

Early cercopithecoid monkeys from the Tugen Hills, Kenya

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The modern Old World Monkeys (Superfamily Cercopithecoidea, Family Cercopithecidae) can be traced back into the late Miocene, but their origin and subsequent diversification is obscured by the scarcity of terrestrial fossil sites in Africa between 15 and 6 Ma. Here, we document the presence of cercopithecids at 12.5 Ma in the Tugen Hills of Kenya. These fossils add 3 My to the known antiquity of crown Cercopithecidae. The two specimens represent one or possibly two species of early colobine, and their morphology suggests that they were less folivorous than their modern relatives.

paleontology | primates | Catarrhini

The early evolutionary history of crown Old World monkeys is poorly documented (1–4). Cercopithecids have a rich Pliocene and Pleistocene fossil record but are unknown before about 9.5 Ma, when early members of the colobine subfamily are first encountered (4–7). The other cercopithecoid subfamily, Cercopithecoidea, is not definitively known until 7.4 Ma, although poorly dated cercopithecine teeth from Menacer, Algeria, might be slightly older (1, 2, 8, 9). The origin of crown Cercopithecidae is surely earlier than this first appearance of colobines (10, 11), but the middle and late Miocene fossil record in Africa is sparse, with few primate fossil sites between 15 and 6 Ma (4, 12). The Ngorora Formation in the Tugen Hills, Kenya, provides one of the few paleontological windows into this time period (6, 12). Two fossil teeth collected from the Kabasero section of the Ngorora Formation, dated at 12.5 Ma, are identified here as belonging to early colobine monkeys. This discovery considerably extends the temporal range of colobines, in particular, and, therefore, of crown cercopithecids. This has obvious significance for studies that use such data as calibration points for estimating divergence dates within the Primate order (10, 13). The fossils described here also provide fresh insights into the ecological context of Old World Monkey origins. The Kabasero colobines coexisted with a large hominoid and late-surviving members of more primitive Miocene lineages, including a stem cercopithecoid (*Victoriapithecus*) and two dendropithecoids (6, 14, 15). Competition between early cercopithecids and these more archaic taxa has often been invoked in explaining the extinction of the latter (16, 17), but only now are these lineages shown to cooccur paleontologically and probably to have been sympatric.

The colobine specimens reported here come from site Baringo Paleontological Research Project (BPRP) no. 38 (Universal Transverse Mercator coordinate: 36N 0816681 0099805) in the Kabasero type section of the Ngorora Formation, in the Tugen Hills succession. The Ngorora Formation is stratigraphically defined by its bounding lavas, the Tiim Phonolite below, and the Ewalel Phonolites above (18). Between are at least 400 m of sediments, ranging in age from about 13 to 8.5 Ma. The Kabasero section is extremely well calibrated by radiometric and paleomagnetic means (19, 20); the precision of the data has suggested modifications to the Geomagnetic Reversal Timescale for this portion of geologic time. The age of the fossiliferous horizon, and hence of the colobines, is particularly well resolved (6). In the 30-m local succession that encompasses the site, there is an ascending

series of three radiometric dates, the middle of which corresponds exactly to the fossiliferous level. Single-crystal, laser-fusion, ⁴⁰Ar/³⁹Ar determinations give bracketing ages of 12.56 ± 0.04 Ma and 12.26 ± 0.07 Ma, and the result for the fossiliferous horizon itself is 12.49 ± 0.02 Ma (6, 20).

The fossil site is one of relatively small extent, where the fossils are apparently sorted clasts in pumice and lithic pebble conglomerates, interbedded with epiclastic, feldspathic sandstone and primary airfall tuffs. Most fossils are, therefore, small, mainly isolated teeth and fragments of bone but including jaws. Despite this, the assemblage is taxonomically very diverse and provides a unique picture of the African fauna at this time (6).

Previously, the earliest record of colobines consisted of the type specimen of *Microcolobus tugenensis* (7, 21), from Ngeringerowa (BPRP no. 25), a site complex near the top of the Ngorora Formation. Although early estimates of this site's age placed it between 8.5 and 10.5 Ma (7), our more recent radiometric dating narrows this range to between 8.8 and 9.5 Ma (4, 6, 15). Colobines are also known from the roughly contemporaneous site of Nakali, Kenya, at around 9.5 Ma (5, 22), where they appear to be represented by the same genus (5). Outside of Africa, the earliest colobine is *Mesopithecus*, which is found at several sites throughout Southern Europe between 8.5 and 6 Ma (1).

Description and Comparison

KNM-TH 48368 is a right lower molar collected during dry screening in 2006, which we believe to be a third molar (M₃) (Fig. 1 and Table 1). The crown is only slightly worn; with a small island of dentin visible on the protoconid, and minimal wear on the hypoconid. It is slightly smaller in overall size than the M₃s of the *M. tugenensis* type specimen, but is morphologically similar. Like *Micropithecus*, *Mesopithecus*, and many extant colobines (2), KNM-TH 48368 displays a very small but distinct hypoconulid. This cusp is not found on M_{1–2} in crown cercopithecids (23), and its presence, along with the absence of a distal wear facet and the distal convexity of the distal root (*Supporting Information*), indicates to us that it is an M₃. The alternative identification of this tooth as an M₁ or M₂ would imply one of the following: either the tooth belongs to a stem cercopithecoid like *Victoriapithecus* (which retain M_{1–2} hypoconulids) or the M_{1–2} hypoconulid was lost independently in colobines and cercopithecines. The former possibility is countermanded by our cladistic and comparative study of the specimen below, and the latter would overturn well-supported inference (23), the refutation of which will require

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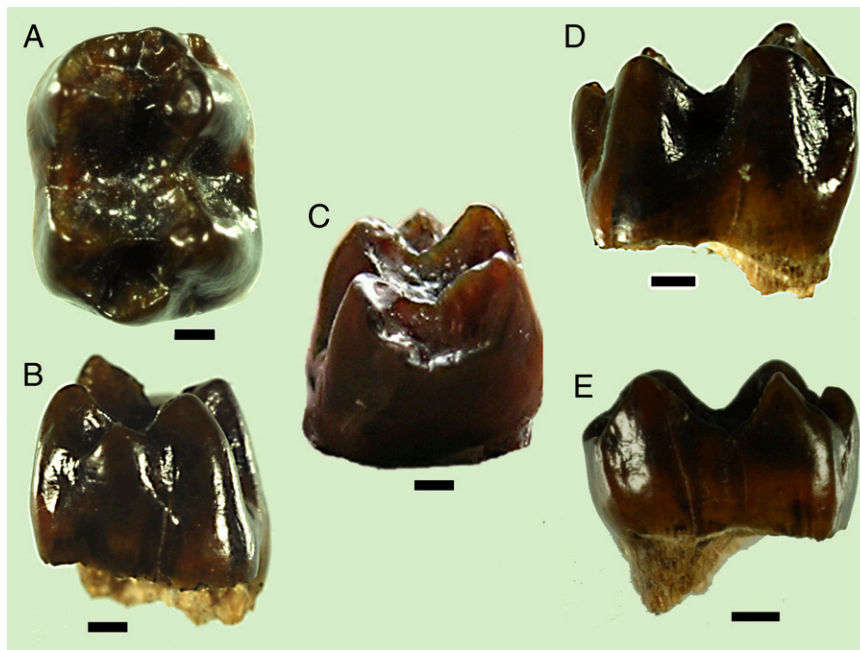


Fig. 1. Mandibular molar KNM-TH 48368; Colobinae gen. et sp. indet. Occlusal (A), distal (B), mesial (C), buccal (D), and lingual (E) views. (Scale bar: 1 mm.)

more definitive evidence than an isolated tooth. Nonetheless, our cladistic and metric comparisons will include treatment of the tooth as both an M_2 and M_3 for the sake of completeness ([Supporting Information](#)).

Pending discovery of further material, we conservatively assign KNM-TH 48368 to Colobinae gen et sp. indet. It resembles *M. tugenensis* and other early fossil colobines (e.g., *Mesopithecus*) in retaining some primitive features (e.g., relatively shorter cusps), but is recognizable as a colobine possessing derived features including tall and sharp transverse lophids, reduced basal flare of the crown, a wide and deep median buccal cleft, buccal cusps with a columnar profile and mesial tilt, a long talonid basin relative to overall crown length, and subequal mesial and distal crown breadths. Unlike M_3 s of *Victoriapithecus*, which is also known from BPRP no. 38 (6, 15), KNM-TH 48368 does not taper distally and despite having a long talonid basin is mesiodistally short, with a small and mesiodistally compressed hypoconulid rather than a large hypoconulid lobe. It exhibits far less basal flare and more marginally placed cusps than *Victoriapithecus* and early cercopithecines.

Like *M. tugenensis*, the present specimen is intermediate in several characteristics compared with extant colobines and cercopithecines. For example, the ratio of cusp height to height of the lingual notch above the crown cervix (NH/NR) approaches the extant colobine range but is within the high end of variation among living cercopithecines (Table 2). The mesial shelf length (MSL) seen in KNM-TH 48368 is similar to that in *Microcolobus*, although the ratio of MSL to overall crown length is at the high end of the colobine range because of the reduction of the hypoconulid and overall reduction in crown length. Numerous other measures of the new specimen fall well within the extant colobine range, particularly those relating to cusp position [basin length (BL)/

overall crown length], flare [mesial cusp proximity/maximum mesial buccolingual breadth (MCP/MW); distal cusp proximity/maximum distal buccolingual breadth (DCP/DW)], and the proportions of the mesial and distal crown breadths (MW/DW). In several instances, the specimen described here appears more primitive than the later *Microcolobus*, which is perhaps to be expected in a specimen 3 Ma closer to the origination of the colobine subfamily. Nonetheless, a cladistic analysis of 19 dental characters confirms the interpretation of KNM-TH 48368 as an early colobine, regardless of whether it is coded as M_2 or M_3 ([Supporting Information](#)).

In addition to KNM-TH 48368, a second isolated tooth from BPRP no. 38 is also recognized here as an early colobine. This lower fourth premolar (KNM-BN 1251) collected from this site in 1972 has been considered to have colobine characteristics in the past (most significantly the taller protoconid compared with metaconid) (6, 7, 15) and is here assigned to that subfamily. In addition to the tall protoconid, KNM-BN 1251 exhibits other colobine features such as reduced flare and a relatively long mesial shelf. Despite primitive features such as a long overall crown length and oblique crown orientation (6, 7), the cladistic analysis of molar and premolar features in this study also confirms that a phylogenetic position within the Colobinae is most likely for KNM-BN 1251 (Fig. 2 and [Supporting Information](#)). Given that this specimen is large relative to KNM-TH 48368, we doubt that they represent the same species, but comparisons of their size ratio to that seen in 26 fossil and extant colobine species show that such a size difference is possible ([Table S5](#)). Accordingly, we tentatively assign both specimens to the same indeterminate colobine species for the time being.

Table 1. Measurements of KNM-TH 48368 and KNM-BN 1251

	P ₄ L	P ₄ B	P ₄ MCP	P ₄ MSL	M ₃ L	M ₃ MW	M ₃ DW	M ₃ MCP	M ₃ BL	M ₃ DCP	M ₃ NH	M ₃ NR
KNM-TH 48368	X	X	X	X	5.9	4.6	4.5	3.4	2.7	3.3	1.5	2.0
KNM-BN 1251	5.5	4.0	2.3	2.4	X	X	X	X	X	X	X	X

See Table 2 for details of measurements. B, maximum buccolingual breadth; L, maximum mesiodistal length; X, unavailable measurement.

Table 2. Lower third molar shape indices

	NH/NR	MCP/MW	DCP/DW	L/MW	MW/DW	SUMS/L	BL/L	MSL/L
KNM-TH 48368	75	74	66	128	102	208	46	29
KNM-BN 1740	112	89	?	141	102	?	?	23
Colobines	116–153	65–80	63–71	120–153	99–108	220–426	38–61	21–32
Cercopithecines	41–76	47–62	49–64	117–152	99–117	180–237	36–41	26–30
<i>Victoriapithecus</i>	76	53	49	141	117	188	35	23

Molar crown shape indices illustrating the mosaic of colobine and primitive cercopithecoid traits in KNM-TH 48368. Ranges in bold indicate those in which the fossil specimen falls. Question marks indicate unknown values. Extant colobine, cercopithecine, and *Victoriapithecus* data are from ref. 23. KNM-BN 1740 is the type specimen of *M. tugenensis* and its data are from ref. 7. Ranges shown for extant colobines and cercopithecines are species means. Data for *Victoriapithecus* are means of *Victoriapithecus macinnesi*. For all indices, the colobine and cercopithecine samples are significantly different ($P < 0.0001$) despite overlap (23). BL, or interlophid distance, is measured between the lowest points of mesial and distal lophids; DCP is between the tips of the entoconid and hypoconid; DW is the widest distance between the sides of the distal cusps; MCP is between the tips of the protoconid and metaconid; MSL is the lowest point of the mesial lophid to the mesial crown margin; MW (maximal mesial width) is the widest distance between sides of mesial cusps; NH, or projection of the metaconid above the lingual notch, is the vertical height from the base of the notch to the point horizontal to the metaconid tip; NR is measured from the base of the notch to the cervical margin directly below it. L, mesiodistal crown length; SUMS, sum of shearing crests.

Discussion and Conclusions

Modern colobine monkeys possess two principal adaptations that permit their high level of folivory: highly developed molar shearing crests that allow them to finely triturate foliage (24) and a sacculated stomach in which fermentation aids in the breakdown of cellulose (25–27). Given their functional synergy, it is tempting to postulate that these two systems evolved simultaneously under selective pressure for increased folivory, but it is not clear that this was the case (3, 26). The less pronounced molar shearing crests of KNM-TH 48368 and other Miocene colobines suggest that they were less folivorous than their modern relatives (3, 7, 28). One of the least

folivorous extant colobines, *Procolobus verus*, is also the smallest (4.2–4.6 kg) and is similar in size to *Microcolobus* and KNM-TH 48368 (~4–5 kg based on molar dimensions) (29). *P. verus* differs from larger African colobines in consuming almost no mature leaves, focusing instead on immature leaves, as well as seeds and fruit (30). With their less advanced dentitions and similar body size, *Microcolobus* and KNM-TH 48368 would clearly have been less folivorous than *Procolobus*. Even the larger Pliocene colobines, which are presumably part of the crown clade, have less developed molar shearing crests than modern genera, implying less folivory (3).

At present, it is not possible to determine whether early stem colobines like *Microcolobus* had acquired the adaptations for foregut fermentation that characterize the modern species, but current evidence indicates that fundamental elements of this system were present in the common ancestor of crown colobines (31, 32). Assuming that Pliocene colobines like *Paracolobus* were members of the crown clade (32), this implies that their foregut fermentation adaptations preceded the evolution of fully modern molar shearing crests. Thus, paleontological and molecular evidence combine to suggest that foregut fermentation was of adaptive utility before highly elaborated molar shearing crests, thereby implying that it originated for some purpose other than folivory of the sort used by modern colobines.

It has been suggested that the initial changes in the colobine dentition may have been partly an adaptation to seed processing (3, 28, 33, 34). The mosaic evolution of colobine molar traits now evident in the fossil record indicates that the first features to evolve were those related to the maintenance of tall, sharp, and broad wedge-like lophids (decreased flare, deep notches, tall cusps, broader and subequal mesial/distal lophids), whereas very high cusps, low crowns, and shearing crest development evolved much later in time (3). This emphasis on sharp, broad, wedge-like lophids and lophids would make early colobines like *Microcolobus* and *Mesopithecus* efficient processors of tough and pliant seeds (33), and molar microwear corroborates that such items were eaten by *Mesopithecus* (28). Such seeds are nutrient-rich if they can be digested (3, 35), and they comprise a significant dietary component for many extant colobines, particularly those of small body size (30, 35, 36). In fact, among extant cercopithecoids, small species are more likely to triturate and digest seeds than to swallow them whole (35). The specialized colobine stomach aids considerably in digesting seeds (26, 35), and on present evidence, it seems a viable hypothesis that it evolved initially for this purpose (26, 34).

If foregut fermentation evolved in one of these small-bodied Miocene colobines because of its value in digesting seeds and unripe fruit, this would have paved the way for subsequent

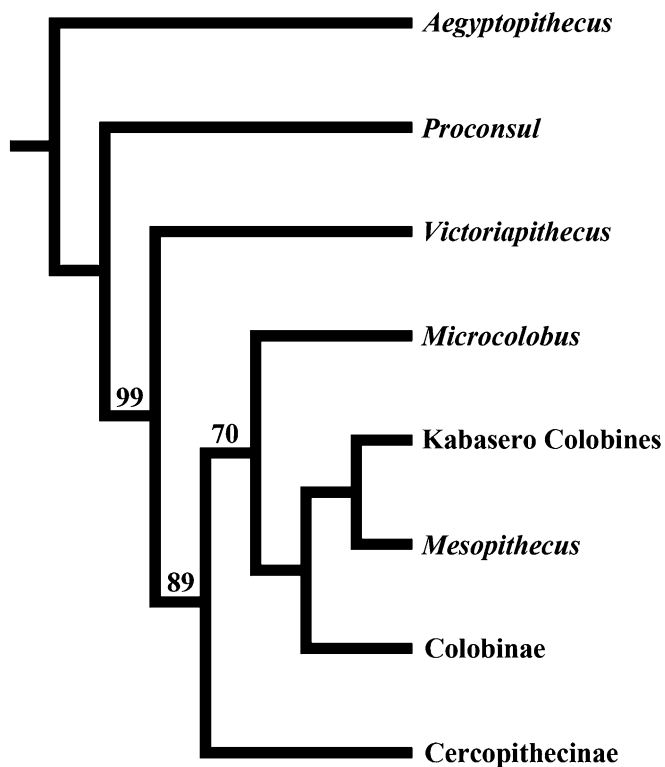


Fig. 2. Phylogenetic placement of the Kabasero colobines, KNM-TH 48368 and KNM-BN 1251. Single-most parsimonious tree resulting from cladistic analysis of 19 molar and premolar traits. The two Kabasero teeth are coded as one taxon, and the molar is coded as an M_3 . For details and results of other assumption sets, see [Supporting Information](#).

selection for increased folivory. Such a shift would require further modifications to the dentition, gut, or body size, and many Pliocene colobines seem to have coupled modest increases in molar-shearing abilities with major increases in body size. These changes may have permitted more folivory, but presumably not as much as in modern species (3, 21). Increasing body size may help to alleviate some of the metabolic challenges involved in digesting foliage (21, 37, 38), but if taken too far, it can compromise access to the terminal branches where leaves are found (39–41). If the large-bodied Pliocene colobines were somewhat folivorous, the shift to true folivory like that exhibited by many modern colobines may have required a reduction in body size for the sake of arboreal foraging efficiency. This would sacrifice the metabolic advantages of large body size and may have necessitated the improved molar shearing abilities seen in modern taxa. Clearly, this is only one of many viable scenarios, but we believe that it is consistent with available evidence.

The adaptations of these early colobines carry broader ecological implications because their emergence has been implicated in the extinction of other catarrhine groups (14, 16, 17, 39, 42). The small ape-like dendropithecoids, as well as the larger proconsuloids, seem to disappear soon after the time when colobines and cercopithecines are thought to diverge (10). It has, thus, been tempting to hypothesize that the adaptations of one or both of these monkey subfamilies placed them in direct competition with the more primitive catarrhines (16, 17, 39, 42). Competitive exclusion is difficult to demonstrate in the fossil record but requires, at minimum, contemporaneity and adaptive similarity (43, 44). Recent discoveries have reduced the chronological gap between the last dendropithecoids and proconsuloids on one hand, and the earliest cercopithecoids on the other (14, 45), and here we show that the three groups were indeed contemporaneous and presumably sympatric. Further illumination of the adaptations of what appears to be a diverse catarrhine fauna at this time (6, 14, 45) will improve our understanding of this important period of faunal change in the catarrhine community.

The fact that this discovery extends the first appearance datum (FAD) for cercopithecids and colobines by about 3 Ma demonstrates, rather disturbingly, the rarity of some higher taxa in the African fossil record and the corresponding imprecision of their existing FADs. This should be taken into consideration when evaluating hypotheses that rely too heavily on such data. For simple geological reasons this site provides the only evidence of fossil monkeys in Africa between about 15 and 10 Ma, but the effects of such missing strata and time periods are rarely sufficiently accounted for in evaluations of faunal change, paleobiogeography, and evolution (46). The representation of African hominoids over this time interval is sparse for the same reasons. Their apparent rarity in Africa at this crucial time is probably more a geological than a biological phenomenon and says little about their biogeographical history.

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1. Delson E (1994) *Colobine Monkeys: Their Ecology, Behaviour, and Evolution*, eds Davies AG, Oates JF (Cambridge Univ Press, Cambridge, United Kingdom), pp 11–43.
2. Delson E (1975) *Approaches to Primate Paleobiology. Contributions to Primatology*, ed Szalay FS (Karger, Basel), pp 167–217.
3. Benefit BR (2000) *Old World Monkeys*, eds Jolly C, Whitehead P (Cambridge Univ Press, Cambridge, United Kingdom), pp 133–179.
4. Gundling T, Hill A (2000) *Old World Monkeys*, eds Whitehead PF, Jolly CJ (Cambridge Univ Press, Cambridge, United Kingdom), pp 180–213.
5. Nakatsukasa M, et al. (2010) Earliest colobine skeletons from Nakali, Kenya. *Am J Phys Anthropol* 143(3):365–382.
6. Hill A, Leakey MG, Kingston JD, Ward SC (2002) New cercopithecoids and a hominoid from 12.5 Ma in the Tugen Hills succession, Kenya. *J Hum Evol* 42(1-2):75–93.
7. Benefit BR, Pickford MH (1986) Miocene fossil cercopithecoids from Kenya. *Am J Phys Anthropol* 69(4):441–464.
8. Leakey MG, Teaford M, Ward CV (2003) *Lothagam: The Dawn of Humanity in Eastern Africa*, eds Leakey MG, Harris JM (Columbia Univ Press, New York).
9. McDougall I, Feibel CS (2003) *Lothagam: The Dawn of Humanity in Eastern Africa*, eds Leakey MG, Harris JM (Columbia Univ Press, New York), pp 43–64.
10. Raaum RL, Sterner KN, Novello CM, Stewart C-B, Disotell TR (2005) Catarrhine primate divergence dates estimated from complete mitochondrial genomes: Concordance with fossil and nuclear DNA evidence. *J Hum Evol* 48(3):237–257.
11. Ting N (2008) Mitochondrial relationships and divergence dates of the African colobines: Evidence of Miocene origins for the living colobus monkeys. *J Hum Evol* 55(2):312–325.
12. Hill A (1999) *Late Cenozoic Environments and Hominid Evolution: A Tribute to Bill Bishop*, eds Andrews P, Banham P (Geological Society of London, London), pp 85–97.
13. Steiper ME, Young NM (2006) Primate molecular divergence dates. *Mol Phylogenet Evol* 41(2):384–394.
14. Rossie JB, Hill A (2005) A new small-bodied ape from the middle Miocene Ngorora Formation, Tugen Hills, Kenya. *Am J Phys Anthropol Suppl* 40:178–179.
15. Gilbert CC, Goble ED, Hill A (2010) Miocene cercopithecoids from the Tugen Hills, Kenya. *J Hum Evol* 59(5):465–483.
16. Simons E, Fleagle JG (1973) The history of extinct gibbon-like primates. *Gibbon & Siamang* 2:121–148.
17. Simons EL (1970) *Old World Monkeys: Evolution, Systematics, and Behavior*, eds Napier JR, Napier PH (Academic, New York), pp 97–137.
18. Bishop WW, Chapman GR (1970) Early Pliocene sediments and fossils from the northern Kenya Rift Valley. *Nature* 226(5249):914–918.
19. Tauxe L, Monaghan M, Drake R, Curtis G, Staudigel H (1985) Paleomagnetism of Miocene East African Rift sediments and the calibration of the Geomagnetic Reversal Time Scale. *J Geophys Res* 90(B6):4639–4646.
20. Deino A, Tauxe L, Monaghan M, Drake RE (1990) 40Ar/39Ar age calibration of the litho- and paleomagnetic stratigraphies of the Ngorora Formation, Kenya. *J Geol* 98:567–587.
21. Leakey MG (1982) Extinct large colobines from the Plio-Pleistocene of Africa. *Am J Phys Anthropol* 58(2):153–172.
22. Aguirre E, Leakey P (1974) Nakali: Nueva fauna de *Hipparion* del Rift Valley de Kenya. *Estudios Geologicos* 30:219–227.
23. Benefit BR (1993) The permanent dentition and phylogenetic position of *Victoriapithecus* from Maboko Island, Kenya. *J Hum Evol* 25(2):83–172.
24. Walker P, Murray P (1975) *Primate Functional Morphology and Evolution*, ed Tuttle RH (Mouton, The Hague), pp 135–150.
25. Kuhn H-J (1964) Zur Kenntnis von Bau und Funktion des Magens der Schlangkaffen (Colobinae). *Folia Primatol (Basel)* 2(4):193–221.
26. Chivers D (1994) *Colobine Monkeys: Their Ecology, Behaviour, and Evolution*, eds Davies AG, Oates JF (Cambridge Univ Press, Cambridge, United Kingdom), pp 205–228.
27. Bauchop T, Martucci RW (1968) Ruminant-like digestion of the langur monkey. *Science* 161(3842):698–700.
28. Merceron G, et al. (2009) Folivory or fruit/seed predation for *Mesopithecus*, an earliest colobine from the late Miocene of Eurasia? *J Hum Evol* 57(6):732–738.
29. Delson E, et al. (2000) Body mass in Cercopithecidae (Primates, Mammalia): Estimation and scaling in extinct and extant taxa. *Anthropol Pap Am Mus Nat Hist* 83:1–159.
30. Davies AG, Oates JF, Dasilva GL (1999) Patterns of frugivory in three West African colobine monkeys. *Int J Primatol* 20(3):327–357.
31. Schienbain JE, Holt RA, Auerbach MR, Stewart C-B (2006) Duplication and divergence of 2 distinct pancreatic ribonuclease genes in leaf-eating African and Asian colobine monkeys. *Mol Biol Evol* 23(8):1465–1479.
32. Jablonski NG, Frost S (2010) *Cenozoic Mammals of Africa*, eds Werdelin L, Sanders WJ (Univ of California Press, Berkeley, CA), pp 393–428.
33. Lucas PW, Teaford M (1994) *Colobine Monkeys: Their Ecology, Behaviour, and Evolution*, eds Davies AG, Oates JF (Cambridge Univ Press, Cambridge, United Kingdom), pp 173–203.
34. Happel RE (1988) Seed-eating by West African cercopithecines, with reference to the possible evolution of bilophodont molars. *Am J Phys Anthropol* 75(3):303–327.
35. Lambert JE (1999) Seed handling in chimpanzees (*Pan troglodytes*) and redtail monkeys (*Cercopithecus ascanius*): Implications for understanding hominoid and cercopithecine fruit-processing strategies and seed dispersal. *Am J Phys Anthropol* 109(3):365–386.

36. Oates JF (1994) *Colobine Monkeys: Their Ecology, Behaviour, and Evolution*, eds Davies AG, Oates JF (Cambridge Univ Press, Cambridge, United Kingdom), pp 75–128.
37. Van Soest PJ (1994) *Nutritional Ecology of the Ruminant* (Cornell Univ Press, Ithaca, NY).
38. Fleagle JG (1985) *Size and Scaling in Primate Biology*, ed Jungers WL (Plenum, New York), pp 1–19.
39. Temerin LA, Cant JGH (1983) The evolutionary divergence of Old World monkeys and apes. *Am Nat* 122(3):335–351.
40. Avis V (1962) Brachiation: The crucial issue for man's ancestry. *Southwest J Anthropol* 18(2):119–148.
41. Grand TI (1972) A mechanical interpretation of terminal branch feeding. *J Mammal* 53(1):198–201.
42. Andrews P (1981) *Aspects of Human Evolution*, ed Stringer CB (Taylor and Francis, London), pp 25–61.
43. Maas MC, Krause DW, Strait SG (1988) The decline and extinction of Plesiadapiformes (Mammalia? Primates) in North America: Displacement or replacement? *Paleobiology* 14(4):410–431.
44. Kelley J (1998) Non-competitive replacement of apes by monkeys in the late Miocene of Eurasia. *Am J Phys Anthropol* 26(Suppl):137–138.
45. Nakaya H, Sawada Y, Kunimatsu Y, Nakatsukasa M, Saegusa H (2006) Late Miocene mammalian fauna including large hominoids from the Nakali Formation, Rift Valley, Kenya. *J Vertebr Paleontol* 26:75A.
46. Hill A (1987) Causes of perceived faunal change in the later Neogene of East Africa. *J Hum Evol* 16(6):583–596.