Partial Cranium of *Cercopithecoides kimeui* Leakey, 1982 From Rawi Gully, Southwestern Kenya

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ABSTRACT   The Rawi Gully, located on the Homa Peninsula in southwestern Kenya, has produced several fossil elements of a large cercopithecid from sediments approximately 2.5 million years old (Ma). Nearly all of these elements appear to represent a single adult male individual of the colobine species *Cercopithecoides kimeui* Leakey, 1982. Part of the face, mandible, dentition, and several small postcranial fragments were collected by the Homa Peninsula Paleoanthropological Project (HPPP) in 1994 and 1995. This individual also appears to be represented by material collected in two previous expeditions to the site, one led by David Pilbeam in the 1970s and an earlier expedition led by L.S.B. Leakey in 1933. This specimen may extend the first appearance of *C. kimeui* by approximately 500 Kyr, and provides the first evidence for much of the male facial morphology in this species. Furthermore, Rawi may represent a more wooded habitat than the other occurrences of *C. kimeui* at Olduvai Gorge, Tanzania, and Koobi Fora, Kenya, indicating that *C. kimeui* may have been relatively flexible in its habitat preferences. Am J Phys Anthropol 122:191–199, 2003. © 2003 Wiley-Liss, Inc.

A series of cercopithecoid fossils recovered by several different expeditions (Kent, 1942; Pickford, 1984; Ditchfield et al., 1999) from the Rawi Gully System located on the Homa Peninsula, southwestern Kenya, appears to represent a single individual. The most recent material from Rawi was collected in two field seasons in 1994–1995, by the Homa Peninsula Paleoanthropological Project (HPPP), and originally identified by Ditchfield et al. (1999) as *Papio* or *Parapapio*, largely on the basis of the low-crowned molar dentition. Preserved in this material is a crushed and mildly distorted partial face of a large male colobine, assignable to the species *C. kimeui* (Fig. 1), along with some cranial vault fragments, some mandibular corpus fragments, vertebral spinous processes, and miscellaneous indeterminate bone fragments (the *Papio* or *Parapapio* cranium mentioned in Ditchfield et al., 1999). All of the 1994–1995 material seems to represent a single individual, as there are refits between pieces collected in different years. A mandibular corpus fragment, collected by a Harvard University expedition led by D. Pilbeam in the 1970s, originally identified as *Papio* (Pilbeam, 1974), most likely belongs to the same individual as several fragments from the 1994–1995 collections refit onto it (Fig. 2). A fragment of the right corpus with an M_3 and a separate edentulous corpus fragment from the left side preserving the area under the P_3–M_1 (Fig. 3) was collected by L.S.B. Leakey in the 1930s (Kent, 1942); these fossils are housed at the British Museum of Natural History, London (BMNH). They were previously identified by E. Delson as a colobine (Napier, 1985), and are likely to be the same individual. The M_3 is reduced distally, a feature rare among the Colobinae, but a good match for the facial material collected in 1994–1995. None of the pieces preserved duplicate those from the other collections, and all of the specimens have identical preservation and a blue-brown coloration uncommon in the Rawi fossil
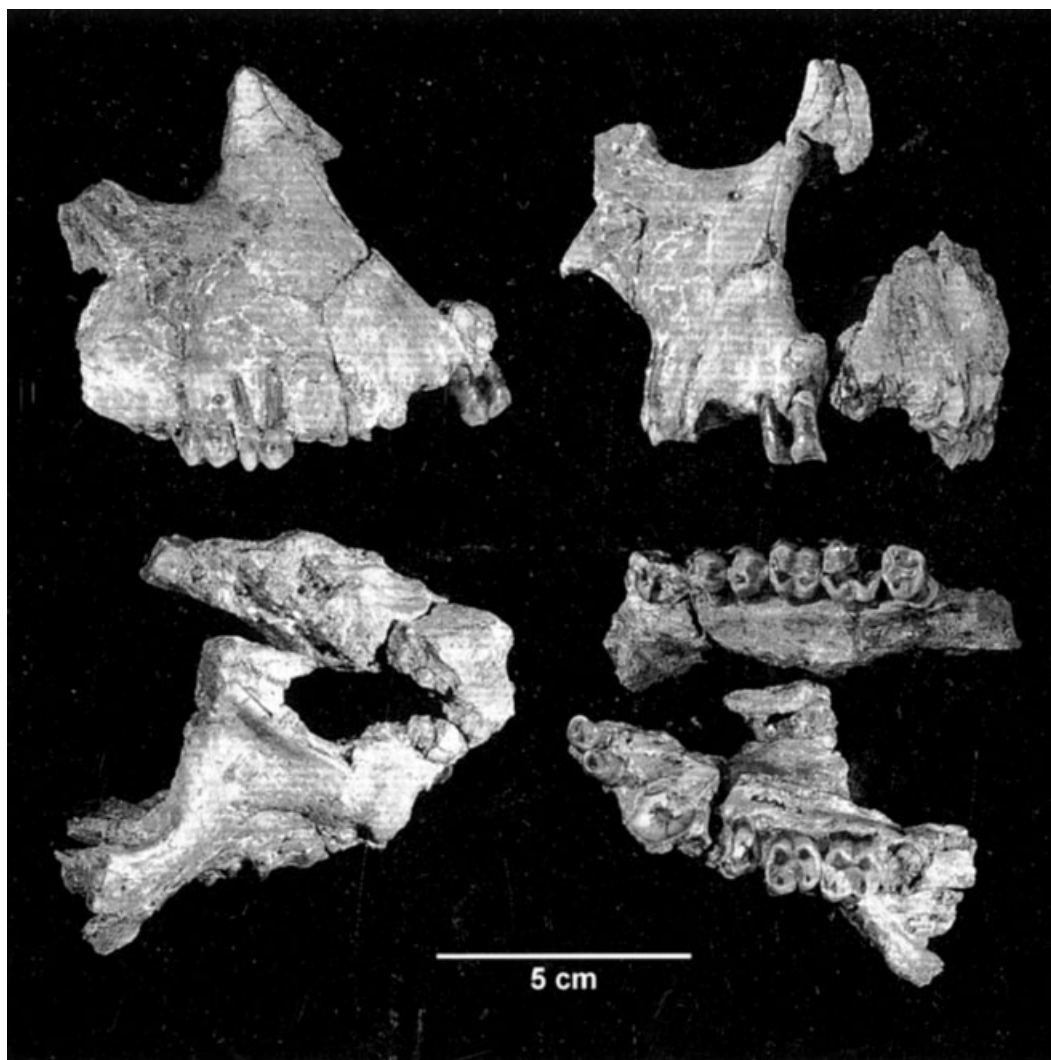
Fig. 1. Face of Rawi colobine. Clockwise from upper left: right lateral, anterior, ventral, and dorsal views.

sample. Therefore, a real possibility exists that all of this material represents a single individual collected over approximately 60 years by three different research teams. Also, in the Leakey collection, there is a femoral fragment preserving the proximal end, which almost certainly represents a second individual. It may also indicate the presence of a second taxon, as it is considerably smaller than would be expected for a colobine the size of the Rawi specimen.

In addition to the material from Rawi, fossil cercopithecids have been recovered from other localities on the Homa Peninsula, including Kanjera (Kanjera North in Ditchfield et al., 1999), the type locality of *Theropithecus oswaldi* (Andrews, 1916). *Theropithecus oswaldi* dominates the Kanjera primate sample, though a colobine tooth has been recovered from the middle Pleistocene bed KN-5. Additionally, the Kanam East Gully has produced a reasonably diverse assemblage of late Pliocene and Pleistocene cercopithecids, including *Colobus* sp., *Cercopithecus* sp., *Lophocebus* sp. (Harrison and Harris, 1996), and

Theropithecus sp. (Delson, 1993). There is also a single specimen of *Cercopithecus* sp. surface-collected by Leakey from Kuguta (Napier, 1985), which has yielded both Plio-Pleistocene and Late Pleistocene faunal elements. The Rawi material, however, represents the first occurrence of *C. kimeui* from the Homa Peninsula.

STRATIGRAPHY, CHRONOLOGY, AND PALEONTOLOGY

The oldest stratigraphic deposits in the Rawi Gully System are the Late Miocene and Early to Middle Pliocene Kanam and Homa Formations (Fm), respectively (Pickford, 1984; Potts, personal communication). The Rawi Fm is composed of two members (lower and upper) and has a planar, weakly erosive contact with the underlying Homa Fm in the Rawi Gully. The lower member consists of an approximately 2.5-m-thick broadly fining upwards sequence of pebble to granule grade matrix-supported conglomerates, passing upwards into a fine- to medium-grained micaceous sandstone
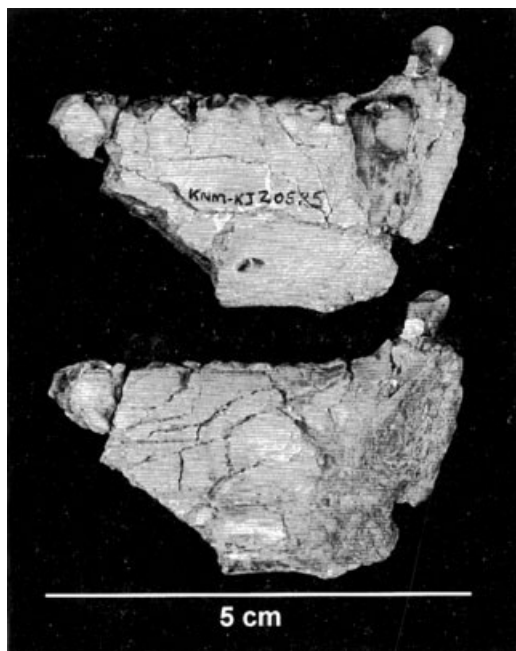
Fig. 2. KNM-KJ 20525 mandible. I$_2$ and distal most segment are from 1994–1995 collections and refit onto mandible collected in the 1960s. **Above:** Lateral view. **Below:** Medial view.

Fig. 3. BM(NH) M18945 mandible. From top to bottom: occlusal, lateral (courtesy E. Delson), and medial (courtesy E. Delson) views.

(Ditchfield et al., 1999). This member appears to represent deposition in a fluvial system, possibly with only seasonal water flow. The upper member is approximately 13.5 m thick, and consists of a series of centimeter-thick couplets of very fine sand and silt interbedded with occasional thin, tabular, fine- to medium-grade sandstones up to 20 cm thick. Well-preserved, often complete fish fossils and reworked evaporite pseudomorphs are common in the Rawi Fm, and the term "Fish Cliffs" has been used to refer to these sediments at both Rawi and the nearby Kanam Central Gully (Kent, 1942). The upper member appears to have been deposited in a shallow lacustrine environment, with periodic desiccation giving rise to evaporite formation and possible fish mass death. The fine sand/silt couplets which characterize the background sedimentation may represent annual seasonal cycles, suggesting rapid deposition. The sheet sands probably represent deposition from streams draining into the lake during times of increased precipitation and runoff.

Extensive trenching by Louis Leakey in the 1930s produced a rich paleontological sample from the upper member of the Rawi Fm (Table 1), including the holotype skeleton of *Giraffa jumae*, a skeleton of *Ceratotherium simum*, an articulated juvenile suid skeleton, a cranium and a mandible (representing two individuals) of *Metridiochoerus andrewsi*, a *Hippopotamus gorgops* cranium, and a nearly complete pygmy hippo mandible (Kent, 1942). While a detailed taphonomic analysis of these materials has not yet been undertaken, the presence of multiple partial skeletons, some with articulated bones, as well as the low w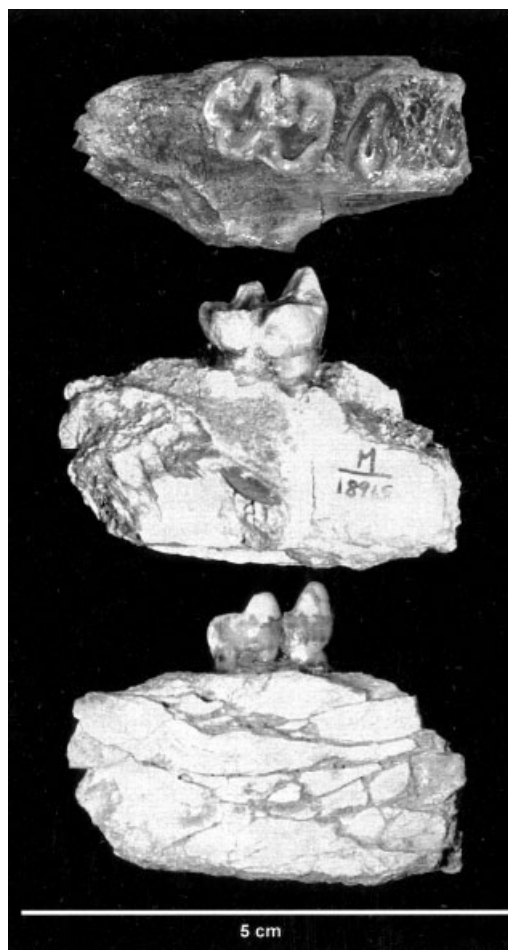eathering stages of the finds, is consistent with sedimentological evidence for rapid burial of fossils. In 1994 and 1995, a survey by the HPPP relocated Leakey's trenches and surface-collected additional fossils. Maxillary, facial, and cranial vault fragments from what was initially described as a *Papio* or *Parapapio* cranium (here identified as *Cercopithecoides kimeui*) were recovered from the "Baboon Cranium Site" approximately 80 m south of Leakey's excavations, at the base of the main vertical cliff of upper-member Rawi Fm sediments (Ditchfield et al., 1999). Ninety-six additional fossils, including fragments of bovid, hippo, suid, tortoise, crocodile, and fish, were observed within 15 m of the cercopithecid fossil. Sieving near the primate specimen recovered microfauna, snail shells, and abundant fish remains. The rediscovery of Leakey's sites and our field observations indicate that most if not all of the Rawi Fm fossils collected to date have eroded from the silts and platy sands of the upper third of the sequence, and may have been deposited over a relatively short period of time (tens to hundreds of years). The faunal sample is suggestive of a variety of habitats, particularly woodland (suggested by the giraffids, tragelaphines, and *No-*

TABLE 1. Macromammalian fauna from Rawi Fm from both Rawi and Kanam Central Gullies[1]

	Rawi Fm, Kanam Central Gully	Rawi Fm, Rawi Gully
Cercopithecoides kimeui		OX
Cercopithecidae		X
Notochoerus cf. *euilus*		O
Metridiochoerus sp.	X	
M. andrewsi		X
Hippopotamidae, pygmy		X
Hippopotamidae, large	O	O
Hippopotamus cf. *gorgops*		X
Giraffidae		O
Giraffa jumae		X
Tragelaphini, size 2	O	X
Tragelaphini, size 3	O	
Reduncini		O
Kobus kob		X
Equidae		O
Rhinocerotidae	O	
Ceratotherium simum		X
Elephantidae	O	OX

[1] O, taxa collected by HPPP; X, taxa collected by previous expeditions.

tochoerus cf. *euilus*) and edaphic grassland (suggested by the hippopotamids and reduncines) (Bishop, 1999). *M. andrewsi*, *C. simum*, and the indeterminate equid may have grazed in open habitats, but the complete lack of alcelaphine and antilopine bovids argues against the presence of large tracts of secondary grassland.

The Rawi Fm has been dated through a combination of bio- and magnetostratigraphy. The presence of the suids *Notochoerus* cf. *euilus* and *Metridiochoerus andrewsi* suggests a biostratigraphic age of between 2.0–3.36 Ma, as *N. euilus* is unknown in sediments younger than 2.0 Ma, and *M. andrewsi* is known from approximately 3.36 Ma (Harris et al., 1988; Bishop, 1994; Behrensmeyer et al., 1997). Normal geomagnetic polarity has been determined for the Rawi Fm (Ditchfield et al., 1999), which was thus probably deposited during a normal subchron within the Gauss Chron, most likely either C2An.1n (2.581–3.040 Ma) or C2An.2n (3.110–3.220 Ma) (Cande and Kent, 1995). The *M. andrewsi* cranium and mandible collected from Rawi exhibit tooth height, length, and complexity intermediate between the most primitive specimens at around 3.0 Ma and more derived specimens between 1.7–2.0 Ma. Thus, the Rawi Fm deposition probably occurred during C2An.1n, providing a minimum date of 2.581 Ma for the *Cercopithecoides* specimen.

DESCRIPTION

Almost all of the cercopithecid material from Rawi appears to represent a single individual assignable to the colobine species *Cercopithecoides kimeui* Leakey, 1982. The face is orthognathic, with short nasal bones and a tall and narrow piriform aperture. Slight maxillary and suborbital fossae are present, as is typical of the genus *Cercopithecoides*. Also typical for the genus is the very shallow midface. Within *Cercopithecoides*, this specimen is consistent

with *C. kimeui* because of its low-crowned and broad molars, which are unlike the molars of *C. williamsi*, *C. kerioensis*, or *C. meavae*. Furthermore, this specimen is substantially larger than specimens assigned to *C. williamsi*, *C. kerioensis*, or *C. meavae*.

In overall size, the face is very large for a colobine. The orbit is approximately 36 mm across, and the distance from nasion to prosthion is estimated to be between 75–80 mm. As the face is quite orthognathic, this was probably a larger animal than the more prognathic species *Rhinocolobus turkanaensis* or *Paracolobus chemeroni*, which have nasion to prosthion distances of 67 mm and 72 mm, respectively (based on the female KNM-ER 1485 and male holotype KNM-BC 3, the only specimens for each species which preserve this measurement). The dentition is in the upper part of, or slightly larger than, the known size range for other specimens of *C. kimeui* from Olduvai, Koobi Fora, and Hadar (Leakey and Leakey, 1973; Leakey, 1982; Frost, 2001; Frost and Delson, in press), except for M^3, which is quite reduced, and the M_3 which is shorter than those of other specimens due to its lack of a hypoconulid (Table 2).

Face

In its morphology, the face shows many features characteristic of the Colobinae, and looks like a larger version of the KNM-ER 4420 male face assigned to *C. williamsi* by Leakey (1982). The face is very orthognathic, with a short and deep rostrum. The inferior border of the zygoma arises from the maxilla superior to the M^1/M^2 contact, and the inferior orbital rim projects a small amount anterior to this point so that the zygoma "undercuts" the orbit slightly. Once again, this is distinct from *Paracolobus* or *Rhinocolobus*, where the zygomata slope anteroinferiorly. The orbits appear relatively large, and were also likely to have been fairly square in outline, but it is impossible to be certain of this, as only the lower portion is preserved. The midface is short relative to the overall height of the face. The zygomata are only 3 cm in height from the inferior orbital rim to the inferior margin at the zygo-maxillary suture, relative to a nasion to rhinion distance of approximately 75–80 mm. The lower face is deep. The alveolar process extends well below the zygoma. From medial to lateral, the inferior border of the zygoma curves superiorly in a gentle arc, laterally away from the face, reaches an apex directly inferior to the lateral border of the orbit, and then continues its arc inferiorly. The zygoma is bent posteriorly due to damage. In life, it would have projected more laterally. The short midface is also reflected in the modest length of the nasals (17.4 mm). The piriform aperture is tall and narrow, reaching well above the base of the orbits. The nasal process of the premaxilla is narrow, forming its lateral border, and reaches up to the nasals, but no higher. The main body of the premaxilla is quite small. In superior view, it probably formed a nearly straight trans-

TABLE 2. Dental dimensions for C. kimeui[1]

Specimen	Sex	I¹ Width	I¹ Length	I² Width	I² Length	C¹ Width	C¹ Length	P³ Width	P³ Length	P⁴ Width	P⁴ Length
RAWI	**m**	**6.8**	**6.1**	**6.7**	**5.7**	**11.1**	**14.2**	**8.4**	**7.3**	**10.0**	**7.3**
ER 398	f						6.9			9.1	7.0
ER 986	?									9.4	7.0
ER 3065	m					11.5	15.0	7.4	6.5	8.3	7.2
Old 068/6514	m									9.0	7.3

Specimen	Sex	M¹ Mwidth	M¹ Dwidth	M¹ Length	M² Mwidth	M² Dwidth	M² Length	M³ Mwidth	M³ Dwidth	M³ Length
RAWI	**m**	**10.9**	**10.4**	**10.3**	**12.1**	**11.0**	**11.7**	**11.1**	**8.2**	**8.9**
AL603-1	f				11.3	10.4	11.2	10.4	8.8	11.7
ER 398	f	9.6		9.0	11.3	11.3	11.6	11.5	10.4	12.5
ER 986	?	9.7	9.5	9.6	11.6	10.5	10.9			
ER 3065	m			9.5	12.0	11.8	12.0	11.7	9.4	12.2
ER 3069	?				10.1	8.9	11.3			
Old 068/6514	m	10.1	9.5	10.9	11.7	10.8	11.7			

Specimen	Sex	I₁ Width	I₁ Length	I₂ Width	I₂ Length	C₁ Width	C₁ Length	P₃ Width	P₃ Length	P₄ Width	P₄ Length
RAWI	**m**			**6.5**	**5.1**	**10.7**	**7.2**				
ER 126	m	6.5		5.9		10.5	7.6		12.4		
ER 967	m	6.9		6.2		10.0	6.3		11.2		9.7
ER 5894	m									6.7	8.8

Specimen	Sex	M₁ Mwidth	M₁ Dwidth	M₁ Length	M₂ Mwidth	M₂ Dwidth	M₂ Length	M₃ Mwidth	M₃ Dwidth	M₃ Length
RAWI	**m**							**10.6**	**9.9**	**12.5**
ER 126	m				10.7	10.8	13.4	10.7	10.6	16.9
ER 1529	?						10.7		9.2	16.0
ER 3069	?							8.5	8.5	15.2
ER 5894	m						12.2			14.8
Old 69/S.194	?				9.5	9.8	11.7			

[1] All width measurements represent maximum bucco-lingual dimension of crown, and all length measurements represent its maximum mesio-distal dimension. For molar teeth, Mwidth represents width taken across mesial loph(id), and Dwidth is width taken across distal loph(id). M₃ dimensions for Rawi specimen are taken from BM(NH) M18945.

verse line joining the canines, yielding a subnasal part of the face that would have been very squared off. Unfortunately, there is considerable distortion to this part of the face, particularly on the left side. On the maxillae, facial fossae are present, and are best preserved on the right. These fossae extend beneath the orbit posteriorly, and abut the canine root anteriorly. Superiorly these fossae are bounded by slight maxillary ridges.

Mandible

The mandible has a steep symphysis, with only weak mental ridges. Unfortunately, the symphysis is broken in the midline, making it impossible to tell whether there was a median mental foramen present. The corpus was broad and shallow, with only weakly excavated corpus fossae. The single mental foramen is inferior to P_4. There was a wide extramolar sulcus and a well-marked oblique line lateral to M_3. In anterior view, the corpus was widest near the base, due to the presence of inferior lateral bulges, or prominentia laterales, near the inferior margin roughly below M_1. This is unlike most *C. williamsi*, where the widest part of the mandible is located at approximately midheight. In the morphology that is preserved, this mandible is similar to the large male *C. kimeui*, KNM-ER 126, but very distinct from the deep, narrow, and posteriorly deepening mandibles of *Paracolobus*, *Rhinocolobus*, *Kuseracolobus*, or *Colobus*.

Dentition

In contrast to the relatively low-crowned molars, the incisors preserve several features that reveal clear colobine affinity, including the presence of enamel on the lingual face of the lowers, caniniform upper laterals, lingual cingula on the uppers, and upper centrals that are nonspatulate in outline. In overall appearance, the dentition is quite a good match for that of the *C. kimeui* holotype NMT 068/6514, and to specimens from Koobi Fora and Hadar (Leakey, 1982; Frost and Delson, in press). The incisors are small relative to the cheek teeth and canine. The upper premolars are broad, with P^4 being rather molariform. As is typical of *C. kimeui*, the molars are low-crowned and broad in comparison to those of other colobines. The mesial molars are large relative to the other teeth. M^2 is the largest molar. Unlike other known specimens of *C. kimeui*, or even any other known large colobine specimen, M^3 is greatly reduced.

I^1. Although fairly worn, I^1 is clearly colobine in its morphology. The crown is not flaring in anterior view, but is more of a parallelogram in outline, with the mesial and lateral edges being parallel and sloping mesially, so that the crown would not have been wider at the tip than at the base. There is a distinct lingual cingulum present. The contact facet for I^2 is near the cervix. Lastly, it is a fairly small tooth relative to both the overall size of the animal and the other teeth.

I^2. This is a fairly caniniform tooth, as is typical of colobines, with a well-developed lingual cingulum. The crown is conical in shape, though the tip is worn, so that its length at the cervix is greater than its length at the occlusal surface. The contact facet for I^1 is located near the cervix.

C^1. None of the crown of the upper canine is preserved, but the roots are large in caliber, clearly marking this specimen as a male. The roots form prominent bulges on the anterior surface of the muzzle and contribute to the superior and anterior border of the maxillary fossa.

P^{3-4}. The overall morphology of the upper premolars is typical of the family. The crown of P^3 is considerably narrower than that of P^4. The P^3 crown is tall, with minimal mesial and distal foveae. The protocone is reduced, as is typical of the extant African colobines and as seems also to be true for the genera *Cercopithecoides* and *Rhinocolobus*, but unlike *Paracolobus* and *Kuseracolobus*, at least in the few specimens where this feature is preserved. P^4 is more molariform than P^3, with a well-developed protocone and distal fovea and talon. A small cuspule is present on the distal limit of the talon.

M^{1-3}. The upper molars are very quadrate in occlusal view, being short, broad, and low-crowned for a colobine, but with a relatively large amount of that height being made up of the cusps. This is unlike papionins, where most of the crown height is below the level of the buccal notch. The cusps are widely spaced on the crown, which is straight-sided with little basal flare. The teeth are relatively "clean" in appearance, lacking accessory cuspules and rugosities. The cross lophs, though not high, are continuous, and make up a relatively large fraction of the total crown width. The lophs are not interrupted by a sulcus in the midline, though this could arguably be due to wear. In the above features they are more like flattened colobine teeth than papionin teeth. M^3 is distally reduced, with the hypocone and metacone being little more than a cingulum. The root is single and crescent-shaped in cross section, with two distal bulges near the apex of the arc.

I_2. The lower second incisor is small and can only be a colobine, as a thick layer of lingual enamel is present. Also, there is the typical colobine distal cuspule, or "lateral prong" (Szalay and Delson,

1979). The cervical margin is relatively even in height all the way around the circumference of the tooth.

M_2. On BMNH 18945, the inferior portions of the roots of M_2 are preserved. It appears as though this tooth may have actually been larger than M_3 in both width and length, a rare feature in colobines and papionins.

M_3. The right M_3 is preserved in BMNH M18945. The crown is fairly quadrate and broad, and the distal lophid is narrower than the mesial. The hypoconulid is nearly absent. This is a phenomenon that is fairly common in the smaller colobines, such as *Presbytis*, but otherwise unknown in the larger forms. However, at least two specimens of *Mesopithecus pentelicus* present a similar pattern, although unilaterally (Delson, 1973: the "holotype" of *M. major* Roth and Wagner, 1854, and the two mandibular fragments from Baltavar (Petho, 1884), presumably of a single individual). The crown is typical of colobines, with a deep lingual notch. The crown is worn considerably, so that dentin is exposed over most of the occlusal surface, with the enamel forming a perimeter, giving the occlusal surface a somewhat *Theropithecus*-like pattern. This pattern is quite similar to that seen in the male mandible from Koobi Fora, KNM-ER 126 (depicted in Leakey and Leakey, 1973). Visible on the left mandibular fragment are the roots of M_3, which is distally reduced.

Femur

The femoral fragment from Rawi almost certainly represents a second individual, and may well represent a second taxon. It is from the Leakey collection at the BMNH, and has not been given an accession number. It is a proximal fragment with the head, neck, and both trochanters, but little of the shaft. The maximum diameter of the head is 20 mm, and the maximum mediolateral breadth across the head, neck, and trochanteric tubercle is 38 mm. This is far smaller than would be expected for a cercopithecid the size of a male *C. kimeui*. In fact, this is smaller than expected for females of *C. kimeui*, based on estimates by Delson et al. (2000) from Koobi Fora of 25 kg (range of estimates, 23–27 kg). The size of the femoral head is within the range for females of extant *Papio*, which range in mass from about 10–15 kg, depending on the subspecies (Delson et al., 2000). The greater trochanter is approximately even with the head in height. It is difficult to accurately assess the angle of the neck relative to the shaft because there is so little shaft preserved, but it was relatively high. Both of these features are typical of cercopithecids adapted to more arboreal locomotor behaviors, and are unlike *T. oswaldi* (the Rawi femur falls in the lower range of female *T. oswaldi* head size).

DISCUSSION

The colobine individual from Rawi almost certainly represents the species *Cercopithecoides kimeui*. It is clearly a large individual relative to others of the species. These specimens are mostly female, however, and comparable male material is lacking, as the possibly male holotype material from Olduvai preserves little of the face (Leakey and Leakey, 1973). The only feature that could be used to separate the Rawi specimen from the rest of the hypodigm would be the reduction of the distal molars. It is quite common among smaller species of *Presbytis* for the M_3 hypoconulid to be variably absent (Szalay and Delson, 1979), but its significance in a species this size is difficult to determine. Until larger samples are available to ascertain the variability of this feature in this species, it is best to include the Rawi material without special taxonomic indication.

C. kimeui was described from Olduvai, Koobi Fora, and Hadar (Leakey and Leakey, 1973; Leakey, 1982; Frost, 2001; Frost and Delson, in press). At Olduvai, it is known by the holotype, a presumably male associated calvaria and right and left maxillae from MLK, Middle Bed II above the Lemuta Member (approximately 1.65–1.52 Ma; Tamrat et al., 1995; Delson and Van Couvering in White, 2000), and possibly by a single isolated right M_2 from Bed III (between 1.33 and approximately 1.2 Ma). At Koobi Fora, it is known from several cranial specimens in the Upper Burgi and KBS Members (and therefore between about 2–1.64 Ma in age; Brown and Feibel, 1991). There are also two specimens from lower strata in the sequence, one each in the Tulu Bor and Lokochot Members, but these are less definitely assigned, as they are incomplete maxillary fragments with molars. They are here considered to be indeterminate large colobines. The specimen from Hadar comes from the Pinnacle Site, which is in the upper part of the sequence, and probably dates between 1.6–1.8 Ma (Eck, personal communication). If our interpretation of the Rawi Fm bio- and magnetochronology is correct, then the Rawi material would represent the earliest occurrence of the species, extending the range by at least 500 Kyr and possibly 1 Myr.

The paleoenvironment in the Olduvai Gorge region during Middle Bed II time has been reconstructed as more open and incorporating more C_4 grass than was the case during Lower Bed II or early Bed I time (e.g., Hay, 1990; Sikes, 1994). At Koobi Fora, the Upper Burgi and KBS paleoenvironments were also generally more open than those of the earlier Tulu Bor Member (Feibel et al., 1991). The Upper Burgi Member probably represented a more wooded and wet environment than the younger KBS Member, with the latter possibly representing savanna or subdesertic steppe based on mammalian faunal analysis, pollen spectra, and carbon isotopic data (Feibel et al., 1991; Reed, 1997). The Upper

Burgi paleoenvironments may also have included more wooded habitat than Middle Bed II at Olduvai Gorge (Kappelman et al., 1997). Paleoenvironmental reconstructions for the Pinnacle Site have not been published. At all localities where *C. kimeui* has been recovered other than Rawi, it is associated with the large baboon *Theropithecus oswaldi*. Like the extant *T. gelada*, *T. oswaldi* has been reconstructed as a terrestrial grazer from several lines of evidence (Jolly, 1972; Lee Thorpe and van der Merwe, 1989; Krentz, 1993; Teaford, 1993; Benefit, 2000). Therefore, from the very limited current sample, *C. kimeui* may be associated with more open habitats. However, its presence at Rawi and perhaps to a lesser extent the Upper Burgi Member suggests that *C. kimeui* was found in a broad array of habitats, ranging from woodland to more open grassland.

Little is known of the functional ecomorphology of *C. kimeui*. There are very few postcrania known, all of which are relatively fragmentary, and none of these have been analyzed functionally. There is a relatively complete skeleton of *Cercopithecoides williamsi* from Koobi Fora, which may represent the most terrestrially adapted colobine known (Birchette, 1982; Ting, 2001). A partial skeleton of *C. meavae* from Hadar also shows a number of features consistent with at least a semiterrestrial habitus (Frost, 2001; Frost and Delson, in press). However, whether *C. kimeui* was similar to these in its postcranial morphology is impossible to tell. Benefit (2000) estimated the percentage of fruit and leaves in the diet of several species of fossil cercopithecids using three different gross morphological characteristics. For *C. kimeui* from both Olduvai and Koobi Fora, she estimated the percentage of leaves in the diet at under 45%, and fruit at nearly 40%. These values are among the lowest for leaves and highest for fruit among all of the Pliocene and Pleistocene colobines included in her analysis.

Delson et al. (2000) estimated the population mean mass of male *C. kimeui* from Koobi Fora at 51 kg (estimates ranged from 35–62 kg in their analysis), based on dentition. If the holotype from Olduvai is indeed male, then their estimate for males of this population would be 47 kg (±20% range, 38–59 kg). Using the equations from Delson et al. (2000) and applying them to the dentition of the Rawi specimen yields a mean estimate of 46 kg (estimates range from 34–50 kg, with a ±20% range of 37–55 kg). The reduced M_3 of the Rawi specimen significantly reduces the estimated weight for this population. If estimates from M_3 are removed, then the mean estimate becomes 49 kg. In any event, the estimated mean male weight is similar at all three sites, and it is clear that *C. kimeui* was a very large colobine. Only the estimates for *Paracolobus mutiwa* are as large, and those for *P. chemeroni* are only slightly smaller. All of the other large colobines, including *C. williamsi*, *Rhinocolobus turkanaensis*, and *Dolichopithecus ruscinensis*, are significantly smaller. Furthermore, based on the estimates from Rawi, it ap-

pears that body size in *C. kimeui* was essentially constant throughout its known temporal range.

In spite of a growing fossil record, the evolutionary history of the African colobines is not well-known (e.g., Szalay and Delson, 1979; Leakey, 1982; Delson, 1994; Jablonski, 2002). The relationship between *Cercopithecoides* and the other fossil and extant colobines is not currently resolved, nor is the relationship among the species within the genus (*C. williamsi*, *C. kimeui*, *C. kerioensis*, and *C. meavae* from Leadu and Hadar). It is clear, however, that there was considerably greater diversity in the Plio-Pleistocene than is present today in terms of the number of taxa, body mass, locomotion, and possibly diet and habitat preference. The Rawi *C. kimeui* material provides the first glimpse at the male facial morphology in this taxon, and in conjunction with material from other sites, provides insight into the paleoecology of this species.

ACKNOWLEDGMENTS

LITERATURE CITED

Andrews CW. 1916. Note on a new baboon (*Simopithecus oswaldi*, *gen.etsp.n.*) from the (?) Pliocene of British East Africa. Ann Mag Nat Hist London 18:410–419.

Behrensmeyer AK, Todd NE, Potts R, McBrinn GE. 1997. Late Pliocene faunal turnover in the Turkana Basin, Kenya and Ethiopia. Science 278:1589–1594.

Benefit BR. 2000. Old World monkey origins and diversification: an evolutionary study of diet and dentition. In: Whitehead P, Jolly CJ, editors. Old World monkeys. Cambridge: Cambridge University Press. p 133–179.

Birchette M. 1982. The postcranial skeleton of *Paracolobus chemeroni*. Ph.D. dissertation, Harvard University.

Bishop L. 1994. Pigs and the ancestors: hominids, suids and environments during the Plio-Pleistocene of East Africa. Ph.D. dissertation, Yale University, New Haven.

Bishop L. 1999. Suid paleoecology and habitat preferences at African Pliocene and Pleistocene hominid localities. In: Bromage TG, Schrenk F, editors. African biogeography, climate change, and human evolution. New York: Oxford University Press. p 216–225.

Brown FH, Feibel CS. 1991. Stratigraphy, depositional environments and palaeogeography of the Koobi Fora Formation. In: Harris JM, editor. Koobi Fora Research Project. Volume 3, stratigraphy, artiodactyls and paleoenvironments. Oxford: Clarendon Press. p 321–346.

Cande SC, Kent DV. 1995. Revised calibration of the geomagnetic polarity time scale for the Late Cretaceous and Cenozoic. J Geophys Res 100:6093–6095.

Delson E. 1973. Fossil colobine monkeys of the circum Mediterranean region and the evolutionary history of Cercopithecidae (Primates, Mammalia). PhD dissertation, Columbia University.

Delson E. 1993. *Theropithecus* fossils from Africa and India and the taxonomy of the genus. In: Jablonski NG, editor. *Theropithecus*: the rise and fall of a primate genus. Cambridge: Cambridge University Press. p 157–189.

Delson E. 1994. Evolutionary history of the colobine monkeys in paleoenvironmental perspective. In: Davies AG, Oates JF, editors. Colobine monkeys: their ecology, behaviour and evolution. Cambridge: Cambridge University Press. p 11–43.

Delson E, Terranova CJ, Jungers WL, Sargis EJ, Jablonski NG, Dechow PC. 2000. Body mass in Cercopithecidae (Primates, Mammalia): estimation and scaling in extinct and extant taxa. Am Mus Nat Hist Anthropol Pap 83:1–159.

Ditchfield P, Hicks J, Plummer T, Bishop LC, Potts R. 1999. Current research on the Late Pliocene and Pleistocene deposits north of Homa Mountain, southwestern Kenya. J Hum Evol 36:123–150.

Feibel CS, Harris JM, Brown FH. 1991. Neogene paleoenvironments of the Turkana Basin. In: Harris JM, editor. Koobi Fora Research Project. Volume 3, stratigraphy, artiodactyls and paleoenvironments. Oxford: Clarendon Press. p 321–346.

Frost SR. 2001. Fossil Cercopithecidae from the Afar Depression, Ethiopia: species systematics and comparison to the Turkana Basin. Ph.D. dissertation, City University of New York.

Frost SR, Delson E. 2002. Fossil Cercopithecidae of the Hadar Formation, Ethiopia, and surrounding areas. J Hum Evol 43:687–748.

Harris JM, Brown FH, Leakey MG 1988. Stratigraphy and paleontology of Pliocene and Pleistocene localities west of Lake Turkana, Kenya. Nat Hist Mus Los Angeles County Contrib Sci 399:1–128.

Harrison T, Harris EE. 1996. Plio-Pleistocene cercopithecids from Kanam East, western Kenya. J Hum Evol 30:539–561.

Hay RL. 1990. Olduvai Gorge: a case history in the interpretation of hominid paleoenvironments in East Africa. In: LaPorte LF, editor. Establishment of a geologic framework for paleoanthropology. Boulder: Geological Society of America. p 23–37.

Jablonski NG. 2002. Fossil Old World monkeys: the Late Neogene radiation. In: Hartwig WC, editor. The primate fossil record. Cambridge: Cambridge University Press. p 255–299.

Jolly CJ. 1972. The classification and natural history of *Theropithecus* (*Simopithecus*) (Andrews, 1916), baboons of the African Plio-Pleistocene. Bulletins of the British Museum (Natural History). Geology 22:1–122.

Kappelman J, Plummer T, Bishop LC, Duncan A, Appleton S. 1997. Bovids as indicators of Plio-Pleistocene paleoenvironments in East Africa. J Hum Evol 32:229–256.

Kent PE. 1942. The Pleistocene beds of Kanam and Kanjera, Kavirondo, Kenya. Geol Mag 79:117–132.

Krentz HB. 1993. Postcranial anatomy of extant and extinct species of *Theropithecus*. In: Jablonski NG, editor. *Theropithecus*: the rise and fall of a primate genus. Cambridge: Cambridge University Press. p 383–422.

Leakey MG. 1982. Extinct large colobines from the Plio-Pleistocene of Africa. Am J Phys Anthropol 58:153–172.

Leakey MG, Leakey REF. 1973. New large Pleistocene Colobinae (Mammalia, Primates) from East Africa. Fossil Vertebr Afr 3:121–138.

Lee Thorpe J, van der Merwe NJ. 1989. Isotopic evidence for dietary differences between two extinct baboon species from Swartkrans. J Hum Evol 18:183–190.

Napier PH. 1985. Catalog of primates in the British Museum (Natural History) and elsewhere in the British Isles, part III: family Cercopithecidae, subfamily Colobinae. London: British Museum (Natural History).

Petho J. 1884. Uber die fossilen Säugethiereste von Baltavár. Jb Kon Ungarische Geol Anst.

Pickford M. 1984. Kenya paleontology gazetteer, volume 1, western Kenya. Nairobi: National Museums of Kenya.

Pilbeam D. 1974. Hominid-bearing deposits at Kanjera, Nyanza Province, Kenya. Unpublished report.

Reed KE. 1997. Early hominid evolution and ecological change through the African Plio-Pleistocene. J Hum Evol 32:289–322.

Roth J, Wagner A. 1854. Die Knochenübereste von Pikerni in Griechlend. Abh K Bayerishe Akad Wiss 2 C1 (Math-Phys) 7:371–388.

Sikes NE. 1994. Early hominid habitat preferences in East Africa: paleosol carbon isotopic evidence. J Hum Evol 27:25–45.

Szalay FS, Delson E. 1979. Evolutionary history of the primates. San Diego: Academic Press.

Tamrat E, Thouveny N, Taieb M, Opdyke ND. 1995. Revised magnetostratigraphy of the Plio-Pleistocene sedimentary sequence of the Olduvai Formation (Tanzania). Palaeogeogr Palaeoclimatol Palaeoecol 114:273—283.

Teaford MF. 1993. Dental microwear and diet in extant and extinct *Theropithecus*: preliminary analyses. In: Jablonski NG, editor. *Theropithecus*: rise and fall of a primate genus. Cambridge: Cambridge University Press. p 331–349.

Ting N. 2001. A functional analysis of the hip and thigh of *Paracolobus chemeroni* and *Paracolobus mutiwa*. M.A. thesis, University of Missouri, Columbia.

White TD. 2000. Olduvai Gorge. In: Delson E, Tattersall I, Van Couvering JA, Brooks AS, editors. Encyclopedia of human evolution and prehistory, 2nd ed. New York: Garland. p 486–489.

APPENDIX
Catalogue

RA94-2

Right partial face, with slightly crushed premaxilla, left and right nasals, right rim of piriform aperture, base of right orbit, trigone of right zygomatic, I^2, M^{1-2}, and roots of C–P^4 and M^3.

Left premaxilla, with a small part of maxilla. Includes base of left piriform aperture rim. Roots of I^1–C. Does not meet with right side due to some damage to face at contact area.

Left M^3.

Left mandible fragment, with roots of the M^3. Does not preserve inferior margin or ramus.

Vault fragments. These show distinct temporal lines, but little else.

RA95-1a

Left maxilla, preserving lower part of face and root of zygomatic process. P^3–M^1 are preserved, as are lingual half of M^2, and root of M^3. It fits across a large contact onto left premaxilla from RA94-2.

RA95-1b

Right I^1. Fits onto root from RA94-2 face, and meets I^2 at its contact facet. Both incisors are in a similar state of wear, which is approximately 1/3 of way down crown. It has an interesting wear pattern, in that when viewed labially, the occlusal surface is concave, superiorly, so that mesial and distal sides are taller than the middle.

RA95-1

Paracone of left M^2. Fits onto M^2 of left maxilla 95-1a.

Vault fragment. Similar temporal line to those from 94.

Cranial fragment, possibly of mandible.

Right I_2. Appears to fit onto KJ 20525 mandible.

Left C_1, male. A small fragment with most of root and crown lacking, but cervix is largely preserved. Approximately same size as KJ 20525 canine.

Right mandible fragment with roots of M_2. Seems to fit by a small contact with back of KJ 20525 mandible.

Several other mandibular corpus fragments and some indeterminate bone fragments.

Spinous process, or transverse process fragment.

KNM-KJ 20525

Right male mandibular corpus fragment with roots of I_1–M_1. Only a small portion of inferior margin is preserved.

BMNH M18945

Right mandibular fragment with M_3. Inferior portions of roots of M_2 can also be observed. May fit onto posterior end of KNM-KJ 20525 and fragment from RA95-1.

BMNH M18946

Left edentulous mandibular corpus fragment preserving mental foramen, distal root of P_3, and roots of P_4 and M_1.

Second individual

BMNH unaccessioned.

Left proximal fragment of a femur, preserving head, neck, greater and lesser trochanters, and approximately 1 cm of shaft distal to lesser trochanter.