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Evolution

Recently recovered *Kenyapithecus* mandible and its implications for great ape and human origins

(Primates/Hominoidea/Miocene/Africa/anatomy)

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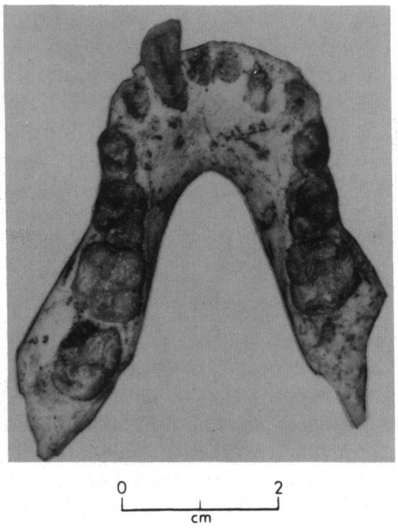
ABSTRACT We report here a *Kenyapithecus africanus* juvenile mandible recovered from middle Miocene (ca. 14–16 million years) deposits of Maboko Island (Lake Victoria), Kenya. Symphyseal and dental attributes of the mandible distinguish *K. africanus*, a species widely regarded as the earliest known member of the great ape and human clade, from other Miocene large-bodied hominoids. The Maboko Island mandible exhibits a markedly proclined symphyseal axis, massive inferior transverse torus, mesiodistally narrow, high-crowned, and strongly procumbent lateral incisor, and molars with cingula restricted to the median buccal cleft. Although the presence of some of these conditions in *Kenyapithecus* was suggested earlier, the fragmentary and ill-preserved nature of previously known specimens led certain authorities to doubt their validity. Our assessment of mandibular and dental morphology indicates that *K. africanus* diverged after *Proconsul* and *Griphopithecus* but prior to the last common ancestor of *Sivapithecus*, extant great apes, and humans. The robustly constructed mandibular symphysis and anterior dentition suggest that incisal biting played as important a role as thick molar enamel in the dietary adaptations of *K. africanus*.

Kenyapithecus africanus (1–3) and *Kenyapithecus wickeri* (4) from middle Miocene deposits of eastern Africa are generally recognized as being among the earliest representatives of the great ape and human clade (5–7). *K. africanus* was initially attributed to *Sivapithecus* (1, 2) and later it was considered to be a direct ancestor of humans (3, 8). The distinctiveness and relationships of *K. africanus* continue to be debated (5–15). Authorities have argued that *Kenyapithecus* is a basal member of the great ape and human clade (6), is specially allied to *Sivapithecus* and *Pongo* (11, 13), or is ancestral to only *Gorilla, Pan,* and *Homo* (7, 14).

An undistorted and nearly complete juvenile mandible of *K. africanus* was recently excavated from middle Miocene deposits on Maboko Island. The fossil was discovered *in situ* in Bed 3 of the Maboko Formation (16), a stratum dated to older than 14.7 and younger than 16 million years old on the basis of geological and faunal evidence (17, 18). The specimen, KNM-MB 20573, is described here and compared with juvenile and adult mandibles of *Proconsul, Sivapithecus, Hylobates, Pongo, Gorilla,* and *Pan*. Aspects of mandibular and dental morphology are used to clarify the affinities and adaptations of *K. africanus*.

DESCRIPTION AND COMPARISONS

KNM-MB 20573 is a juvenile mandible with left I_2 (second incisor), left and right dp_3–M_1 (deciduous third premolar through first molar), and unerupted left M_2 exposed within its crypt (Fig. 1, Table 1). The crown morphology of an unworn isolated right M_2 found adjacent to the mandible is identical to the left M_2 and is considered here to belong to the same individual (Fig. 2 *Right*). The mandibular symphysis and corpus are preserved intact and undistorted, but almost all of the ramus is missing from both sides.



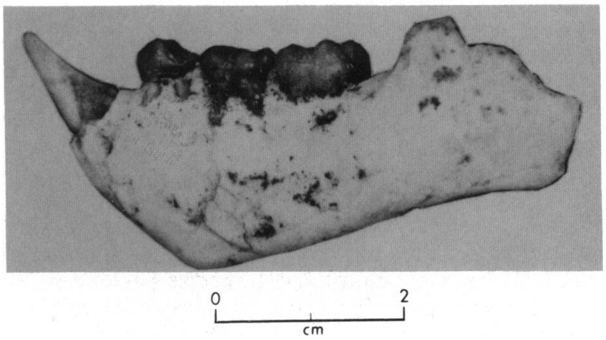


FIG. 1. *K. africanus* juvenile mandible (KNM-MB 20573): occlusal (*Upper*) and left lateral (*Lower*) views.

Unerupted germs of the permanent canine and premolars are evident from radiographic examination (Fig. 3). The specimen exhibits the same dental eruption sequence found among extant apes, with M_2 erupting after I_2. Comparison with the dental development of extant pongids (19) suggests that KNM-MB 20573 represents an individual of between 6 and 7 years. The second molar length of KNM-MB 20573 is most comparable to the mean for female *Pongo pygmaeus* (20), suggesting an adult body weight of approximately 36 kg.

The incisor and canine alveoli form a rounded anterior component of the dental arcade, and dp_3–M_1 are arrayed in

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Table 1. Dimensions of the KNM-MB 20573 mandible, left I_2–M_1, and right M_2

Dimension	mm
I_2 maximal mesiodistal diameter	5.6
I_2 labiolingual diameter	7.8
I_2 crown height	13.4
dp_3 maximal mesiodistal diameter	7.1
dp_3 trigonid buccolingual diameter	4.9
dp_3 talonid buccolingual diameter	4.5
dp_4 maximal mesiodistal diameter	8.7
dp_4 trigonid buccolingual diameter	6.6
dp_4 talonid buccolingual diameter	7.1
M_1 maximal mesiodistal diameter	10.3
M_1 trigonid buccolingual breadth	9.1
M_1 talonid buccolingual breadth	9.3
M_2 mesiodistal diameter	12.6
M_2 trigonid breadth	11.5
M_2 talonid breadth	11.0
Maximal symphyseal length (infradentale–gnathion)	25.0
Minimal symphyseal length (horizontal projection)	21.5
Symphyseal height (vertical projection)	21.1
Maximal symphyseal thickness (perpendicular to maximal symphyseal length)	20.5
Corpus height at dp_4	19.5
Corpus breadth at dp_4	13.5
Corpus height at M_1	16.6
Corpus breadth at M_1	14.2
External bi-M_1 breadth	38.1

a straight line, as in extant great apes. As a result, the dental arcade is U-shaped. The sublingual planum of the Maboko mandible is moderately long and broad but only slightly concave. *Sivapithecus indicus* (7) differs from *Kenyapithecus* in having a sublingual planum that is narrower and more deeply hollowed at the midline.

The symphysis (Fig. 3) is robustly constructed and its long axis is strongly proclined, forming an angle of only 38 degrees to the alveolar margins of dp_3–M_1. In contrast, the symphyseal axes of *Proconsul, Sivapithecus,* and *Ouranopithecus* are more vertically oriented (Fig. 4). *Kenyapithecus* shares with *Sivapithecus* (7, 14), *Ouranopithecus* (23), and extant great apes a posteriorly directed genioglossal fossa and strongly developed inferior transverse torus that extends further posterior than the weak superior transverse torus. In contrast, *Proconsul* lacks an inferior transverse torus (2, 3) but has a strongly developed superior transverse torus and an inferiorly directed genioglossal fossa.

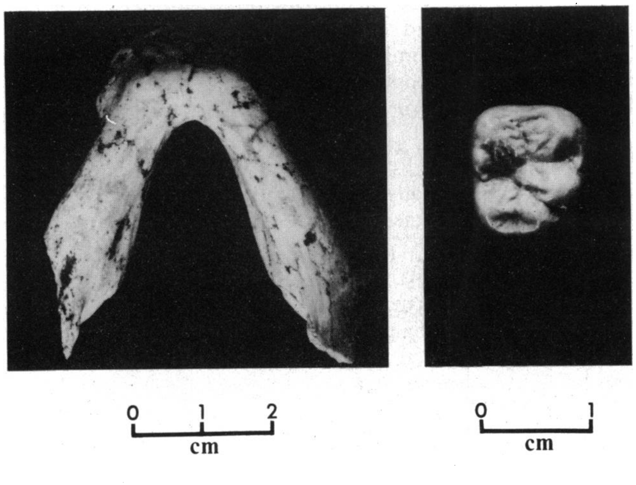

FIG. 2. Inferior view (*Left*) and right M_2 occlusal view (*Right*) of KNM-MB 20573.

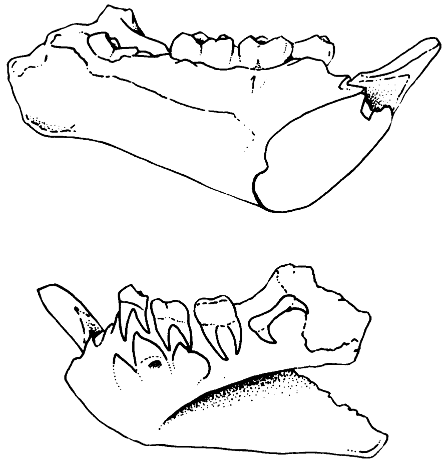

FIG. 3. (*Upper*) Medial view of left half of KNM-MB 20573, showing cross section of symphysis. (*Lower*) Left inferolateral view of KNM-MB 20573 (traced from radiograph), showing positions of unerupted tooth germs [from left to right: C_1 (canine), P_3 (third premolar), P_4, M_2].

Externally, the subincisor plane is bounded on either side by jugae of the unerupted permanent canines and is marked superiorly by paired incisive fossae. Inferiorly, the mandibular body is swollen, shows impressions for digastric attachments, and diverges posteriorly (Fig. 2). The external surface

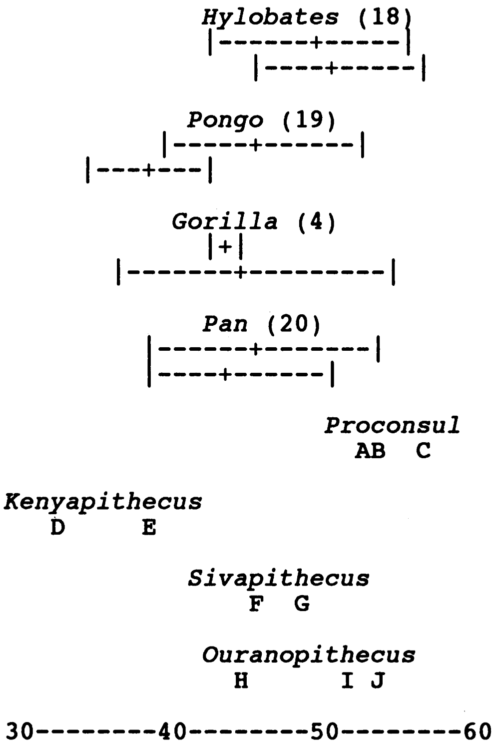

FIG. 4. Orientation of symphyseal axis relative to molar occlusal plane (scale at the bottom in degrees). Numbers in parentheses are sample sizes. Ranges of extant hominoid genera are for juveniles retaining dc_1–dp_4 (upper range of each pair) and for adults with complete permanent dentition (lower range). Note that within each modern genus juveniles and adults exhibit similar orientations of the symphyseal axis. Fossil specimens are as follows: A = KNM-SO 396, *Proconsul major* (7); B = KNM-SO 1112, *Proconsul africanus* (21); C = KNM-RU 7290, *P. africanus* (5); D = KNM-FT 45, *K. wickeri* (22); E = KNM-MB 20573, *K. africanus*; F = GSP 9564, *S. indicus* (7); G = GSP 15000, *S. indicus* (7); H = RPl 75, *Ouranopithecus macedoniensis* (23); I = RPl 56, *O. macedoniensis* (23); and J = RPl 197, *O. macedoniensis* (23).

of the corpus is marked by a hollowed contour below dp_3 and dp_4 and posteriorly by an oblique line which is contiguous with the origin of the ascending ramus (Fig. 1). The mental foramen is positioned low on the corpus and opens anteriorly. A prominent bulge caused by the underlying germ of P_3 is present on the corpus, immediately superior to the mental foramen. A homologous prominence on the anterolateral corpus of *S. indicus* juvenile GSP 11536 was erroneously attributed to the permanent canine (24).

The corpus of KNM-MB 20573 is robust with an index of 69% for buccolingual thickness/height at dp_4. A similar value of corpus robusticity at dp_4 (71%) is observed for *S. indicus* juvenile GSP 11536. Juvenile *Proconsul* mandibles KNM-ME 1 (25), KNM-MO 26 (21), and KNM-SO 541 (21), in contrast, are more gracile, with robusticity indices ranging from 51% to 62% at dp_4. A similar degree of difference in mandible robusticity has been observed between adult *Sivapithecus* and *Proconsul* (7). Corpus height of KNM-MB 20573 decreases distally, its height below M_1 being only 79% of symphyseal height in vertical projection.

Alveoli for the central incisors are labiolingually thick but mesiodistally compressed and are smaller and more anteriorly positioned than I_2 alveoli. The unworn lateral incisor is mesiodistally narrow, labiolingually thick, high-crowned, and procumbently implanted (Fig. 1; Tables 1 and 2). The I_2 exhibits weak lingual relief, including a feebly developed median pillar and basal cingulum. The distal margin is only slightly curved, and it lacks the strong flare usually seen in *Pongo, Gorilla*, and *Pan*. The relative breadth (I_2 mesiodistal diameter/M_1 mesiodistal length) of the KNM-MB 20573 I_2 is comparable to that of *Hylobates* and *Proconsul* but is narrower than that of extant great apes (Table 2). The *K. africanus* I_2 crown is labiolingually thick relative to M_1 length, as for *Proconsul nyanzae, Pongo*, and *Pan*, and is unlike the thinner crowns of *Proconsul africanus, Hylobates*, and *Gorilla* (Table 2). Unworn I_2 crowns of both *Proconsul africanus* and *K. africanus* are slightly taller relative to M_1 length than those of *Pan* and *Pongo*, moderately taller than those of *Gorilla*, and much taller than those of *Hylobates* (Table 2). The most distinctive feature of the KNM-MB 20573 I_2 is its strongly procumbent implantation, which is in line with the orientation of the symphyseal axis. The incisor alveolar process of *S. indicus* mandible GSP 9564 appears to be procumbent (7), but is bent forward with respect to the main symphyseal axis inferior to the alveoli. Moreover, procumbency of the incisor alveolar process is not evident in GSP 15000, in which the incisors follow the more vertical symphyseal axis.

The dp_3 crown is oval and buccally flared. The protoconid is positioned centrally on the longitudinal axis of the crown, at approximately one-third of the total mesiodistal diameter of the crown from the mesial margin. No paraconid is present on the dp_3 of KNM-MB 20573, but the occlusal outline of the crown bears a beak-like angular extension where the preprotocristid joins the mesial margin. A distinct metaconid is closely apposed against the lingual face of, and set distal to, the tip of the taller and larger protoconid. The two cusps are connected by a protolophid. A ribbon-like wear facet is present on the preprotocristid. On the buccal aspect, enamel extends slightly farther inferiorly on the mesial than distal root. A low and weakly developed hypoconid and minute entoconid border the simple talonid basin.

The dp_3 preprotocristid of KNM-MB 20573 resembles that of *S. indicus* and extant great apes in being mesiodistally shorter and less steeply inclined than that of *Proconsul*. The dp_3s of *Kenyapithecus, Sivapithecus*, and extant great apes also differ from the dp_3 of *Proconsul* in having a much shorter buccal extension of enamel onto the mesial root. The Maboko specimen resembles extant African ape dp_3s but differs from *Pongo* and *Sivapithecus* dp_3s in the configuration of the mesial fovea. As for *Gorilla* and *Pan*, the premetacristid is short, intersecting the lingual margin a short distance mesial to the metaconid apex, and an oblique crest runs mesiolingually from the protoconid, dividing the anterior fovea. Mesial to the oblique crest, the anterior fovea is bordered lingually by the short and horizontal mesiolingual margin. In contrast, the premetacristid of *Sivapithecus* and *Pongo* is long and extends further mesially, creating an expansive anterior fovea bounded buccally by the preprotocristid and lingually by the premetacristid. No oblique crest divides the anterior fovea of GSP 11536. The dp_3 of *Kenyapithecus* and extant great apes differs from that of *S. indicus* (GSP 11536) in being less molariform due to the low and poorly developed entoconid and hypoconid and in having a more simple talonid basin.

The dp_4 is molariform, exhibits a Y-5 arrangement of cusps, and differs from M_1 and M_2 in being more elongated and much narrower mesially than distally (Table 1). The KNM-MB 20573 dp_4 differs from *Proconsul* and *Hylobates* dp_4s and is more similar to the dp_4s of extant great apes in having a more buccally positioned hypoconulid. The *Kenyapithecus* dp_4 differs from the dp_4s of *Proconsul* and Pasalar *Griphopithecus* (26–28) in having only a tiny remnant of cingulum restricted to the mesial aspect of the median buccal cleft. The distal lophid connecting the hypoconulid and entoconid is more distinct, and the distal fovea is better defined than in *Proconsul*. The dp_4 enamel is coarsely crenulated.

First and second molar occlusal surfaces are strongly crenulated. Tiny shelves of enamel at the base of the median buccal cleft represent cingular remnants. The M_1 of KNM-MB 20573 is much smaller than M_2 (M_1/M_2 area = 64%), as in *Proconsul* (M_1/M_2 area = 58–80%; ref. 29). In contrast, first and second molars of *Sivapithecus* (M_1/M_2 area = 70–85%) and extant great apes (M_1/M_2 area = 73–115%) are more similar in size (29). The second molar is broader relative to length than the first (Tables 1 and 3). As for *Proconsul major* [KNM-CA 1298, KNM-LG 47,

Table 2. Relative proportions of unworn lateral incisors of *Kenyapithecus, Proconsul* (21), and extant apes

Species	n	Relative breadth*	Relative thickness†	Relative crown height‡
Hylobates lar	7	56 (48–60)	65 (61–69)	91 (81–97)
Pongo pygmaeus	2	76 (70–82)	76 (73–78)	116
Gorilla gorilla	2	62 (61–63)	68 (65–70)	104 (91–117)
Pan troglodytes	5	73 (65–77)	87 (79–92)	114 (104–127)
Proconsul africanus	2	52 (49–55)	69 (65–73)	139
Proconsul nyanzae	2	56 (55–57)	82 (79–85)	
K. africanus KNM-MB 20573		55	76	130

Data are means, with ranges in parentheses.

*I_2 mesiodistal breadth × 100/M_1 mesiodistal length.

†I_2 labiolingual thickness × 100/M_1 mesiodistal length.

‡I_2 labial crown height × 100/M_1 mesiodistal length.

KNM-LG 452 (30), and KNM-SO 415], *Pan*, *Gorilla*, and *Pongo*, the M_2 of KNM-MB 20573 is nearly as buccolingually wide as mesiodistally long (Table 3). In contrast, M_2s of *Afropithecus* (31, 32), *Sivapithecus*, Pasalar *Griphopithecus*, *Dryopithecus*, *Ouranopithecus*, *Proconsul africanus*, and *Rangwapithecus* tend to be more narrow (Table 3). As for *Afropithecus* and *Proconsul*, metaconid and protoconid apices are set closer together relative to mesial crown width than those of *Sivapithecus*, *Gorilla*, and *Pan*. Second molar cusp relief measured as the height of the median lingual notch relative to height of the crown below the notch is similar to relief in *Griphopithecus*, *Dryopithecus*, and *Pan*, greater than relief in *Proconsul*, *Sivapithecus*, and *Ouranopithecus*, and less than relief in *Rangwapithecus* and *Gorilla* (Table 3). The sum of shear crest lengths is similar to that of *Sivapithecus* and *Proconsul* and greater than that of *Afropithecus* (Table 3).

PHYLOGENETIC IMPLICATIONS

There has been a long history of problems with delineation of the distinctive features of *Kenyapithecus* (including *Sivapithecus africanus* and *Ramapithecus wickeri*), as well as with recognition of the genus in the fossil record. *Kenyapithecus* was originally described on the basis of maxillary material from Fort Ternan (4). The type specimen of *Sivapithecus africanus* BMNH 16649 (1, 2), a maxilla which may derive from Maboko Island (33), was transferred to *Kenyapithecus* (3) because it shares molars with reduced cingula and thick enamel with the Fort Ternan maxilla. However, many workers attributed the Fort Ternan material to *Ramapithecus wickeri* (22, 34, 35) while BMNH 16649 was treated as *Dryopithecus (Sivapithecus) sivalensis* (36, 37), *Proconsul nyanzae* (15, 21, 38), or *Sivapithecus africanus* (9, 10, 39). Although most researchers now recognize the Fort Ternan and Maboko fossils as *K. wickeri* and *K. africanus*, respectively, some authorities would place material from both sites into a single species (9, 40), while others would potentially regard them as different genera (11, 13). In addition to the type series of *Kenyapithecus* from Fort Ternan (4, 22, 34, 35), Maboko, and other western Kenyan localities (1–3, 12, 13, 33, 41), the genus has been suggested to be present at Nachola (11), Muruyur (42), and Esha (43) in central and northern Kenya, and at Candir and Pasalar in Turkey (26, 27, 44).

Traditionally, *Kenyapithecus* was defined on the basis of features of the maxilla and upper dentition which are similar to those of *Sivapithecus* (1–4, 9, 10). Recently, maxillary features have been found that are purported to distinguish *Kenyapithecus* from *Sivapithecus*. Material attributed to *K. africanus* from Nachola (11) has been alleged to possess a subnasal pattern similar to that of *Gorilla*, *Pan*, and *Homo* in which the incisive foramen is constricted and the premaxilla is obliquely oriented relative to the palatal process (13). *Sivapithecus* and *Pongo*, in contrast, share a subnasal pattern in which the palatal process intersects the premaxilla at a shallow angle (45). Consequently, *Kenyapithecus* has been interpreted to be divergent from *Sivapithecus* and *Pongo* but to conform to the morphological pattern expected for the last common ancestor of *Gorilla*, *Pan*, and *Homo* (14). However, fossils from Nachola are only tentatively attributed to *K. africanus*; differences in the occlusal morphology of Nachola and Maboko molars (11) may indicate that they belong to different species and possibly genera. A definitive assessment of the generic affinities of the Nachola material must await a more detailed description of the fossils.

The robust construction of the mandibular corpus and strong development of the inferior transverse torus shared by *K. africanus* (KNM-MJ 5, KNM-MB 20573) and *K. wickeri* (KNM-FT 45) are derived with respect to conditions in the extant Hylobatidae and earlier Miocene Proconsulidae. Highly diagnostic mandibular features such as the long and low mandibular symphysis of KNM-MB 20573 were previously observed for *K. wickeri* (KNM-FT 45; ref. 22) and *K. africanus* (KNM-MJ 5; ref. 41), but they were questioned due to the fragmentary and distorted nature of the remains (5, 8). Although the incisor alveoli of KNM-FT 45 indicate a procumbent orientation of the incisors, it was suggested that the incisor roots may have been strongly anteroposteriorly curved (22). Therefore, a procumbent orientation for the lower incisors of *Kenyapithecus* was not fully appreciated until the discovery of KNM-MB 20573. Failure to acknowledge these features as distinctive for *Kenyapithecus* contributed to subsequent confusion as to which fossils belong to the genus (21, 26, 27, 44).

Additional features which distinguish *Kenyapithecus* from *Sivapithecus* and other fossil apes are apparent from consideration of the deciduous premolar morphology of KNM-MB 20573. The dp_3 of *K. africanus* is nearly identical to that of extant great apes, but it is less derived and molariform than that of *Sivapithecus indicus* (24). The dp_4 of the Maboko mandible differs from that of *Griphopithecus darwini* from Pasalar (26–28) in retaining only a slight remnant of the buccal cingulum. From consideration of dp_3 and dp_4 morphology of *Kenyapithecus* it is concluded that *K. africanus* is derived relative to *Proconsul* and *Griphopithecus* and could be ancestral to all great apes, including *Sivapithecus*. In contrast, the derived condition of the *Sivapithecus* dp_3 corroborates other lines of evidence which indicate that it could not have been ancestral to *Gorilla*, *Pan*, and *Homo*.

Table 3. Proportions of relatively unworn second molars

Species	*n*	L/MW*	NH/NR†	Sums/L‡
K. africanus KNM-MB 20573	1	110	90	214
Proconsul africanus	4	119 (118–121)	51 (45–65)	209 (204–216)
Proconsul nyanzae	4	119 (113–126)	58 (50–65)	213 (200–223)
Proconsul major	7	113 (105–120)	56 (46–64)	215 (201–229)
Afropithecus	2	119 (118–121)		190 (177–202)
Rangwapithecus	5	128 (117–133)	96 (74–154)	221 (204–237)
Sivapithecus§	4	114 (102–123)	62 (47–68)	209 (189–227)
Ouranopithecus§	2	118	57 (53–61)	200
Dryopithecus§	3	115 (114–118)	73 (70–76)	218 (213–226)
Griphopithecus§	4	116 (112–122)	104	200 (190–206)

Data are means and ranges.

*Mesiodistal length × 100/mesial width.

†Vertical height from the base of the median lingual notch to the metaconid apex × 100/crown height directly below the base of the median lingual notch.

‡Sum of shear crest lengths × 100/mesiodistal length.

§Measurements are approximations based on casts in the collection of the National Museums of Kenya.

FUNCTIONAL INFERENCES

Previous reconstructions of the functional anatomy of *K. wickeri* attributed abbreviation of the facial skeleton and reduction of canine and incisor size to mastication of hard food items between thick-enamelled molars (8, 22, 34, 35). Although then known only from partial alveoli (22), lower incisors of *Kenyapithecus* were thought to be very small and not to have played an important role in food preparation (8, 35). However, the I_2 of KNM-MB 20573 (and KNM-MB 14, a virtually identical right I_2 collected by L. S. B. Leakey in 1949) demonstrates that the lower incisors of *K. africanus* were moderately large and procumbent. In addition, it is now known that large canines attributable to male *Kenyapithecus* individuals occur at both Fort Ternan and Maboko (12). The small canines of each species, which were once thought to be characteristic of the genus, are likely to represent female individuals (12).

The combination of a moderately large anterior dentition and strong inferior transverse torus suggests that the incisors and canines played a significant role in the feeding adaptations of *K. africanus*. Strain gauge tests of primate mandibles reveal that the inferior transverse torus resists anteroinferiorly directed bending moments during incisal biting (46). The first appearance of a massive inferior transverse torus in hominoids seems to be correlated therefore with biomechanical stresses associated with procumbent implantation of the incisors. Similarly procumbent incisors and robust canines enable the bearded saki (*Chiropotes satanas*) and orangutan to open fruits and nuts with outer coverings too durable for the more gracile dental apparatus of other primates (47, 48). Thick molar enamel and lateral buttressing of the corpus (46) indicate strong occlusal loading on the posterior dentition as well, consistent with the nutcracking adaptation suggested for *Sivapithecus* (49).

The appearance of mandibular features which typify the earliest members of the great ape and human clade (6) is therefore plausibly correlated with increased exploitation of hard fruits and nuts (49), cracked open by a specialized anterior dentition and comminuted between thick-enamelled molars.

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