foramen on the mandible, a higher and thicker mandibular body in full adults, relatively larger and puffer cheek teeth, a M₃ with five (exceptionally 6) distinct cusps, and a slight cingulum on the lingual aspect of the incisors (Swindler 2002).

The undistorted portions of the facial skeleton preserved are closely similar to that of present-day *Colobus*, featuring a relatively shallow maxilla and the maxillary root of the zygomatic arch rising above the M². The preserved portion of the left zygomatic arch suggests a flat and broad cheek area. There appear to have been two small infraorbital foramina located immediately below the inferior orbital margin on the left, and one larger foramen on the right. The muzzle is square in cross-section, largely because of the prominence of the canine eminences on the muzzle dorsum. The palate is deep and is broadest at the level of the fourth premolar and first molar. Apart from the prominent incisive foramina, the palatine foramina are not evident.

The specimen differs slightly from modern *Colobus* in the conformation of the nasal region and in the morphology of the P³s. In KNM-BK 42141, the nasal aperture is small and inverted-tear-shaped, and the nasal bones are long and appear to have sloped gently and linearly from caudal to rostral. These conditions contrast to those in modern *Colobus* where the nasal aperture exhibits a long, narrow elliptical form and the nasal bones are more abbreviated. The

P³s of KNM-BK 42141 are strongly caniniform, to a greater extent even than modern *Colobus* males with very large C¹s. Variability in the size of the canine complex in male (as well as female) colobus monkeys is well-known and appears to be related to social organization and predator deterrence (Hayes et al. 1996). It is unfortunate that the small size of the sample of fossil *Colobus* does not permit speculation on the variability in this complex in the past. Measurements of KNM-BK 42141 and those of modern male *C. guereza* are presented in Table 8.

KNM-BK 62 (Figure 9): The specimen represents a portion of the upper facial skeleton of a female, with a nearly complete upper dentition. The premolars and molars are well preserved on both sides, but the crowns of the C¹ and I¹-I² have been lost. The posterior margins of the maxillae, the floor of the right orbit, and most of the palatal surface are obscured by a dense, grey-beige siltstone. The left maxilla has been displaced posteriorly during fossilization. This has rendered the palate and nasal aperture asymmetrical, but the maxillae themselves are relatively undistorted. The maxillary root of the zygomatic arch is preserved on the left but not the right.

The very small size of the base of the C¹ and its root clearly indicate that KHM-BK 62 was a female. The lingual cusps of the molar teeth are slightly and evenly worn, exposing small dentinal lakes. The maxilla of the specimen closely resembles that of a modern female *Colobus guereza* in being relatively shallow with the zygomatic arch rising superior to the M¹-M². There appear to have been two infraorbital foramina located immediately below the inferior orbital margin on the left; the number present on the right cannot be discerned. Measurements of KNM-BK 62 are provided in Table 8.

KNM-TH 46347 (Figure 10): The specimen represents an associated male partial right maxilla and partial mandible together with several nondescript bone fragments. The partial maxilla and small attached portion of the premaxilla support the broken crowns of the right I¹-I², and the C¹ through the M². The tip of the C¹ is broken off, but the cheek teeth are in good condition—except for a light covering of calcareous matrix on the lingual surfaces—and are virtually unworn. The small portion of the premaxilla preserved includes the right inferior margin of the nasal aperture. The adjacent rostral and orbital portions of the maxilla are mostly missing, except for the dental alveoli. The palatal portion of the maxilla is preserved nearly to the midline, but is deficient posterior to the level of the M². The palate appears to have been deep and somewhat arched. The mandible is represented by the rostral portion of the bone. The symphysis of the mandible and most of the mandibular body on the left side are complete and undistorted; the mandibular body on the right is missing posterior to the level of the M₂ and has been compressed slightly toward the midline. On the left, the I₁-I₂ and C₁ are present but their crowns are not well preserved or measurable. The left P₃, P₄, and M₁ are present, but the lingual aspects of the bases of the premolars have been slightly abraded; the mesial lophid only of the left M₂ is present. On the right side,

TABLE 8. MEASUREMENTS (in mm) OF CRANIODENTAL REMAINS OF *COLOBUS* SP. INDET.*

Variable	KNM-BK 42141	KNM-BK 62	KNM-TH 46347	KNM-TH 47127	<i>C. g. occidentalis</i> mean (males; n=41)	<i>C. g. occidentalis</i> mean (females; n=35)
C ¹ MDL			9.29		9.08	7.42
C ¹ BLL			7.02		6.71	5.68
P ³ MDL	5.36	4.52	5.55		5.15	4.89
P ³ BLL	5.20	5.11	5.94		5.44	5.26
P ⁴ MDL	5.31	4.36	4.25		5.00	4.87
P ⁴ BLL	5.82	5.66	5.92		6.54	6.42
M ¹ MDL	6.36	5.97	5.79		6.78	6.62
M ¹ BLL (mesial)	5.94	5.61	5.82		6.32	6.20
M ¹ BLL (distal)	6.06	5.46	5.86		6.00	5.91
M ² MDL	7.10	6.19	6.97		7.20	7.03
M ² BLL (mesial)	7.05	6.41	6.68		7.18	6.96
M ² BLL (distal)	6.29	5.77	5.48		6.63	6.44
M ³ MDL	6.83	6.77			7.26	7.17
M ³ BLL (mesial)	6.51	5.99			6.92	6.61
M ³ BLL (distal)	5.70	5.20			6.26	6.06
P ³ -M ³ L	31.93	28.66				
M ¹ -M ³ L	20.60	18.95				
Palatal length	23.66					
Upper bimolar breadth	35.04					
Biporionic width	52.07					
Piriform aperture height	13.72					
Piriform aperture width	8.62					
Maxilla height	20.47	17.08				
Rhinion to orbitale distance	17.17					
Foramen magnum width	12.27					
I ₁ MDL			3.22		4.06	4.04
I ₁ BLL			2.71		3.51	3.41
I ₂ MDL			3.81		4.44	4.41
I ₂ BLL			3.19		3.33	3.35
C ₁ MDL			6.59		7.86	6.90
C ₁ BLL			6.54		5.05	4.47
P ₃ MDL			6.62	6.30	10.81	9.08
P ₃ BLL			4.47	4.01	4.97	4.57
P ₄ MDL				5.43	5.77	5.54
P ₄ BLL				4.16	4.42	4.38
M ₁ MDL			6.28		6.98	6.74
M ₁ BLL (mesial)			4.67	4.57	5.23	5.18
M ₁ BLL (distal)			4.97		5.59	5.55
Mandibular symphysis length				21.04		
Mandibular symphysis thickness				8.29		

*KNM-BK 42141 is a male partial cranium; KNM-BK 62 is a female upper facial skeleton; KNM-TH 46347 is an associated male partial cranium and mandible, and KNM-TH 47127 is a female partial mandible. Dental measurements of modern *C. guereza occidentalis* (Hayes et al. 1995) are provided for comparison. Abbreviations as in Table 2.

I₁-I₂ are well preserved and measurable, the crown of the C₁ has been broken near the base, and only the roots of the P₃, P₄, and M₁ remain. The several bone fragments associated with the jaws are not described because they are too fragmentary to be conclusively diagnosed.

The large sizes of the C₁ and P₃ crowns indicate that KNM-TH 46347 was a male. The relatively unworn condition of the P₃ and M₁ indicate that the animal was a full adult at death. The morphology of the P₄ distinguishes this specimen from *C. freedmani*, which exhibits a more sectorial

P₄ with a small, distally offset lingual cusp (Jablonski and Leakey 2008c). The upper jaw and maxillary teeth of the specimen are very similar in morphology to those of small male individuals of modern *Colobus guereza*. Like modern *C. guereza* also, the mandible of KNM-TH 46347 features a broad symphysis that is squared off at the incisive alveoli. The symphysis of KNM-TH 46347 is slightly longer and sloped more posteriorly than those of most modern *Colobus*. The incisors and incisive alveoli of KNM-TH 46347 exhibit the proclined appearance of modern colobines that engage



Figure 9. KNM-BK 62. *Colobus* sp. indet., female partial cranium with nearly complete upper dentition, basal (occlusal) view.

in leaf-stripping. The bone of the mandible is relatively thin throughout, especially in the region of the premolar and molar alveoli. The teeth preserved in KNM-TH 46347 are similar to those of modern *Colobus* males, especially in their possession of large and highly caniniform lower premolars and very small M_1 s. The measurements of KNM-TH 46347 are provided in Table 8.

KNM-TH 47127: The specimen consists of a partial right mandible of a female with P_3 , P_4 , the protolophid of M_1 , and an associated M_3 , which was cleaned from surrounding matrix. The mandible is broken at mid-symphy-

sis and again along an oblique line from the hypolophid of M_1 to below the level of M_3 . The mandible is shallow; the superior and inferior symphyseal shelves are small. Female status is judged by the reduced sectoriality of the P_3 and the small size of the C_1 alveolus. The P_4 is narrow and the lingual cusp is situated opposite the buccal one, as is more commonly the case in modern *C. guereza* (Swindler and Orlosky 1974). The M_3 is moderately worn. Measurements of the specimen are provided in Table 8.

KNM-BK 56 (Figure 11): The specimen represents a poorly preserved mandible of a very old male individual. The body of the mandible is mostly complete on the right, but is deficient inferiorly on the left below the premolars and molars. The symphyseal area is preserved, but has been badly distorted by crushing. Both mandibular rami are missing. The teeth present in the mandible have been worn to an extreme extent, resulting in extreme thinning of the alveolar bone supporting them. On the right, the C_1 , P_3 , P_4 , M_2 , and M_3 are preserved; on the left, the lower C_1 , P_3 , P_4 , and small portions of the M_2 and M_3 are preserved. On both sides, the I_1 - I_2 and M_1 s appear to have been lost before death, with marked concavities in the M_1 region of the mandible on both sides attesting to having occurred long before the individual's demise.

Despite its advanced age at death, KNM-BK 56 can be judged as a male because of the large sizes of the bases of the C_1 s and the honing facet of the P_3 s. Taking the chronological age of the animal into account, the shape of the mandible is very similar to that of modern *Colobus guereza*, with its distinctively long and proclined symphysis that is squared off at the incisive alveoli. Because of the animal's advanced age, the bone of the mandible was considerably thinner than that seen in most modern adult colobus monkeys. Its condition is, however, completely compatible with the normal age changes observed in the skulls of living colobines of similar age. The poor condition of the mandibular bone and the heavily worn condition of the teeth precluded measurement.

KNM-TH 46355 (Figure 12a-c): The specimen is a partial mandible, which is preserved in several fragments. The



Figure 10. KNM-TH 46347. *Colobus* sp. indet., male partial maxilla and associated partial mandible. a) right lateral view of maxilla; b) left lateral view of mandible; and, c) basal (occlusal) view of mandible.



Figure 11. KNM-BK 56. *Colobus* sp. indet., male partial mandible, very old individual, occlusal view. Note heavy wear of P_4 and M_1 consistent with wear caused by habitual leaf-stripping.

sex of the specimen cannot be determined. The largest fragment is a portion of the left corpus bearing the M_1 and M_2 . A second small bony fragment of the right corpus consists

of the alveolar bone supporting the M_2 only. The left C_1 , P_4 , and M_3 are preserved as isolated elements in fair condition, as are the right P_4 and M_1 . The roots and partial crowns of the I_1 - I_2 are also preserved, but are too worn and fragmentary to be measured. The better-preserved elements of KNM-TH 46355 are very similar in morphology to those seen in modern *Colobus guereza*. Measurements of this specimen are provided in Table 9.

KNM-TH 46356 (Figure 12d, e): The specimen consists of the posterior portion of the left side of the mandible of a small individual. Only the crown of the lower second molar is intact in its alveolus. The ramus is nearly complete, with only the medial portion of the mandibular condyle missing. The bone at the gonion and along the inferior surface of the corpus has been weathered away.

The morphology of the specimen with its high and up-right ramus is entirely consistent with that of female *Colobus guereza*; but the very small size of this specimen recommends the more cautious designation of *Colobus* sp. indet. Measurements of the specimen are provided in Table 9.

KNM-TH 47048: The specimen represents most of the right side of the body of the mandible of a juvenile individual, complete with the lower first and second deciduous molars, lower first molar and the developing crown of the second molar (unerupted but visible in crypt). The morphology of the teeth and mandible is very similar to that of juvenile *Colobus guereza*, but the small size of the specimen, again, recommends the designation of *Colobus* sp. indet. Measurements of the specimen are provided in Table 9.

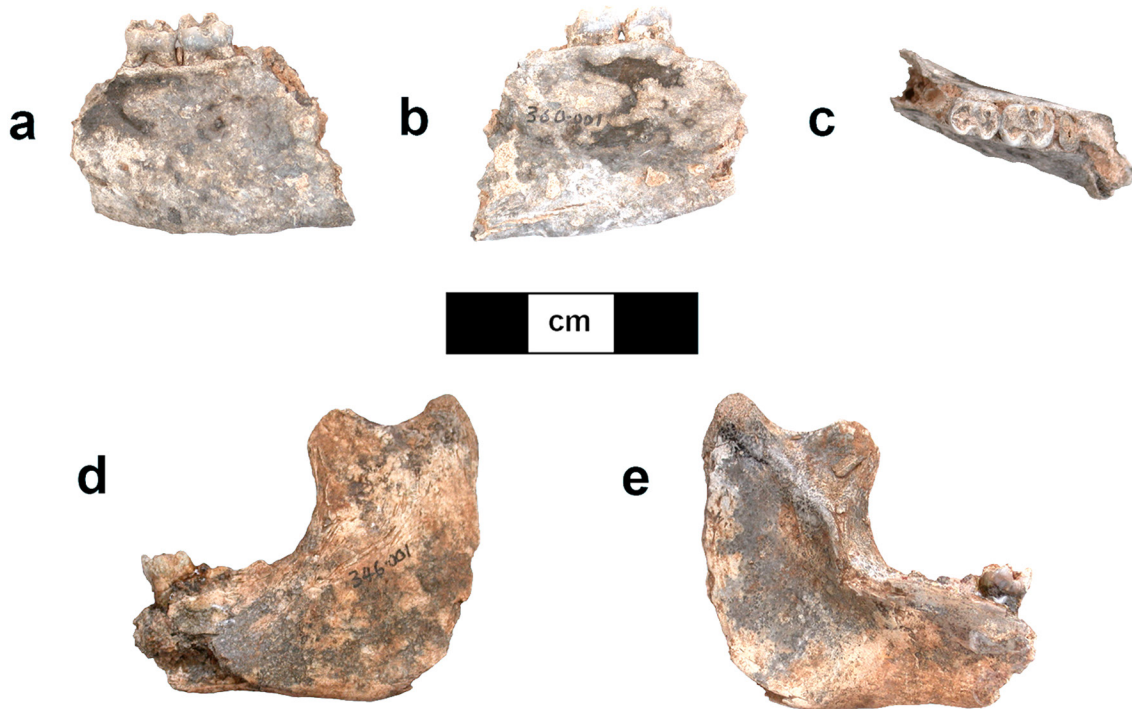


Figure 12. *Colobus* sp. indet. partial mandibles. a) KNM-TH 46355. Fragment of left side of mandible with M_1 - M_2 , indeterminate sex, lateral view; b) same, medial view; and c) same, occlusal view; d) KNM-TH 46356. Left partial mandible of probable female, lateral view; and, e) same, medial view.

TABLE 9. MEASUREMENTS OF THE LOWER TEETH FROM PARTIAL MANDIBLES AND ISOLATED TEETH OF COLOBYS SP. INDET., WITH COMPARISONS OF DENTAL MEASUREMENTS FROM MODERN *C. GUEREZA OCCIDENTALIS* (Hayes et al. 1995).*

Variable	KNM-TH 46355	KNM-TH 46356	KNM-TH 47048	KNM-TH 47128	KNM-TH 47126	KNM-TH 47129	<i>C. g. occidentalis</i> mean (males; n=41)	<i>C. g. occidentalis</i> mean (females; n=35)
C ₁ MDL	6.51						7.86	6.90
C ₁ BLL	6.86						5.05	4.47
P ₃ MDL							10.81	9.08
P ₃ BLL							4.97	4.57
P ₄ MDL	5.80						5.77	5.54
P ₄ MDL	3.83						4.42	4.38
M ₁ MDL	6.38						6.98	6.74
M ₁ BLL (mesial)	4.43		4.28				5.23	5.18
M ₁ BLL (distal)	4.63		4.48				5.59	5.55
M ₂ MDL	7.03	6.39			6.89		7.35	7.12
M ₂ BLL (mesial)	5.27	4.41			5.43		6.04	5.97
M ₂ BLL (distal)	5.49	5.00			5.49		6.26	6.13
dI ₁ mdl				2.96				
dI ₁ bli				4.15				
dI ₂ mdl				3.37				
dI ₂ bli				5.07				
dM ₁ mdl (mesial)			5.85					
dM ₁ bli			3.26					
dM ₂ mdl			5.77			6.50		
dM ₂ bli (mesial)			3.89			5.30		
dM ₂ bli (distal)						4.94		

*KNM-TH 46355 is a partial mandible and associated isolated lower teeth of indeterminate sex; KNM-TH 46356 is a partial mandible of a female; KNM-TH 47048 and KNM-TH 47128 are partial mandibles of juvenile of indeterminate sex; KNM-TH 47126 is an isolated lower second molar; and KNM-TH 47129 is an isolated lower deciduous second molar. Abbreviations as in Table 2; measurements of deciduous teeth are in lower case and are denoted by a “d” inserted before the tooth identifier.

KNM-TH 47128: The specimen consists of a partial right mandible of a juvenile, with di_1 , di_2 , root of the dc_1 , erupting P_3 , and heavily worn dm_1 . The mandible is shallow but thick with the crowns of developing teeth. The di_1 and di_2 are typical of those of modern *Colobus guereza*: the di_1 bears a narrow, symmetrical crown, while the di_2 exhibits an asymmetrical (distally inclined) crown and occlusal surface. Measurements of the specimen are provided in Table 9.

KNM-TH 47126: The specimen is a right M_2 crown. The buccal cusps are moderately worn. The distal shelf is relatively long and in all aspects of morphology the tooth is very similar to that of modern *Colobus*, especially *C. guereza*. Measurements of the specimen are provided in Table 9.

KNM-TH 47129: The specimen is a left dm_2 with broken roots. The buccal cusps are slightly worn. The morphology of the tooth is closely comparable to that of modern

Colobus, and is most likely *C. guereza*. Measurements of the specimen are provided in Table 9.

KNM-BK 57: The specimen consists of the three lower right molars and their surrounding mandibular alveolar bone. The first molar and its supporting bone have been rotated slightly toward the buccal side, rendering its mesiodistal dimension unmeasurable. The mandibular bone on the buccal and lingual surfaces is cracked and slightly expanded.

The size and morphology of the molar teeth are very similar to those of modern *Colobus*. Measurements of the teeth of the specimen are provided in Table 10.

KNM-TH 47036: The specimen represents a fragment of a left mandibular corpus of an adult individual, with most of the lower second and the complete lower third molar intact. The bone of the mandible has been badly crushed; very little of its original anatomy can be discerned

TABLE 10. DENTAL MEASUREMENTS (in mm) OF SPECIMENS OF COLOBUS SP. INDET. (all species are of unknown sex).*

Specimen	Tooth	BLL (mesial)	BLL (distal)	MDL
KNM-BK 57	M ₁	4.89	5.15	
KNM-BK 57	M ₂	5.66	5.92	7.01
KNM-BK 57	M ₃	5.65	5.26	8.69
KNM-TH 47055	P ⁴	5.86		4.81
KNM-BK 58	M ³	7.05	5.77	6.75
KNM-TH 47043	P ₄	3.99		5.45
KNM-TH 46354	P ₄	4.26		6.01
KNM-BK 61	M ₂	5.48	5.47	7.11
KNM-TH 47035	M ₂		6.02	7.16
KNM-TH 47042	M ₂	5.15		
KNM-TH 47040	dM ²	5.78	5.22	6.40

*Abbreviations as in Table 2.

and none of its features can be measured. As with KNM-BK 57, the size and morphology of the specimen are consistent with those of modern *Colobus*.

KNM-TH 47031: The specimen represents the tip of the left C¹ of a male; it was too fragmentary to be measured.

KNM-TH 47055: The specimen represents a lightly worn left P⁴, missing only its mesial root. Measurements are provided in Table 10.

KNM-BK 58: The specimen is an unworn and complete left M³, with a small remnant of alveolar bone adhering to its large palatal root. Measurements are provided in Table 10.

KNM-TH 47043: The specimen is a heavily worn left P₄, with its buccal alveolus and partial lingual alveolus preserved. Most of the detail of the crown morphology has been lost as a result of normal wear, but the caniniform shape of its mesiobuccal surface identifies it unambiguously as belonging to a male *Colobus*. Measurements are provided in Table 10.

KNM-TH 46354: The specimen is the unworn crown of a left P₄. The surface of the enamel has been etched. Measurements are provided in Table 10.

KNM-BK 61: The specimen represents an isolated right M₂ with complete roots. Measurements are provided in Table 10.

KNM-TH 47035: The specimen is the partial crown of a left M₂. The lingual aspect of the metaconid is missing, rendering the mesial breadth dimension of the tooth unmeasurable. Measurements are provided in Table 10.

KNM-TH 47042: The specimen represents the protolepid of a left M₂. The preserved morphology closely resembles that of modern *Colobus*. Measurements are provided in Table 10.

KNM-TH 46358: The specimen is a left M₃, exhibiting typical *Colobus* morphology with a well-formed hypoconulid. The specimen could not be measured because of exten-

sive erosion of the enamel surface by weathering.

KNM-TH 47040: The specimen is a right dM², with a complete lingual root. The lingual cusps are slightly worn and the mesial face bears a small interproximal wear facet. The morphology of the tooth is closely comparable to that of modern *Colobus*. Measurements of the teeth are provided in Table 10.

Postcranial Material

KNM-TH 47032 (Figure 13a, b): The specimen represents the left proximal humerus of an adult. The humeral head is typically cercopithecoïd, being nearly hemispherical and directed posteriorly and cranially. In posterior view, the greater tuberosity does not project above the level of the head of the humerus. The cranial and lateral faces of the greater tuberosity bear clearly defined facets for the origins of *mm. supraspinatus* and *infraspinatus*. The lesser tuberosity is much smaller than the greater and is situated more inferiorly; the origin of *m. subscapularis* on the tuberosity is moderately elevated and evenly round. The intertubercular groove is well defined superiorly, but rapidly flattens below the surgical neck. The deltoid crest is a sharp and strongly raised continuation of the lateral lip of the intertubercular groove. On the medial aspect of the shaft, extending from the inferior aspect of the lesser tuberosity, is a moderately raised crest that represents the origin of *m. latissimus dorsi*. The preserved portion of the shaft is very straight. All aspects of the anatomy of the specimen are consistent with that of a modern *Colobus*. The diameter of the humeral head is 19.33mm.

KNM-TH 46346: The specimen a complete left third metacarpal, comparable in size and morphology to that of a female *Colobus guereza*. The base of the bone is compact, and bears articular surfaces identical to those of the modern species. The shaft is very straight and expands slightly in diameter from proximal to distal. The head is large and

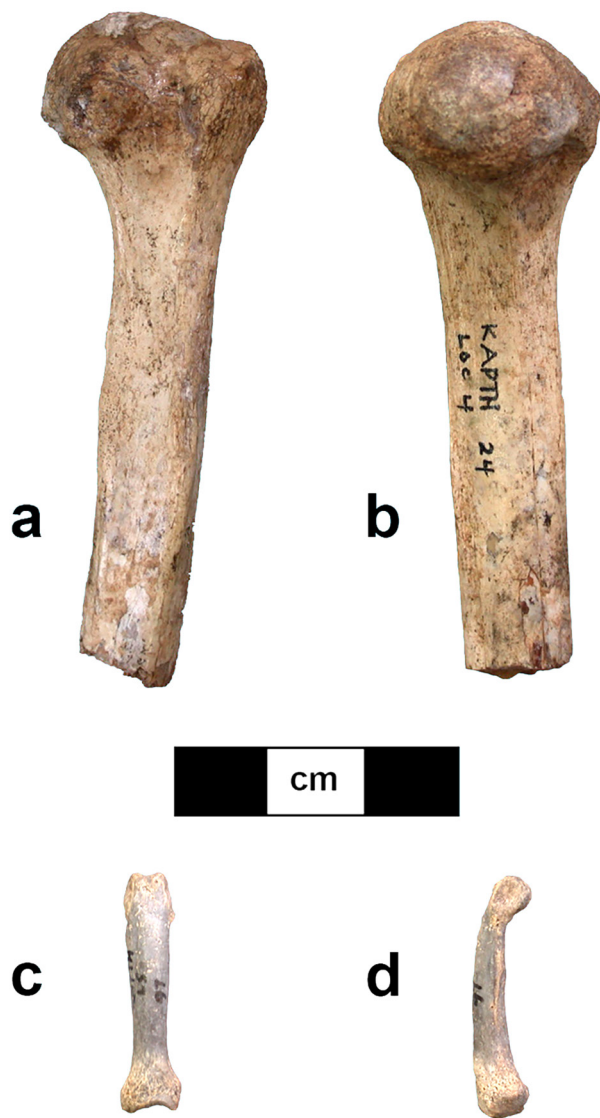


Figure 13. *Colobus* sp. indet. postcrania. a) KNM-TH 47032. Left proximal humerus, indeterminate sex, anterior view; b) same, posterior view; c) KNM-TH 47037. Left proximal manual phalanx, digit IV, dorsal view; and, d) same, medial view.

rounded; its dorsal surface bears prominent bilateral crests for the insertion of the tendons of *m. extensor digitorum*. The length of the bone is 38.09mm.

KNM-TH 47037 (Figure 13c, d): The specimen represents the complete left proximal manual phalanx of digit IV and completely comparable in size and morphology to female *Colobus guereza*. The shaft is straight, and only slightly ventrally curved. The length of the element is 25.17mm.

KNM-TH 47033: The specimen represents the base of the left proximal manual phalanx of digit V; its morphology is consistent with that of modern *Colobus*.

Remarks

The Kapthurin Formation *Colobus* is a small morph of the genus that is closely comparable to *C. guereza* based on the

limited material available. In details of dental morphology, the Kapthurin Formation *Colobus* is distinguished from Early Pleistocene *C. freedmani* from the Okote Member of Koobi Fora by the mesial position of the P_4 metaconid, the morphological configuration most common in *C. guereza*. Further comparative study of the Kapthurin Formation *Colobus* material is recommended in order to ascertain whether the form represents the oldest known sample of fossil *C. guereza* and, possibly, the descendant species of *C. freedmani*. Until recently, the only other conclusively diagnosed fossil of the species had been described from near Wad (Wadi) Medani in central Sudan, of presumed Pleistocene age. In recent years, the fossil record of *Colobus* has expanded dramatically with the collection and description of hundreds of new specimens, mostly from Middle Awash localities (Brasil et al. 2023a). These new remains complement significantly those previously described from Pleistocene sites in eastern and east-central Africa, including that from Asbole, Ethiopia (Frost and Alemseged 2007; Jablonski and Frost 2010). We concur with the author of a recent report that the Pleistocene was a time of rapid geographic dispersal and speciation. The large collections of Pleistocene-aged *Colobus* fossils now recognized from sites throughout eastern and northeastern Africa, including the Middle Awash, Koobi Fora, the current collection from the Kapthurin Formation, and others, now invite detailed comparative study in order to better understand the evolution of *Colobus* and the origins of the co-occurrence of *Colobus* with *T. oswaldi* and *Chlorocebus*. (Brasil et al. 2023a; Jablonski and Leakey 2008c).

COLOBINAE GEN. ET SP. INDET.

Kapthurin Formation Material

Six specimens from the Kapthurin Formation can be identified as colobine, but cannot be diagnosed further because of incompleteness. Three of these are isolated teeth; three are fragmentary postcranial elements. Measurements of the teeth are provided in Table 11.

Craniodental Material

KNM-TH 47041: The specimen is the isolated left I^1 of a colobine. The tooth is moderately worn and cannot be given a taxonomic diagnosis.

KNM-TH 47044: The specimen represents the isolated unworn right C_1 of a very small female individual. The morphology of the tooth is that of a colobine based on similarities in the shape of the talonid heel, but a specific assignment cannot be made.

KNM-TH 47045: The specimen is the isolated left lower third molar of a very small colobine, possibly associated with KNM-TH 47044. The tooth is complete except for the apex of the distal root. The cusp tips are sharp and extremely well defined; the lingual notches are deep.

Postcranial Material

KNM-TH 46351: The specimen consists of three fragments of a left distal humerus. The morphology of the medial

TABLE 11. MEASUREMENTS (in mm) OF ISOLATED TEETH OF COLOBINAE GEN. ET SP. INDET.*

Specimen	Tooth	Sex	BLL (mesial)	BLL (distal)	MDL
KNM-TH 47041	I ¹	U	5.25		5.05
KNM-TH 47044	C ₁	F	5.16		3.20
KNM-TH 47045	M ₃	?	4.98	4.78	8.20

*Abbreviations as in Table 2.

portion of the distal epiphysis is mostly preserved, permitting identification of the specimen to the subfamilial level (Jablonski and Leakey 2008c). The most highly diagnostic feature on the specimen is its large and retroflexed medial epicondyle, which is similar in morphology to those seen in modern African colobines. The specimen was too fragmentary to be measured.

KNM-TH 46359: The specimen consists of the proximal portion of the shaft of a left femur, in two pieces. The only diagnostic feature on the bone is its lesser trochanter, which is typically colobine in its strong triangular form, which rises sharply from the proximal shaft. The kidney-bean-shaped facet for attachment of *m. psoas major* is also typical of that seen in colobines. There were no measurable features on the bone.

KNM-BK 55: The specimen represents the shaft of a left femur, which preserves only the lesser trochanter. The shaft is long, uncurved, and nearly round in diameter throughout most of its length. The lesser trochanter is typical of that of colobines, rising steeply to a triangular form with a rounded apex (Jablonski and Leakey 2008c; Jablonski et al. 2008b). The dorsoventral diameter of the shaft is 11.35mm; the mediolateral diameter of the shaft is 11.45mm.

CERCOPITHECIDAE INDET.

Kapthurin Formation Material

The fossils listed below could be not be assigned to a more precise category than Family, and were too fragmentary to measure.

Craniodental Material

KNM-BK 59: fragment of calvaria.

KNM-BK 60: fragment of cranial bone.

KNM-TH 47025: fragment of a left temporal bone, and a glued set of fragments representing small portions of the parietal and occipital squama of a juvenile individual.

KNM-TH 47050: fragment of cranial bone, probably the parietal, of a juvenile individual.

KNM-TH 47047: fragment of molar.

DISCUSSION

The later Middle Pleistocene sediments of the Kapthurin Formation document the presence of a near-modern eastern African monkey fauna featuring *Chlorocebus*, *Colobus*, and, probably, *Papio*, along with the stalwart fixture of the later Pliocene and Pleistocene, *Theropithecus oswaldi*, represented by its largest morph, *T. o. leakeyi*. The *Chlorocebus* and *Colobus* from the Kapthurin Formation are closely similar to modern vervets and guerezas and, as such, provide valuable information about the environment of the Baringo Basin in the eastern Rift Valley during the Middle Pleistocene.

The Kapthurin Formation *Chlorocebus* is closely comparable to modern *Ch. pygerythrus*, the vervet, which is distributed patchily in woodlands and in woodland-savanna ecotones from the Ethiopian highlands to South Africa (IUCN et al. 2016). Investigations as to whether the Kapthurin Formation *Chlorocebus* represents *Ch. pygerythrus* or *Ch. aethiops* are warranted. The considerable overlap in size and craniodental morphology between the two species, as recently documented by an exhaustive comparison of samples of extant and fossil forms (Taylor et al. 2023), will complicate this study. Studies of dental microwear on the Kapthurin Formation specimens have not been conducted, but the kind and degree of dental wear macroscopically observable in the fossils are comparable to those seen in modern eastern Africa vervets, suggesting that the Kapthurin Formation representatives could comparably be classified also frugivorous, nectarivorous, and florivorous omnivores (Whitten 1988).

Of all the cercopithecoidean remains from the Kapthurin Formation, those of *Colobus* may provide the best insight into the radiation of their modern relatives. The specimens of *Colobus* sp. indet. from the Kapthurin Formation represent a small arboreal morph of the species that would have been 10–15% smaller than the smallest and most widespread of the living subspecies of black-and-white colobus, *C. guereza occidentalis*. The Early Pleistocene colobus known from Koobi Fora, *Colobus freedmani*, is also a small morph that displays morphological affinities to black-and-

white colobus, but which lacks key guereza apomorphies of the P_4 and the postcranium. Further comparative study is required to establish if the Kapthurin Formation colobus—possibly along with that from Asbole—may represent a phyletic link between *C. freedmani* and the modern guereza radiation. What is clear from the Kapthurin Formation *Colobus* remains is that, by the Middle Pleistocene, the likely antecedents of today's black-and-white colobus monkeys appear to have been engaged in the same feeding behavior as their modern counterparts. Evidence of classic leaf-stripping behavior is seen in the wear patterns of the P_4 and mesial molars in specimens representing older individuals, most particularly the old male represented by KNM-BK 56 (Morbeck 1979; Swindler 2002). This suggests that, in the region represented by sediments of the Kapthurin Formation by the Middle Pleistocene, *Colobus* had established its niche as an arboreal leaf-eater, pursuing the low-energy strategy characteristic of modern African colobines (DeSilva 1992). Studies of the dental wear of the Kapthurin Formation fossil *Colobus* are required to determine whether the monkeys utilized seeds as well as leaves, because many modern guerezas include high proportions of seeds in their diet. For colobines in Africa, establishment and maintenance of the arboreal “hypometabolic” niche, *sensu* DeSilva (1992), characterized by seed- and leaf-consumption, long periods of arboreal inactivity during digestion, and overall low energy output was critical to the survival of the lineage. Compared to their terrestrial and semiterrestrial relatives of the Plio-Pleistocene, the arboreal colobines of the Pleistocene faced no direct competition for food from ruminant ungulates.

The *Chlorocebus* and *Colobus* monkeys from the Kapthurin Formation, especially the well-preserved partial crania of *Chlorocebus* sp. indet. and *Colobus* sp. indet., are significant with respect to the taphonomic history of the site. The collections of *Chlorocebus* and *Colobus* fossils from the Kapthurin Formation include friable and easily consumed portions of the face and calvaria, suggesting that monkey bodies at the site were, at least some of the time, not subjected to extensive scavenging. As suggested by Leslie et al. (2016) and modeled by Tryon (2010), this may relate to intermittent periods of rapid but relatively gentle sedimentation (Leslie et al. 2016; Tryon 2010).

Theropithecus oswaldi leakeyi from the Kapthurin Formation represents one of the last and certainly best examples of the craniodental morphology of the species before its apparent extinction about 0.25 Ma. *Theropithecus o. leakeyi* in the Kapthurin Formation was the archetypal Pleistocene giant, which used its massive masticatory apparatus to process the large quantities of vegetation it required. By the ~509–545 ka interval in the Kapthurin Formation, the species probably faced a metabolic crisis, having to spend more time seeking and chewing moderate quality vegetation to maintain its large body mass and relatively large brain and to sustain successful pregnancies. The reasons for the extinction of the species have been much discussed (Dunbar 1993; Lee and Foley 1993), but in the Baringo Basin during the deposition of the Kapthurin Formation, *T. o.*

leakeyi probably faced competition as a graminivore from tragelaphine and reduncine bovids, which occur in great diversity in the formation and are among the most abundant taxa found in the formation (Cornelissen et al. 1990). In the late Early and Middle Pleistocene, the physical and ecological situations of monkeys in eastern Africa fundamentally changed (Jablonski and Leakey 2008a; Leakey et al. 2008). In the Pliocene and Plio-Pleistocene, monkeys were prominent among the terrestrial mammalian herbivores, and some of the most common species (e.g., *T. oswaldi* and *Cercopithecoides kimeui*) were grass-eaters sympatric with ungulates. By the Middle Pleistocene, however, graminivorous monkeys literally lost ground in forest fringe and open environments to ungulates. In the long run, *T. o. leakeyi*—even with its massive masticatory apparatus and highly specialized bilophodont molars—was no match for less highly encephalized bovids equipped with hooves, foregut fermentative digestion, and highly specialized masticatory apparatuses (Jablonski and Leakey 2008a). The early local appearance of the grassland specialist Grévy's zebra (*Equus grevyi*) (O'Brien et al. 2021) provides additional support for this hypothesis.

The monkeys poised to succeed *T. o. leakeyi* in ecotonal and open eastern African environments by the end of the Pleistocene, the common baboons of the genus *Papio*, are represented in the Kapthurin Formation only by a small handful of dental remains. More fossils of the species are needed to establish morphological equivalence, but the Kapthurin Formation's *Papio* remains are compatible with those of the modern anubis baboon, and suggest that regional differentiation of the genus was occurring by the Middle Pleistocene.

The monkeys of the Kapthurin Formation were not the only non-human catarrhines present, and their co-occurrence with *Pan* (McBrearty and Jablonski 2005) is highly significant. Modern chimpanzees are widely regarded as denizens of tropical rainforests, but they are known to live in a range of environments from closed-canopy everwet forests to heterogeneous habitats composed of gallery forests, woodlands, bamboo thickets, and grasslands (Russak and McGrew 2008). All of the monkey species known from the Kapthurin Formation (except for *T. o. leakeyi*) live in sympatry with chimpanzees at three long-term behavioral observatories, Kibale, Budongo, and Mahale, which are often characterized as having relatively open habitats (Russak and McGrew 2008). The same observatories share many of the same herbivore genera (*viz.*, *Tragelaphus*, *Potamochoerus*, *Syncerus*, *Cephalophus*, *Phacochoerus*, and *Hippopotamus*) and carnivores (*viz.*, *Crocota*, *Panthera*) as those preserved in Kapthurin Formation sediments (McBrearty et al. 1996; Russak and McGrew 2008). Viewed in its totality, the mammalian fauna of the late Middle Pleistocene Kapthurin Formation provide a glimpse of the modern ecotonal ecology of equatorial eastern Africa. In the Baringo Basin and in other basin systems of eastern Africa, the mammalian fauna includes species favoring woodland, stream margin, and grassland habitats (Leslie et al. 2016). In such diverse habitats, the catarrhine primates are divided between ex-

clusively arboreal primates (colobus monkey) and forms that are more versatile and opportunistic in their locomotion and diet (vervets, common baboons, chimpanzees, and hominins). With the exception of *T. o. leakeyi*, the large-bodied, strongly terrestrial, and largely graminivorous cercopithecoidea of the Plio-Pleistocene had been replaced by the later Middle Pleistocene in equatorial eastern Africa by hooved herbivores (Jablonski and Leakey 2008a).

CONCLUSIONS

The rich fossil record of Cercopithecoidea from the Kaphthurin Formation is significant because it documents the presence of monkey fauna in ecotonal equatorial Africa very similar to that of the present day by the later Middle Pleistocene in the eastern Rift Valley. The monkeys present in the Kaphthurin Formation collection, from the exclusively arboreal colobus monkeys to the probably exclusively terrestrial theropithecids, support the interpretations of the Baringo Basin as a lush and diverse environment in the later Middle Pleistocene.

The only Plio-Pleistocene remnant in the cercopithecoidea assemblage, *T. o. leakeyi*, is seen in the Kaphthurin Formation in one of its last appearances and largest, with respect to body mass. The presence of these grazing giants and the common baboon, but the absence of the terrestrial grazing colobines common earlier in the Pleistocene, highlights the transition in the nature of the mammalian herbivore fauna in East Africa in the later Middle Pleistocene to one dominated by ecological generalists and migrating ungulates (Faith et al. 2012; Jablonski and Leakey 2008a; Leslie et al. 2016).

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DATA AVAILABILITY

All of the original data for this project have been deposited with ScholarSphere and can be accessed via <https://scholar.sphere.psu.edu/>, managed by the Penn State University Libraries.

CONFLICTS OF INTEREST

The authors declare no conflicts of interest.



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