A NEW LATE MIOCENE SPECIES OF *PARACOLOBUS* AND OTHER CERCOPITHECOIDEA (MAMMALIA: PRIMATES) FOSSILS FROM LEMUDONG'O, KENYA

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ABSTRACT

The Colobinae (Mammalia: Primates) are relatively unknown from the middle to late Miocene of eastern Africa. When they appear in the Pliocene fossil record they are unambiguous and fairly diverse taxonomically, geographically, and ecologically. The primate fauna from the late Miocene of Lemudong'o is dominated by colobines and therefore represents one of the richest fossil assemblages yet published of this subfamily at 6 Ma. At least three species of colobine, including a new species of *Paracolobus*, are represented in this collection. Given the paleoecological reconstruction for Lemudong'o Locality 1, and the postcranial morphology of the cercopithecids, colobines in this area of Africa were occupying a relatively closed or forested habitat, and exhibiting a primarily arboreal habitus, which contrasts with previous hypotheses suggesting that colobines prior to the Pliocene were terrestrial and occupying more open habitats.

Introduction

The cercopithecoids (Old World Monkeys) are commonly thought to have split molecularly from the hominoids (apes) 25–23 Ma, presumably in Africa (Kumar and Hedges, 1998), although a recent analysis suggests that it may have been 34–29 Ma (Steiper et al., 2004). During the early- to mid-Miocene, hominoids dominated the primate fossil record. Cercopithecoids are represented only by isolated teeth and jaw fragments, the oldest being from 19-Ma sediments at Napak, Uganda (Pilbeam and Walker, 1968).

The prevalence of hominoids over cercopithecoids started to shift 15 Ma, as is seen at the site of Maboko, Kenya, where significant numbers of cercopithecoid fossils have been recovered (Benefit, 1993, 1999). The Maboko cercopithecoid specimens are attributed to the genus *Victoriapithecus* and show a combination of traits that are primitive relative to the modern colobines and cercopithecines, and traits that are derived relative to the hominoids. Therefore, Benefit (1993) elevated the *Victoriapithecus* fossils to their own family, the Victoriapithecidae, a sister taxon to the Cercopithecidae that encompasses the Colobinae and Cercopithecinae. The latest known *Victoriapithecus* specimens are from the 12.5-Ma Ngorora Formation in Baringo, Kenya (Hill et al., 2002).

This family-level recognition of the *Victoriapithecus* fossils has been argued to elevate the Colobinae and Cercopithecinae to family level distinction as well (Jablonski, 2002, and references therein). Here, I follow the traditional taxonomic ranking and leave the Colobinae and Cercopithecinae differentiated at the subfamily level within the family Cercopithecidae.

The early evolutionary history of the Cercopithecidae remains relatively unknown. The Colobinae are particularly enigmatic in Africa until the Pliocene when they appear to have undergone a radiation of large-bodied forms. The earliest known African colobine specimens are *Microcolobus tugenensis* from Ngeringerowa in the Tugen Hills, Kenya, and a molar from Nakali, Kenya (Benefit and Pickford, 1986). These specimens indicate that colobines and cercopithecines diverged morphologically sometime before 9 Ma. This compares favorably with molecular data that place the split between colobines and cercopithecines at 17.9–14.4 Ma (Raaum et al., 2005).

Outside of eastern Africa, colobines of late Miocene age are known from Wadi Natron, Egypt (*Libypithecus*, perhaps also at Sahabi, Libya), Menacer, Algeria ("?*Colobus*" *flandrini*), and especially the many specimens of *Mesopithecus* from Eurasia (e.g., see Szalay and Delson, 1979; Delson et al., 2000; Jablonski, 2002).

The lower Nawata beds at Lothagam, Kenya, represent the best known late Miocene African cercopithecid assemblage published to date (Leakey et al., 2003). This collection is dominated by papionins (cercopithecines) that constitute 79% of the cranial collection (Leakey et al., 2003, p. 202). The colobines are relatively rare and are best represented by a partial cranium and mandible attributed to the new species *Cercopithecoides kerioensis* (Leakey et al., 2003, p. 216). This skull, KNM-LT 9277, is of unknown provenience, so its age is also unknown, and it may well derive from sediments much younger than the late Miocene (ibid.).

The secure ~7–6-Ma colobine specimens from Lothagam consist of largely isolated teeth and jaw fragments, a fragment

of frontal bone, and a calcaneus (Leakey et al., 2003, p. 218–219). These were all attributed to "Colobinae species B" largely due to their similarity in size, which is slightly larger than the extant *Colobus guereza* (*abyssinicus*) (Leakey et al., 2003, p. 219; revised taxonomy, Grubb et al., 2003, p. 1343). These specimens do not preserve enough morphology to allocate them to genus, and therefore are of limited value to phylogenetic reconstructions. Most of the colobines from Lothagam derive from younger deposits.

The more complete and similarly aged cercopithecid fossils from Lemudong'o (Ambrose, Nyami, et al, 2007) fill an unknown gap in the evolutionary history of the colobines. There are 281 primate specimens recovered from the site of Lemudong'o. Six other specimens are from the associated sites of Kasiolei and Enamankeon. As described by Ambrose, Bell, et al. (2007) these sites are of equivalent age to Lemduong'o Locality 1 and are therefore considered penecontemporaneous at 6 Ma.

All of the specimens are identified to either Colobinae or Cercopithecidae subfamily indeterminate, indicating that the assemblage may be entirely dominated by colobines. This stands in sharp contrast to other late Miocene and early Pliocene sites where colobines are extremely rare (Grine and Hendey, 1981; Harris et al., 2003, p. 47–48; Leakey et al., 2003; Haile-Selassie et al., 2004). The slightly younger (5.65 Ma) Lukeino Formation is also reported to have a dominance and diversity of colobines in the primate fauna (Pickford and Senut, 2001), although these have not yet been fully published. The 4.4-Ma site of Aramis, Ethiopia also has an unusually high colobine representation, however this is more evenly split between colobines and cercopithecines (WoldeGabriel et al., 1994, p. 333; Frost, 2001a).

Although the Narok/Lemudong'o fossils are in some ways more complete than those found at Lothagam, they are still highly fragmentary. Among 174 dentognathic specimens, only 14 are multiple teeth in jaws. Of these 14, four are juvenile. Isolated colobine teeth are not usually taxonomically diagnostic below the subfamily level. Consequently, taxonomic diagnoses rely heavily on jaw and cranial morphology. The alpha taxonomy of this assemblage, which is the focus of this article, is therefore based on a rather small subset of the total assemblage.

Of the 107 postcranial elements recovered, only one was found in association with craniodental material. Although postcranial elements are not highly taxonomically informative, they do provide insights into the locomotor repertoire of the individual. For cercopithecoids, morphological variation in the distal humerus, proximal ulna, and proximal femur have proven to covary with locomotor habitus most closely. Therefore, the more complete humeral, ulnar, and femoral specimens from Lemudong'o will be discussed.

There are at least three colobine species represented at Lemudong'o Locality 1. The first and best-represented is a new species of *Paracolobus* that is intermediate in size between the other two taxa. The second is a much smaller species of indeterminate colobine morphology. The third is represented only by a few isolated teeth, but is a much larger indeterminate colobine.

Abbreviations

KNM   Kenya National Museum.
NK   Narok District, indicates fossils that are from localities within this district, including Lemudong'o Localities 1 and 2, Enamankeon Localities 1, 2, and 3, and Kasiolei Locality 1.

Dental abbreviations follow the convention of upper case letters = maxillary teeth, lower case = mandibular teeth.

Systematic Paleontology
Order PRIMATES Linnaeus, 1758
Suborder ANTHROPOIDEA Mivart, 1864
Infraorder CATARRHINI E. Geoffroy, 1812
Family CERCOPITHECIDAE Gray, 1821
Subfamily COLOBINAE Blyth, 1863 (1825)
Genus *PARACOLOBUS*

Diagnosis
Following the revised diagnosis of Leakey (1982), the *Paracolobus* face is wide with a moderately long and broad muzzle. The nasal aperture is long with relatively thick lateral margins and a straight lateral profile. The mandibular body is deep and slender with no median mental canal on the symphysis. The premolars are relatively large. The P3 has a small protocone. The maxillary molars are wide relative to length and flare at the cervix. The postcranial elements mainly display features typical of arboreal colobines, but some traits appear to be intermediate between colobine and terrestrial cercopithecine morphology. *Paracolobus* differs from *Cercopithecoides* in having a deep slender mandible and P3 protocone. *Paracolobus* differs from *Rhinocolobus* in the short wide muzzle and may have had relatively larger cheek teeth compared with cranium size.

Type species
Paracolobus chemeroni (Leakey, 1969).

Remarks
Only two named species were previously known for *Paracolobus*, and both date to approximately 2 Ma: *P. chemeroni*, the type species named by R. E. F. Leakey (1969), and *P. mutiwa*, named by M. G. Leakey (1982). *Paracolobus chemeroni* is primarily known from one specimen, KNM-BC 3, a skull lacking the posterior and inferior portions of the cranium but preserving the frontal, face, maxilla, and complete mandible. A partial skeleton is associated with this cranium. Analysis of the postcranial morphology indicates that *P. chemeroni* is somewhat of a locomotory chimera. Although most of its anatomical features match those usually seen in aboreal colobines, a few others are more common to terrestrial colobines (Birchette, 1982). A mandibular corpus from 2.5-Ma deposits in the Afar Region of Ethiopia is also tentatively assigned to *P. chemeroni* (Frost, 2001b, p. 194).

Paracolobus mutiwa is known from the Omo and Lake Turkana drainage system (Leakey, 1982). The type specimen is KNM-ER 3843, a female right maxilla and premaxilla with P4–M3 and some cranial fragments. The hypodigm consists of jaw fragments and isolated teeth from the Omo, Ethiopia, and KNM-ER 125 (a right mandible with m2–3) from Area 130 of Koobi Fora, Kenya. Although there are no postcranial elements included in the original hypodigm of *P. mutiwa*, Leakey (1982, p. 168) maintained a locomotory mix of arboreality and terrestriality for the entire genus.

Paracolobus chemeroni is known only from a male specimen, and *P. mutiwa* from one male and one female specimen. These two species are quite similar in overall size, although *P. mutiwa* is slightly larger (Leakey, 1982, p. 162). The two species differ from each other in that *P. chemeroni* has a higher muzzle, maxillary

fossa, and a wider molar region. The gonial region of the mandible in the largest specimen of *P. mutiwa*, L35-59, is expanded, a trait that has been interpreted to possibly be sexually dimorphic in another colobine, *Rhinocolobus* (Frost and Delson, 2002, p. 722).

A small collection of colobine fossils from Laetoli, Tanzania has also been referred to *Paracolobus* sp. indet. (Leakey and Delson, 1987). These specimens are mostly fragmentary jaws and teeth as well as two postcranial elements (femora). The mandibles are referred to *Paracolobus* because they lack the round robusticity and shallow depth of the mandibular corpus of *Cercopithecoides*. They differ from *Rhinocolobus* in that they appear to have bigger teeth relative to cranial size than *Rhinocolobus*, although this is difficult to demonstrate quantitatively because the specimens are so fragmentary (Leakey and Delson, 1987, p. 98). The Laetoli collection does not contain a mandible complete enough to determine the shape of the gonial region, and therefore it is unknown whether or not this structure expands posteriorly in this assemblage. Although they have some characters that most closely align them with *Paracolobus*, these specimens are smaller than both *P. chemeroni* and *P. mutiwa*, and may represent a new taxon (Leakey and Delson, 1987).

The femoral specimens from Laetoli are referred to *Paracolobus* because they are morphologically similar to the partial skeleton of *Paracolobus chemeroni* (KNM-BC 3), and different from *Cercopithecoides* (Leakey and Delson, 1987, p. 99).

The following new species diagnosis relies solely on craniodental features and not postcranial morphology, as the former are less influenced by epigenetic factors than the latter, given what is currently known about the genetic influences on skeletal morphology.

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PARACOLOBUS ENKORIKAE sp. nov.
Figures 1–3

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Specific diagnosis

Paracolobus enkorikae lacks the significant mandibular gonial expansion seen in *Kuseracolobus*, *Microcolobus*, and *Rhinocolobus*. The mandibular corporeal cross section is less robust and less rounded than is seen in *Cercopithecoides*, but rather deep and somewhat slender as in *Kuseracolobus*, *Paracolobus*, and *Colobus*, but not as slender as is seen in *Rhinocolobus*. The mandibular corpus is of uniform depth, although the inferior margin undulates slightly, reminiscent of both *Colobus* and *Paracolobus*. The anterior surface of the mandibular symphysis lacks both the mental ridges seen in *Procolobus* and the median mental foramen seen in *Procolobus*, *Rhinocolobus*, and *Cercopithecoides*. *Paracolobus enkorikae* has an inferior transverse torus, unlike *Microcolobus*. Unlike *Rhinocolobus* but similar to *Kuseracolobus*, *Paracolobus* and *Procolobus*, *P. enkorikae* has prominentia laterales.

Dentally, the mandibular canines of *P. enkorikae* do not curve labially, unlike *Mesopithecus* and *Colobus*. *Paracolobus enkorikae* has a P3 protocone, similar to *Paracolobus* but different from *Cercopithecoides*. *Paracolobus enkorikae* has a relatively long male p3, as is seen in *Colobus polykomos* and *Paracolobus chemeroni*, compared to *Victoriapithecus* and *Kuseracolobus*. As in *P. chemeroni*, the incisors of *P. enkorikae* are small relative to the first molar, especially in the mandibular dentition, relative to *Victoriapithecus* and *Colobus polykomos*.

The combination of the mandibular corporeal cross-sectional shape, the lack of a posteriorly expanding mandibular gonial

region, the lack of mental ridges or median mental foramen, the presence of prominentia laterales, the slightly undulating inferior mandibular margin, and the presence of a P3 protocone aligns this new species most closely with known species of *Paracolobus*.

Paracolobus enkorikae differs from *P. mutiwa* and *P. chemeroni* most markedly in terms of size, as it is considerably smaller. On average, the dental linear measurements for *P. enkorikae* are 15% smaller than the means published for *P. mutiwa* and on average 30% smaller than *P. chemeroni* (KNM-BC 3) (See Table 2). *Paracolobus enkorikae* is approximately the same size as modern *Colobus polykomos* or slightly larger. *Paracolobus enkorikae* also differs from *P. mutiwa* in that it lacks the documented slight posterior expansion of the mandibular body, a character *P. enkorikae* shares with the type species of this genus, *P. chemeroni*.

Etymology

Enkorika is the name of the village near the site of Lemudong'o whose residents have generously hosted and supported our research in the area. This new species is named in their honor.

Holotype

KNM-NK 44770 (Figure 1) is a nearly complete mandible found in 2003 by Gabriel Ekalale in situ in the mudstones just below the speckled tuff in Area 7 at Lemudong'o Locality 1 (Ambrose et al., 2007a). This specimen preserves the right and left sides of the mandible, eight associated isolated maxillary teeth, fragmentary radius with the articular ends, right humeral shaft and separate (non-conjoining) right distal humerus. The mandible is missing the left gonial angle and ramus but preserves the entire mandibular corpus from the left m3 through the symphysis to the right m1. The symphysis is slightly distorted. The right corpus is broken and missing the inferior aspect below the m1–3. Mandibular crowns preserved: left m3–left canine, right i1, right c-p3, right p4 roots, and right m1–3. Maxillary crowns preserved: left I1–2, M1, and RI2–M1.

Hypodigm

KNM-NK 36515, right mandibular corpus with i1, c, and m1–2, left mandibular corpus with i1–p3, m2–3, left maxilla with P3–M3; KNM-NK 36586, left maxilla with broken C root, P3–4 and M2–3; KNM-NK 36587, left and right mandibular fragments with left c–m3, left i1–right i2, right p3, and right m1–2, right maxillary fragment with P3–M3; KNM-NK 40885, left mandibular corpus with m2; KNM-NK 41301, right mandibular corpus with m2–3; KNM-NK 42276, mandibular corpus with left i1, right p3–m3; KNM-NK 42346, associated left I1–right C and M1; KNM-NK 42376, associated maxillary P4–M2; KNM-NK 42388, right and left maxillary canine fragments; KNM-NK 44866, right and left m3 (antimeres); KNM-NK 44870, right p3.

Horizon

All specimens are from Lemudong'o Locality 1. Specimens for which exact provenience is known indicate that they derive from the mudstones and speckled tuff above the sands (Ambrose, Kyule, and Hlusko, 2007).

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Description

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Mandible

As noted above, KNM-NK 44770 (Figure 1) is a nearly complete mandible. All of the crowns are preserved save for the incisors and right p3–4. The symphysis is distorted and although
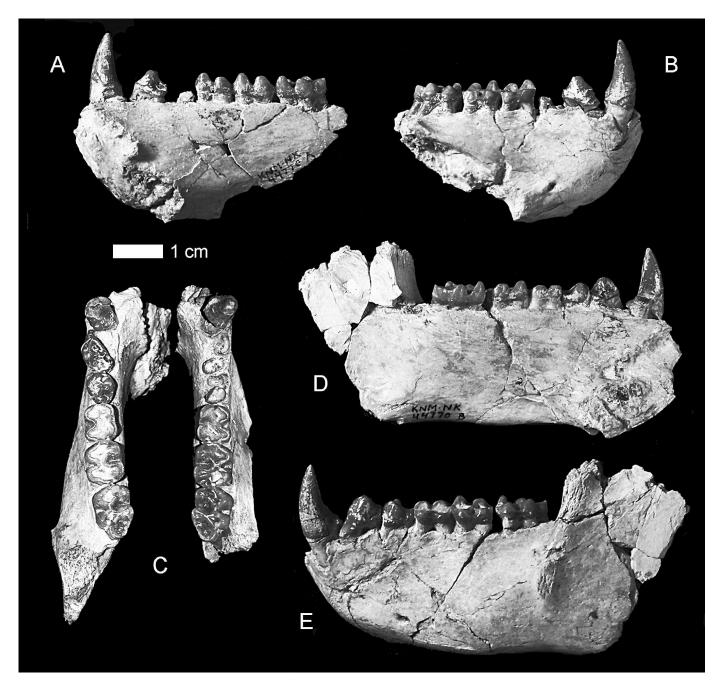
Figure 1. KNM-NK 44770, holotype of *Paracolobus enkorikae*. A, lingual view of the right mandible, mesial is to the left. B, buccal view of the right mandible, mesial is to the right. C, occlusal view, mesial is to the top. D, lingual view of the left mandible, mesial is to the right. E, buccal view of the left mandible, mesial is to the left. Scale bar = 1 cm.

both sides clearly join, the mandibular arch is distorted when they are in articulation.

There is a lateral mental foramen under the mesial root of p4 on both sides of KNM-NK 44770 as it is in KNM-BC 3, and there is no median mental foramen on the anterior aspect of the symphysis. The symphysis is deeper than is seen in *Colobus* with the inferior transverse torus extending to the p4/m1 contact.

The lingual surface of the mandibular symphysis is almost evenly divided from superior to inferior by the genioglossal pit. Modern *Colobus* has a more inferiorly located genioglossal pit

compared to *P. enkorikae*. Both tori on KNM-NK 44770 are well developed, unlike *Microcolobus* that lacks an inferior transverse torus. The anterior surface of the KNM-NK 44770 symphysis is smooth and fairly straight, with no breaks in slope as is seen in some other fossil colobines, and no rugosity like KNM-KP 29255, *Cercopithecoides* sp. indet. (Harris et al., 2003, p. 48). The incisor row would have been rather narrow in life, more so than is seen in modern *Colobus*. Additionally, KNM-NK 44770 does not have a significant retromolar space, as is seen in *Colobus* and other fossil taxa, such as *Kuseracolobus*.
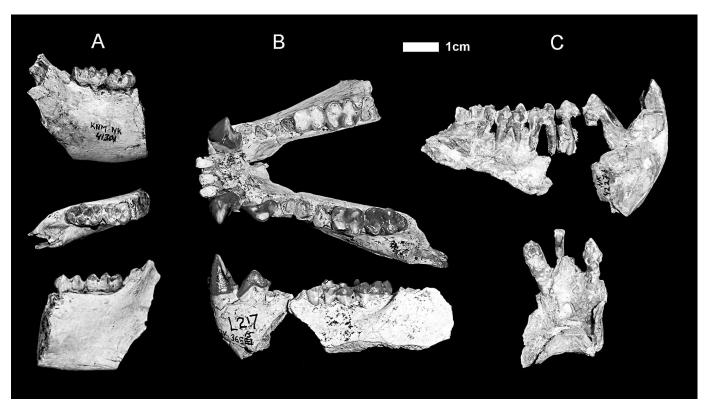
Figure 2. Mandibular material referred to *Paracolobus enkorikae*. A, KNM-NK 41301: (from top to bottom) buccal, occlusal, and lingual views. B, KNM-NK 36515: top, occlusal view; bottom, buccal view, mesial to the left. C, KNM-NK 42276: symphysis and right tooth row; top, buccal view; bottom, lingual view of symphysis. Scale bar = 1 cm.
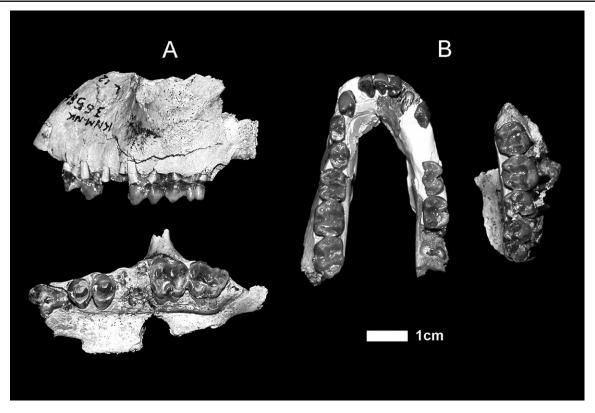

Figure 3. Maxillary and mandibular material referred to *Paracolobus enkorikae*. A, KNM-NK 36586: top, left buccal view; bottom, occlusal view, mesial is to the left. B, KNM-NK 36587: left, occlusal view of the mandible (the white material is molding putty to hold the specimens in approximate anatomical position); right, occlusal view of the maxillary specimen, mesial is towards the bottom. Scale bar = 1 cm.

Table 1A. Measurements of maxillary dental specimens from Lemudong'o Locality 1 by taxon.*

	KNM-NK	M3 md	M3 bl	M2 md	M2 bl	M1 md	M1 bl	P4 md	P4 bl	P3 md	P3 bl	C md	C bl	I2 md	I2 bl	I1 md	I1 bl
small	36516	6.55	7.21	7.05	8.14	7.10	7.42	5.06	6.81	4.58	5.88	—	—	—	—	—	—
	36550	6.19	6.35	6.05	6.61	5.85	6.06	—	—	3.82	5.23	6.00	4.28	—	—	—	—
	41321	7.06	7.48	7.89	8.14	7.30	7.42	4.77	6.93	—	—	6.72	4.75	—	—	—	—
	Average	6.66	7.01	7.00	7.63	6.75	6.97	4.92	6.87	4.20	5.56	6.36	4.28	—	—	—	—
P. enkorikae	36586	9.40	8.43	9.04	9.00	—	—	5.40	7.73	5.09	6.05	—	—	—	—	—	—
	36587	7.75	7.70	8.28	8.63	—	7.27	5.29	7.09	4.55	5.95	—	—	—	—	—	—
	42388	—	—	—	—	—	—	—	—	—	—	8.72	5.83	—	—	—	—
	44770	—	—	—	—	8.27	7.43	6.19	7.95	6.00	7.28	(7.29)	(5.41)	4.41	4.71	5.66	4.90
	Average	8.58	8.07	8.66	8.82	8.27	7.35	5.63	7.59	5.21	6.43	8.20	6.07	4.41	4.71	5.66	4.90

* Measurements in mm; parentheses = estimate; lower case letters = mandibular; upper case letters = maxillary; md = mesiodistal length; bl = buccolingual width (across the mesial loph(id) for molars, or labiolingual width for incisors); canine md length is the long—axis of the crown in cross—section.

Table 1B. Measurements of mandibular dental specimens from Lemudong'o Locality 1 by taxon.*

	KNM-NK	m1 or m2 md	m1 or m2 bl	m3 md	m3 bl	m2 md	m2 bl	m1 md	m1 bl	p4 md	p4 bl	p3 md	p3 bl	c md	c bl	i2 md	i2 bl	i1 md	i1 bl
Large	36555	—	—	—	—	—	—	10.03	7.77	(8.05)	5.53	11.49	5.62	—	—	—	—	—	—
	36502	10.13	8.04	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	42347	9.68	7.75	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	44860	—	—	—	—	—	—	—	—	—	—	—	—	9.82	7.63	—	—	—	—
	44867	—	—	—	—	—	—	—	—	—	—	11.56	5.66	—	—	—	—	—	—
	44868	—	—	—	—	—	—	—	—	(8.17)	5.66	—	—	—	—	—	—	—	—
	Average	9.91	7.90	—	—	—	—	10.03	7.77	8.11	5.60	11.53	5.64	9.82	7.63	—	—	—	—
Small	36514	—	—	8.50	5.27	6.46	6.06	6.01	5.13	5.03	4.50	5.25	4.63	—	—	—	—	—	—
	41305	—	—	8.72	—	6.86	—	6.14	5.24	—	—	—	—	—	—	—	—	—	—
	Average	—	—	8.61	5.27	6.66	6.06	6.08	5.19	5.03	4.50	5.25	4.63	—	—	—	—	—	—
P. enkorikae	36515	—	—	9.93	6.73	8.30	6.91	7.55	6.04	—	—	9.05	4.17	7.84	5.78	2.61	4.55	2.64	4.81
	36587	—	—	9.47	6.85	8.19	6.83	7.58	—	5.89	4.97	5.87	3.80	5.45	3.85	2.97	4.82	3.49	4.57
	40885	—	—	—	—	8.53	7.20	—	—	—	—	—	—	—	—	—	—	—	—
	41301	—	—	10.12	6.71	8.50	—	—	—	—	—	—	—	—	—	—	—	—	—
	42276	—	—	10.87	—	7.93	—	7.45	—	6.92	—	9.72	4.78	—	—	—	—	2.86	4.82
	44770	—	—	10.21	7.34	8.12	7.15	7.07	5.93	5.92	5.44	9.08	4.46	7.68	5.41	—	—	—	—
	44866	—	—	11.84	7.57	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	Average	—	—	10.40	7.04	8.26	7.02	7.41	5.99	6.24	5.21	8.43	4.30	6.99	5.01	2.79	4.69	3.00	4.73

* Measurements in mm; parentheses = estimate; lower case letters = mandibular; upper case letters = maxillary; md = mesiodistal length; bl = buccolingual width, or labiolingual width for incisors; canine md length is the long-axis of the crown in cross-section.

In terms of the dentition, the canine of KNM-NK 44770 is large and the p3 has a long flange and significant wear facet for honing against the upper canine, indicating that this specimen is a male. The premolars and molars have the deep occlusal relief typical of colobines and are fairly worn. The p4 has a well developed talonid and is more square in occlusal outline than are *Colobus* p4s. The p3 is also buccolingually wider than *Colobus*, making both premolars appear more robust than in modern *Colobus*. The canine is similar in height to male *Colobus*, but straighter compared to the labially curved canines seen in *Colobus* males and *Mesopithecus*.

KNM-NK 36587 (Figure 3B) is an associated set of maxillary and mandibular fragments. This specimen is smaller than KNM-NK 44770 but morphologically similar. KNM-NK 36587 is presumed to be female based on its small size. The preserved molar crowns demonstrate the deep occlusal relief typical of colobines.

KNM-NK 42276 (Figure 2C) is a partial mandible preserving the symphysis with the left canine (broken), left i1, and right p3–m3 that join to the jaw fragments. The other three incisors are present but do not conjoin. The incisors are not flared and quite narrow. The right p3 has a heavily worn honing facet. Overall, KNM-NK 42276 is similar in size to KNM-NK 44770. The genioglossal is centered, as in KNM-NK 44770 but deeper, and unlike *Colobus*. The anterior surface of the symphysis is straight with no break in slope and essentially no rugosity, but a slight delineation of a triangle with apex at incisor midline running back to the inferior aspect of the mandibular body below the p3. KNM-NK 44770 has the same flattish surface, but not the slight ridge that delineates it as in KNM-NK 42276. KNM-NK 42276 also has a sharper inferior margin on the symphysis, whereas KNM-NK 44770 is more rounded. Otherwise, these two specimens share the same morphology. The teeth of KNM-NK 42276 are broken and cracked. The incisors are heavily worn. There is no median mental foramen.

KNM-NK 41301 (Figure 2A) is a partial right mandible with a break mesial to m2 and distal to the lateral ramal eminence of the ascending ramus. This specimen is virtually identical to, but slightly smaller than, KNM-NK 44770. The mandibular body is preserved, showing the depth of the corpus and lack of posterior expansion. The m2 is slightly worn and the m3 unworn save for slight wear facets.

Table 2. Measurements of *Paracolobus enkorikae* compared to *P. chemeroni*, *P. mutiwa*, and *Paracolobus* sp. from Laetoli, and *Victoriapithecus macinnesi* and *Colobus polykomos*.[*]

Maxillary	M3 md	M3 bl	M2 md	M2 bl	M1 md	M1 bl	P4 md	P4 bl	P3 md	P3 bl	C md	C bl	I2 md	I2 bl	I1 md	I1 bl
P. chemeroni	13.16	12.21	11.75	11.93	11.15	10.86	8.10	9.63	8.59	9.37	14.16	11.28	6.4	7.63	6.41	6.93
n =	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
P. mutiwa	14.00	11.4	12.2	13.0	10.4	10.8	7.7	10.2	(7.8)	9.5	—	—	—	—	—	—
n =	1	1	1	1	1	1	1	1	1	1						
Laetoli	10. 5	10.3	9.9	10.0	9.9	8.7	7.1	9.0	7.4	7.7	—	—	—	—	—	—
n =	1	1	2	2	4	2	1	1	1	1						
P. enkorikae	8.58	8.07	8.66	8.82	8.27	7.35	5.63	7.59	5.21	6.43	8.20	6.07	4.41	4.71	5.66	4.90
n =	2	2	2	2	1	2	3	3	3	3	2	2	1	1	1	1
V. macinnesi	6.45	7.14	7.28	8.06	6.17	6.59	4.65	6.5	4.45	5.4	7.6♂ 5.2♀	5.9♂ 4.3♀	3.61	3.95	5.13	4.1
n =	43	43	57	55	38	34	9	9	6	6	40♂ 44♀	40♂ 44♀	15	17	42	46
C. polykomos ♂ n =	7.6	6.9	7.5	7.4	7.0	6.5	5.2	6.7	5.3	5.6	9.8	6.5	4.6	4.4	5.1	4.7
	43	44	48	48	49	49	47	48	49	48	40	38	42	42	43	44
C. polykomos ♀ n =	7.3	6.5	7.2	6.9	6.8	6.2	5.1	6.2	5.1	5.4	7.0	5.5	4.4	4.3	4.9	4.5
	27	27	29	28	30	29	28	29	29	29	23	23	26	26	28	29
Mandibular	**M3 md**	**M3 bl**	**M2 md**	**M2 bl**	**M1 md**	**M1 bl**	**P4 md**	**P4 bl**	**P3 md**	**P3 bl**	**C md**	**C bl**	**I2 md**	**I2 bl**	**I1 md**	**I1 bl**
P. chemeroni	16.04	10.03	12.44	9.5	11.28	7.77	9.53	7.09	14.28	7.68	11.57	8.13	5.22	6.25	5.09	5.79
n =	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
P. mutiwa	17.2	9.9	12.8	9.0	11.4	7.8	—	—	—	—	—	—	—	—	—	—
n =	7	7	8	8	6	4										
Laetoli	14.4	9.0	11.4	8.8	9.7	6.9	—	—	—	—	—	—	—	—	—	—
n =	2	2	4	3	6	3										
P. enkorikae	10.40	7.04	8.26	7.02	7.41	5.99	6.24	5.21	8.43	4.30	6.99	5.01	2.79	4.69	3.00	4.73
n =	6	5	6	4	4	2	3	2	4	4	2	2	2	2	3	3
V. macinnesi	8.87	6.33	7.38	6.72	6.12	5.26	5.58	4.72	7.2♂ 5.5♀	4.4♂ 4.1♀	6.6♂ 4.5♀	4.9♂ 3.4♀	3.05	3.86	3.37	3.76
n =	75	72	86	85	40	39	41	49	11♂ 9♀	14♂ 9♀	47♂ 28♀	47♂ 28♀	29	30	37	43
C. polykomos ♂ n =	9.6	6.3	7.7	6.3	7.2	5.5	6.1	4.9	9.1	5.2	6.9	6.9	3.8	4.8	3.7	4.4
	43	44	47	45	47	45	48	46	44	45	37	36	37	38	38	38
C. polykomos ♀ n =	9.4	6.0	7.4	5.9	7.0	5.2	5.9	4.7	7.1	4.9	5.6	5.3	3.7	4.7	3.7	4.2
	26	24	30	30	30	31	30	30	28	29	26	27	23	24	27	26

[*] Measurements in mm; parentheses = estimate; lower case letters = mandibular; upper case letters = maxillary; md = mesiodistal length; bl = buccolingual width (across the mesial loph(id) for molars, or labiolingual width for incisors); canine md length is the long-axis of the crown in cross-section. Data for *Paracolobus*. sp. from Laetoli is from Leakey (1982, p. 163–164), which is a more taxonomically conservative representation, and thus smaller sample size, than those data presented in Leakey and Delson (1987, p. 106–107) (Delson, pers. com.). Data for *P. chemeroni*, KNM-BC 3 measurements taken by the author, right and left sides averaged. Data for *P. mutiwa* are from Leakey (1982, p. 163–164). *Victoriapithecus macinnesi* data are from Benefit (1993, p. 94–96), pooled measurements from beds 3 and 5, male and female data presented separately for canine honing complex. *C. polykomos* male and female data from Swindler (2002, Appendix 1, tables 129–132, p. 230–231).

KNM-NK 36515 (Figure 2B) is a partial mandible with left m3, m2, roots of m1 and p4 (not shown), p3–right i1 crowns, right canine, p3–4 roots, and m1–2 crowns, and mesial m3 root. All teeth are very worn. The superior torus and genioglossal pit of the symphysis are preserved and are similar to KNM-NK 44770 but smaller. The left p3 honing facet is only slightly worn and the flange is shorter. This p3 morphology and the gracile canines suggest that it is a female.

Summary

Paracolobus enkorikae mandibles are similar in size or slightly larger than modern *Colobus polykomos*. There is significant sexual dimorphism in the canine/p3 honing complex and males are larger than females in overall size. Estimates of sexual dimorphism are based on a limited number of specimens, but is at most 20%. This range of variation is easily encompassed in the range of variation in modern *Colobus polykomos*, who have an average sexual dimorphism of 5% (Swindler, 2002, calculated from tables 129–132, p. 230–231).

Morphologically, the *P. enkorikae* mandibular body is fairly deep, similar to modern *Colobus*, but not as slender as *Rhinocolobus*. *Paracolobus enkorikae* has an undulating inferior mandibular margin when viewed from lateral, similar to *Colobus* and *Paracolobus chemeroni*, with a slight deepening just below m2, slight shallowing below m3, and then a slight increase in depth posteriorly, but it lacks the significant posterior expansion seen in other colobines such as seen in *Kuseracolobus*, *Rhinocolobus*, *Microcolobus*, and specimens of *P. mutiwa*. The mandibular corpus is not robust like *Cercopithecoides* but does have prominentia laterales where the lateral aspect of the ascending ramus originates below the m3.

The symphysis has a rounded slope on the anterior surface with a slight break just below the midpoint. There are no rugosities or mental ridges on the anterior symphysis. The lingual side of the symphysis has a characteristic cercopithecoid shape with both inferior and superior transverse tori, unlike *Microcolobus*. The genioglossal pit is deep and located at the midpoint, unlike the more inferiorly located genioglossal pit of *Colobus polykomos*. The inferior transverse torus extends to the p4/m1 contact. The superior transverse torus extends to mid p3 and is more inferiorly sloping compared to *P. chemeroni*. The KNM-BC 3 superior transverse torus is well-developed and shelflike extending posteriorly to mid p4.

Maxillae

There are four maxillary specimens attributed to *P. enkorikae*. Only two of these, KNM-NK 36586 and KNM-NK 36587, are relatively complete (Figure 3A and 3B, respectively). The other two specimens are associated isolated teeth and will be discussed in the dentition section below.

KNM-NK 36586 (Figure 3A) was the first fossil found at the site in 1995, discovered by M.D. Kyule. This is a left maxilla with LC root, LP3–4 crowns, LM1 roots, LM2–3 crowns. The palate is preserved from M1 to midline and then anterior, and includes the edge of the incisive foramen at mid P3. The canine root is large, suggesting this specimen is probably a male. The hard palate ends just distal to M3, which is unlike the extended hard palate of *Paracolobus chemeroni* that extends beyond M3. The M3 has a reduced distal buccolingual width but it is mesiodistally elongate with a third pair of cusps. The P3 is bicuspid with a well-developed protocone. The root of the zygomatic arch is at M2, like *Paracolobus* and *Colobus*. This indicates that *P. enkorikae* has a more prognathic face than is seen in *Kuseracolobus* and is more similar to *Paracolobus chemeroni*. The depth of palate is like *Colobus*.

KNM-NK 36587 (Figure 3B) is a maxillary fragment preserving the right P3–M3 and some alveolar bone. The cortical bone is missing on the buccal surface, exposing the roots. The palate is preserved almost to midline from P3–M2, showing that the palate was similar in depth to *Colobus* and narrow. The M3 is not mesiodistally reduced, as it is in the smaller specimens that are attributed to a separate species (see below). The P3 has a protocone. The P4 is bilophid and the molars have the deep cusp relief characteristic of colobines. All three molars have varying degrees of a protocone shelf development and a pit on the buccal surface in the notch between the protocone and hypocone. The M1 crown is broken and missing the mesial half of the paracone. Although it is difficult to say with certitude because of the missing cortical bone, the root of the zygomatic process is superior to the mesial root of M2, as in KNM-NK 36586.

Summary

The maxilla of *P. enkorikae* is smaller but morphologically quite similar to *P. chemeroni*. The root of the zygomatic arch originates superior to the M2 indicating that *P. enkorikae* was probably comparable to *P. chemeroni* in the prognathism of the snout. The root of the zygomatic process in *Kuseracolobus* is above M1, which implies it had a shorter snout. The *P. chemeroni* hard palate extends farther back than in *P. enkorikae*, beyond the M3, but in *P. enkorikae* it ends right at the distal edge of M3.

The postcanine tooth row in *P. enkorika* is more convex than in *P. chemeroni*, with its widest breadth at M2, whereas *P. chemeroni* has relatively straight maxillary postcanine tooth rows.

Dentition

Seven of the 11 specimens attributed to *P. enkorikae* consist of isolated or associated teeth not in jaws. Of these, four are mandibular and three maxillary. The following descriptions are based on these isolated teeth as well as those in the jaws described above. Measurements for all teeth are presented in Table 1.

The mandibular dentition is typically colobine in having deep occlusal relief, bilophid molars, and a paraconid on the p3. KNM-NK 40885 is a left m2 with some mandibular bone surrounding it. This has the deep cusp relief of a colobine and is associated with *P. enkorikae* because of its size (Table 1). KNM-

NK 44866 is a pair of antimeric third molars with colobine cusp relief also associated with *P. enkorikae* because of size.

The KNM-NK 36587 mandibular molars that are associated with the maxillary specimens described above have steep cuspal relief and fairly deep grooves on the buccal side between the protoconid and hypoconid with a deep pit, but no interconulid. The molars are relatively unworn, the m3 has only small wear facets on the cusp tips, m2 has small dentine pits, and m1 is only moderately worn.

The p3 specimens of *P. enkorikae* are more narrow than *P. chemeroni* and *C. polykomos*, and more similar proportion-wise to *Victoriapithecus*. The m3 distal lophid is wider than the mesial lophid, a condition common to Asian colobines and sometimes considered primitive for the subfamily, although it is not seen in most African colobines after the late Pliocene (Szalay and Delson, 1979, p. 383).

Variation in the relative sizes of cercopithecid central and lateral incisors is high, but in terms of length, I1 is longer than I2 in both *P. enkorikae* and *Victoriapithecus*, whereas they are subequal in *P. chemeroni* and *C. polykomos*. The breadth decreases from i2 to i1 in *P. chemeroni* and *C. polykomos*, whereas in *Victoriapithecus* and *P. enkorikae* it is about the same. *Paracolobus enkorikae* I1 and I2 have almost the same buccolingual breadth, with I1 being slightly broader, which is the same for *Victoriapithecus* and *C. polykomos*, and different from *P. chemeroni*.

The maxillary specimens also include: KNM-NK 42388, a pair of canines; KNM-NK 42376, associated teeth that are digested and not measured for Table 1; and KNM-NK 42346, associated maxillary teeth.

The distal loph of the M3 of *P. enkorikae* is reduced in buccolingual width but is mesiodistally elongated. The M3 metacone is reduced and about the same size as the paracone, and there is a 3rd cusp pair (accessory cusps) in all known specimens of this new species.

Paracolobus enkorikae has relatively buccolingually narrow maxillary canines compared to other cercopithecids, save for female *Victoriapithecus macinnesi*. The length of the maxillary C is also relatively short compared to the other teeth, more like the proportions seen in female *Victoriapithecus macinnesi*.

Paracolobus enkorikae is quite similar in its dental proportions to *Victoriapithecus*, especially in terms of buccolingual widths (Figures 4 and 5). However, the strong dimorphism of the mesiodistal length of the male p3 is more like that seen in *P. chemeroni* than *Victoriapithecus* (Figure 4). The male maxillary canines of *P. enkorikae* appear to be less mesiodistally long than in male *P. chemeroni*, male *Kuseracolobus aramisi*, male *C. polykomos*, and male *Victoriapithecus macinnesi*.

Discussion

The remains of *P. enkorikae* are quite fragmentary, however they show that 6 Ma in the Narok area there was a colobine with close affinities to *P. chemeroni*, although it was considerably smaller, more like the size of modern *C. polykomos*. *Paracolobus enkorikae* has features that may be more primitive than *P. chemeroni*, such as sharing overall dental proportions with *Victoriapithecus macinnesi* relative to the other taxa compared in Figures 4 and 5. The shape of the mandibular corpus suggests that this genus may have closer evolutionary affinities to the modern *Colobus* monkeys than do many of the better known larger Plio-Pleistocene colobines such as *Rhinocolobus*, *Cerco-*
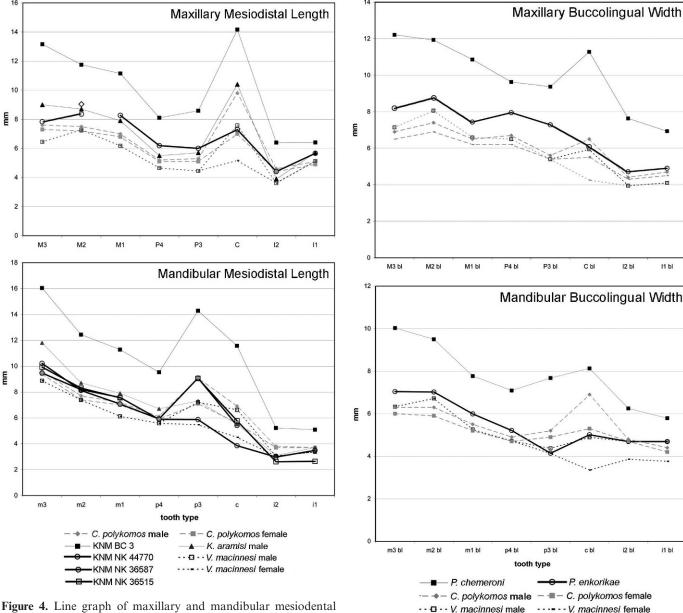
Figure 4. Line graph of maxillary and mandibular mesiodental tooth lengths of *P. enkorikae* and comparative specimens. Measurements are in mm.

pithecoides, and *Kuseracolobus*. A better understanding of the genetic and non-genetic influences on mandibular corpus shape needs to be gained before the taxonomic significance of this variation can be adequately assessed.

<div align="center">

Family CERCOPITHECIDAE Gray, 1821
Subfamily COLOBINAE Blyth, 1863 (1825)
Genus and species indeterminate
SMALL TAXON
Figure 6

</div>

Referred material

KNM-NK 36514 right mandible with p3–m3; KNM-NK 36516 left maxilla with P3–M3; KNM-NK 36550 maxillary fragment with right C–P3 and left M1–3; KNM-NK 41305 mandibular fragments with right m2–3 and left p4–m2; KNM-NK 41321 right maxillary fragment with P4–M3 and associated left M2 and left C.

Figure 5. Line graph of maxillary and mandibular buccolingual tooth widths of *P. enkorikae* and comparative specimens. Measurements are in mm.

Description

The premolar cusp relief of KNM-NK 36514 (Figure 6A) is sharp, even when compared to other colobines. There is a mental foramen below p4. The honing wear on the p3 is only on the surface superior to the paraconid, and not on the flange, which is uncommon. The mandibular body is relatively shallow and gracile. The inferior half of the labial surface and the entire lingual surface of the mandibular symphysis is preserved. The inferior transverse torus extends distally/posteriorly to the mid-point of the p4. The inferior transverse torus is diminutive but present, therefore ruling out an affinity to *Microcolobus*. The genioglossal pit is shallow and located inferiorly compared to *P. enkorikae*, and is more similar to modern *Colobus*. The inferior edge of the symphysis is well delineated, and not rounded as in *P.*
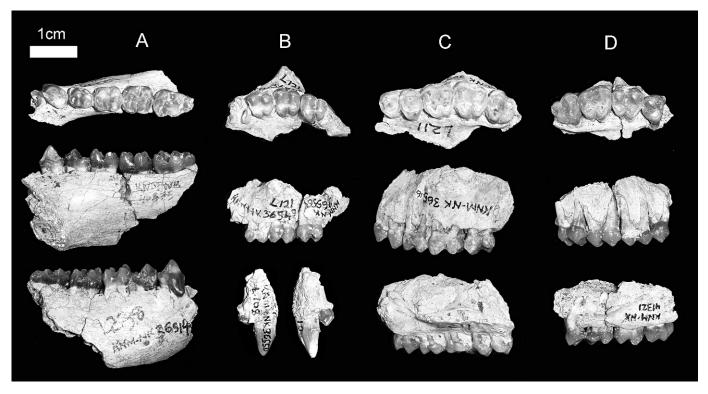
Figure 6. Specimens attributed to the small taxon of Colobinae gen. et sp. indet. A, KNM-NK 36514: from top to bottom: occlusal, lingual, and buccal views. B, KNM-NK 36550: top: occlusal view, mesial to left, middle: buccal view, mesial to the left, bottom left: buccal view, bottom right: lingual view. C, KNM-NK 36516: top to bottom: occlusal, buccal, and lingual views. D, KNM-NK 41321: top to bottom: occlusal, buccal, and lingual views. Scale bar = 1 cm.

enkorikae. Although the symphysis is damaged, it suggests that the shape of the mandible would have been more V-shaped than is common in modern colobines, such as *Colobus.*

KNM-NK 41305 (not shown) is approximately the same size as KNM-NK 36514 but the m3 is slightly longer mesiodistally. The right m1–3 are preserved but the m1 is missing the mesiobuccal side of the protoconid. The entire lingual half of the m2 is missing. The m3 metaconid is broken and missing the mesiolingual aspect, and the buccal enamel of the protoconid is spawled off. Only the superior half of the mandibular corpus is preserved and is identical to KNM-NK 36514. This specimen also has the distal half of the left p4 crown, broken left m1, and left m2 with the surrounding alveolar bone.

Although some of the palate of KNM-NK 36516 (Figure 6C) is preserved, neither the midline nor the anterior part of the greater palatine groove is present. The distal half of the M3 is reduced. The palatal depth is comparable to *Colobus* but the tooth row is more buccally arched. The P3 is more oval in shape than in *Colobus* with a well developed ridge on the mesial aspect and a protocone (bicuspid). The root of the zygomatic process is above the M2 suggesting that this colobine was fairly prognathic.

The fragmentary fossils that comprise KNM-NK 36550 (Figure 6B) were originally accessioned with different KNM-NK numbers that can be seen in the photographs. The zygomatic root is above the M1/M2 contact. The molars have the deep occlusal relief typical of colobines. The M3 is reduced distally. This maxilla is a good size and morphological match for the KNM-NK 36514 and KNM-NK 41305 mandibles, although they are not from the same individuals.

The zygomatic root of KNM-NK 41321 (Figure 6D) is located above M2, and the tooth row is convex as is KNM-NK 36516. KNM-NK 41321 and KNM-NK 36516 are also approximately the same size. The lateral aspect of the greater palatine groove is preserved and again looks like KNM-NK 36516. Maxillary P4 are more asymmetrical than in *Colobus.* An isolated LM2 and LC are associated.

Measurements for all teeth are presented in Table 1.

Discussion

Aside from the size differences between these specimens and those attributed to *P. enkorikae,* there are several morphological differences. The small maxillae have relatively shorter molar rows relative to the premolars, and the maxillary postcanine tooth row is more convex than in *P. enkorikae.* The hard palate of the smaller taxon (e.g., KNM-NK 36516 and KNM-NK 41321) ends at M2 whereas in *P. enkorikae* the hard palate extends to and beyond the M3. The mandible of the smaller taxon lacks the deep genioglossal pit of *P. enkorikae,* as well as the deep mandibular body. These morphological differences coupled with the lack of size overlap indicates that these smaller specimens represent another colobine species.

Due to their fragmentary nature, the taxonomic affinity of these specimens is uncertain. However, they do not share any obviously derived similarities with the known Pliocene genera. When compared to northern African specimens of *Libypithecus,* they are similarly distinct. These Lemudong'o specimens do not show the prognathism or increase in maxillary molar size from
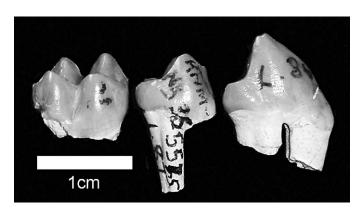
Figure 7. Specimens attributed to the large taxon of Colobinae gen. et sp. indet. KNM-NK 36555, buccal view, mesial is to the right. Scale bar = 1 cm.

anterior to posterior, characteristic of *Libypithecus*. The maxillary tooth row is more buccally curved than in *Colobus* and many other colobines. It is not known whether or not the mandibular corpus expanded posteriorly like *Kuseracolobus* or was uniform in depth like *P. enkorikae*.

Family CERCOPITHECIDAE Gray, 1821
Subfamily COLOBINAE Blyth, 1863 (1825)
Genus and species indeterminate
LARGE TAXON
Figure 7

Referred material

KNM-NK 36502 left m1 or m2; KNM-NK 36555 mandibular dentition with Lp3–4, Rp3–m1, probably associated with KNM-NK 36502; KNM-NK 42347 right m1 or m2; KNM-NK 44860 lower left canine; KNM-NK 44867 right p3; KNM-NK 44868 left p4.

Description

All of these specimens are isolated or associated teeth. There are no jaws. Based on the preservation, it is most likely that these specimens derive from the sands below the more fossiliferous mudstones, from which *P. enkorikae* is predominantly found. Measurements for all teeth are presented in Table 1. These specimens are roughly the size of a female *Papio cynocephalus* (Swindler, 2002, table 124, p. 227).

The morphology of these crowns is typical for colobines, with deep occlusal relief, bilophodont molars, and a paraconid on the p3. Although they are morphologically similar to the other colobines from Lemudong'o, they are attributed to a different taxon because they are considerably larger (Table 1). Figure 7 shows three associated teeth, KNM-NK 36555. The p3 of this set has a short flange, typical of females. When compared to *P. enkorikae*, this female specimen is 25% longer than the length of the male KNM-NK 44770 p3 and the first molar is about 65% longer than the m1 of the small taxon.

The morphology of these teeth does not show any features unusual for a colobine, and no jaw or cranial specimens have been recovered to date. Therefore, the most specific designation that can be made is to Colobinae genus and species indeterminate.

Postcrania
Figure 8

There are 107 non-dentognathic specimens attributed to the Cercopithecoidea from the late Miocene sediments in the Narok District. These include small cranial fragments (*n* = 5), vertebral
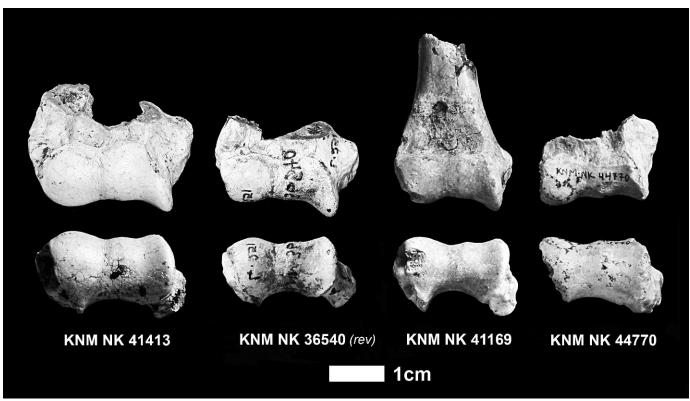

Figure 8. Distal humeral specimens, labeled in figure. Top row: ventral view. Bottom row: inferior view. Scale bar = 1 cm.

Table 3. Ratios and angle measurements for distal humeri from Lemudong'o.[*]

KNM-NK Specimen No.	Epicondyle ratio	Epidondyle angle	Relative flange length
36540	18	32°	57
41169	7.9	55°	58
41413	13.7	49°	50
44770	—	35°	—

   [*] See text for explanation.

and axial fragments ($n = 7$), phalanges ($n = 20$), metapodials ($n = 11$), carpals/tarsals/patella ($n = 14$), ulnae ($n = 9$), radii ($n = 14$), humeri ($n = 17$), tibiae ($n = 5$), and femora ($n = 5$). All are fragmentary. Only one fragment of distal humerus was found in association with craniodental material, KNM-NK 44770, the type specimen for *P. enkorikae* (see above).

Although isolated and fragmentary cercopithecoid postcranial specimens are not typically useful for alpha taxonomy, some elements demonstrate morphological traits that correlate with various locomotor repertoires in modern cercopithecids (e.g., Birchette, 1982; Rose, 1993; Elton, 2001; Frost and Delson, 2002). Animals are functionally integrated units, and therefore interpretations of locomotor patterns based on partial anatomical information must be done with caution. With this caveat in mind, morphological variation in the primate elbow joint and femur has been demonstrated to correlate with habitual arboreality and terrestriality and can therefore provide information about the locomotor habitus of extinct taxa (Birchette, 1982; Rose, 1993; Elton, 2001).

The Narok collection includes only three complete distal humeri: KNM-NK 41413, KNM-NK 41169, and KNM-NK 36540. These specimens are similar in size (Figure 8) and slightly larger than modern *Colobus guereza* (*abyssinicus*) *kikuyuensis*. Given the similarities between these more complete humeri and KNM-NK 44770, the type specimen of *P. enkorikae*, these humeral specimens may be conspecific (see Figure 8).

Three features of the distal humerus have been suggested to be indicative of the locomotory repertoire in Old World Monkeys: the relative inferior projection of the trochlear keel (flange length), the orientation of the medial epicondyle (epicondyle angle), and epicondyle ratio. The measurements and indices are presented in Table 3.

When compared to Frost and Delson (2002, fig. 12, p. 709), the relative flange-length index categorizes these Lemudong'o specimens with the arboreal *Procolobus*, *Nasalis*, and *Colobus*. This compares with those values reported for *Paracolobus chemeroni* (Birchette, 1982, p. 166).

The epicondyle ratio aligns KNM-NK 41413 and KNM-NK 36540 well within the range of *Procolobus* and *Colobus*. KNM-NK 41169 is located at the lower end of the *Colobus* range, and aligns more with terrestrial genera. However, the more terrestrial-looking epicondyle ratio of KNM-NK 41169 is paired with a relative flange length that looks like more arboreal extant genera (Frost and Delson, 2002, fig. 10, p. 707). This proportion of articular surface compares to that reported for *Paracolobus chemeroni* (Birchette, 1982, p. 163–164).

The epicondyle angles for KNM-NK 41413 and KNM-NK 36540 also fall within the range of variation seen in two modern arboreal colobines, *Colobus guereza* and *Presbytis*. KNM-NK 41169 is within the confidence range for *Colobus guereza*, but

better aligns with the variation seen in terrestrial species such as *Chlorocebus aethiops*, *Theropithecus gelada* and *Macaca fascicularis* (Frost and Delson, 2002, fig. 11, p. 708). Again, this compares with the medial epicondyle retroflexion reported for *Paracolobus chemeroni* (Birchette, 1982, p. 161).

These three humeri and the less complete KNM-NK 44770 fall within the range of variation expected for one colobine species that is slightly larger than a modern *Colobus guereza*. Based on dental morphology, KNM-NK 44770 is presumed to be male. The size of the distal humerus aligns with this interpretation, as this specimen is relatively large compared to the three humeri. KNM-NK 41169 is much smaller and may have been a female of the same species.

Ulnae have also proven useful in differentiating terrestrial from arboreal extant colobines. In particular is the retro- or anteflexion of the ulnar olecranon process, as the former is more common in terrestrial taxa and the latter in arboreal taxa (Birchette, 1982, p. 240–242). The ulnae from Lemudong'o Locality 1 have anteflexed olecranon processes, anatomy that is often associated with arboreality in cercopithecoids.

The postcranial specimens thus lend further support to the congeneric interpretation of *P. enkorikae* and *P. chemeroni*, as they both share the same combination of distal humeral and proximal ulnar morphology. The large size difference between these two species suggests that this unusual combination of postcranial features is not an allometric phenomenon.

Femora have also been used to reconstruct locomotor regimes (Frost and Delson, 2002). There is only one relatively complete proximal femur from Lemudong'o, KNM-NK 41175 (not shown). The relative greater trochanter projection for this specimen yields an index of 37.9, which is similar to the arboreal *Colobus guereza* and *Procolobus badius* (Frost and Delson, 2002, fig. 15, p. 712).

Although fragmentary, the postcranial remains from the late Miocene sediments in Narok suggest that the colobines represented in this sample were arboreal. The majority of specimens are within the size range of variation expected for one colobine species similar in sexual dimorphism and slightly larger than modern *Colobus kikyuensis*, and may belong primarily to the new species *P. enkorikae*.

Conclusions

Prior to the recent discovery of, and intense research at, several late Miocene fossil localities in eastern Africa, little was known about the earliest colobines outside of extremely sparse and fragmentary remains (Jablonski, 2002). With its unusually high proportion of colobines, Lemudong'o Locality 1 represents a unique window into the late Miocene evolution of colobines.

Within the Narok material, at least three colobine species are represented: one small, one large, and one intermediate in size belonging to the new species *Paracolobus enkorikae*. These have non-overlapping size ranges, and there are distinct morphological dentognathic differences between *P. enkorikae* and the small taxon.

The two previously recognized species of *Paracolobus* are known from significantly younger deposits: *P. chemeroni* dates from 3.2 Ma (Deino and Hill, 2002, p. 150) and *P. mutiwa* dates from 3.36 to 1.88 Ma (Jablonski, 2002). The new species described here dramatically increases the time range for this genus. The similarities between *P. enkorikae* and *Victoriapithecus* and lack of

autapomorphic features does not preclude this genus from being ancestral to any of the Pliocene genera.

These three colobine taxa also inform our understanding of the paleoecology and paleobiology of colobines in the late Miocene. It has been argued that the earliest colobines were predominately terrestrial, in sharp contrast to the largely arboreal habitus of the extant representatives of this clade (Harris et al., 2003; Leakey et al., 2003). There are two lines of disparate evidence used to bolster this interpretation. The first is that two of the Pliocene colobine genera (*Cercopithecoides* and *Paracolobus*) are often described as having some terrestrial adaptations in their postcranial skeletons (Birchette, 1982). The second line of evidence is that the earliest known cercopithecoid, *Victoriapithecus* from the middle Miocene of Kenya, was a terrestrial frugivore (Benefit, 1999, and references therein). If terrestrial substrate use is primitive for the colobine clade, then the current arboreality in Asian and African colobines arose independently through parallel evolution.

However, the presence of an apparently modern type of arboreality in *Rhinocolobus* (Jablonski, 2002) and the arboreal *Kuseracolobus hafu* (Hlusko, 2006) in the early Pliocene indicate that the most parsimonious scenario is that of an arboreal last common ancestor. *Paracolobus chemeroni*'s unique features have been somewhat of an enigma, especially since they are characterized by only one specimen, KNM-BC 3.

The *P. enkorikae* fossils from Lemudong'o therefore provide an important new insight into the precursors to the radiation of large-bodied colobines seen in the Pliocene. The Lemudong'o mudstone-fossil-horizon fauna is best characterized as representative of a fairly closed, if not forested environment (Ambrose, Bell, et al., 2007). This cercopithecoid assemblage is comprised entirely of colobines or specimens that are indeterminate of subfamily. Therefore, there were at least three colobine species living within close proximity of each other, which were possibly sympatric. The combination of these features with postcranial anatomy most similar to modern arborealists suggests that the earliest colobines, or at least some of their descendants in the late Miocene, were occupying an ecological niche quite similar to modern colobines. Or, these fossils indicate that at least a subset of colobines living about 6 Ma inhabited a niche similar to their extant sister taxa.

Acknowledgments

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