and electron microprobe analysis. Slotted copper grids were glued over areas of interest, and the samples were removed by immersion in acetone. Samples were prepared for TEM by ion-beam milling, with a Gatan ion-beam mill. TEM was carried out on a JEOL 2010 HRTEM, operating at 200 kV. A Link ISIS energy-dispersive x-ray analysis system, equipped with a Link Pentafet ultrathin window energy-dispersive spectrometer, was used to obtain in situ mineral analyses with the Cliff-Lorimer thin film approximation for data reduction. Experimental k factors were used throughout.

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Equatorius: A New Hominoid Genus from the Middle Miocene of Kenya

**Steve Ward,[1] Barbara Brown,[2] Andrew Hill,[3] Jay Kelley,[4]
Will Downs[5]**

A partial hominoid skeleton just older than 15 million years from sediments in the Tugen Hills of north central Kenya mandates a revision of the hominoid genus *Kenyapithecus*, a possible early member of the great ape–human clade. The Tugen Hills specimen represents a new genus, which also incorporates all material previously referable to *Kenyapithecus africanus*. The new taxon is derived with respect to earlier Miocene hominoids but is primitive with respect to the younger species *Kenyapithecus wickeri* and therefore is a late member of the stem hominoid radiation in the East African Miocene.

An important issue in hominoid systematics concerns the origin of the great ape and human clade. Estimated divergence times among the lineages of extant great apes and humans based on comparative genetics suggest that the last common ancestor of this clade may have lived during the Middle Miocene (about 16 to 11 million years ago) (*1*). The African Middle Miocene hominoid *Kenyapithecus* has been considered to be either an early member of the clade or its sister taxon (*2–4*). Most recent analyses, however, consider *Kenyapithecus* to be too primitive to be closely related to extant great apes and humans (*1*, *5–7*).

Two species of *Kenyapithecus* are currently recognized: *K. wickeri*, from the type locality at Fort Ternan in western Kenya, and *K. africanus*, from several localities in western Kenya, the Tugen Hills, and Nachola in the Samburu region (Fig. 1). All sites producing fossils referable to the genus range in age between 15.5 and ~14 million years ago. The fossils from Fort Ternan, at ~14 million years, are younger in age than all known *K. africanus* specimens. The genus *Kenyapithecus* has been controversial since its initial diagnosis (*8*), in part because of the small sample of *K. wickeri* specimens but also because of a paucity until recently of similarly aged large hominoid fossils from Africa and elsewhere. Consequently, the congeneric status of *K. wickeri* and *K. africanus*, as well as hypotheses that place either of these taxa in the ancestry of modern apes and humans have been questioned (*1*, *5–7*, *9–14*).

Here we describe a partial hominoid skeleton from locality BPRP 122 at Kipsaramon, a Middle Miocene site complex in the Muruyur Formation that is exposed along the northern crest of the Tugen Hills, west of Lake Baringo in central Kenya. The skeleton, KNM-TH 28860, provides new evidence regarding the taxonomic diversity and phylogenetic relationships of Middle Miocene hominoids in Africa.

KNM-TH 28860 is the first Middle Miocene hominoid with associated teeth and postcranial remains (Figs. 2 and 3; Table 1). The specimen includes most of a mandible preserving all teeth except the right central incisor, right canine, and right second molar. Also included are the left maxillary central incisor and both lateral incisors. Postcranial elements include portions of the scapula and sternum, a clavicle, numerous rib fragments, most of the right humerus and the head of the left humerus, a complete right radius, half of the right ulna and parts of the left ulna and radius, five carpal bones, and portions of several fingers. Also preserved are one complete lower thoracic vertebra and other fragmentary thoracic vertebrae. Regressions of dental and long bone dimensions on body mass in a variety of extant primates (*15*) suggest a body mass of approximately 27 kg.

The maxillary central incisor crown is relatively broad mesiodistally in proportion to its height (Fig. 2). There is a low but distinct basal lingual tubercle and a distinct, continuous lingual cingulum on the mesial, distal, and basal margins. The I^2 crown is highly asymmetrical, with a lingual cingulum that "spirals" apically from the mesial to the distal margins of the crown (Fig. 2). The mandibular canine is low-crowned relative to basal crown dimensions, and its size and morphology indicate that KNM-TH 28860

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[1] Department of Anatomy, Northeastern Ohio Universities College of Medicine, Post Office Box 95, Rootstown, OH 44272, USA, and Division of Biomedical Sciences, Kent State University, Kent, OH 44242, USA. [2] Department of Orthopaedic Surgery, Northeastern Ohio Universities College of Medicine, Rootstown, OH 44272, USA. [3] Department of Anthropology, Yale University, New Haven, CT 06520, USA. [4] Department of Oral Biology, College of Dentistry, University of Illinois at Chicago, Chicago, IL 60612, USA. [5] Bilby Research Center, Northern Arizona University, Flagstaff, AZ 86011, USA.

was a male (*16*). Molar buccal cingulae are absent except for tiny remnants at the base of the buccal cleft and on the mesiobuccal surface of the protoconid of M_1. The mandible preserves a well-developed inferior transverse torus and a long sublingual planum (Fig. 3).

The sternebrae are broad and flat. The preserved portions of the scapula are sufficient to determine that the acromion projected well beyond the glenoid and that the axillary margin was longer than the vertebral. The clavicle is not markedly twisted along its long axis. The humerus has a posteriorly oriented and flattened head. There is a pronounced deltopectoral crest, the shaft is retroflected, and the medial epicondyle is posteriorly deflected and relatively small. The ulnar olecranon is proximally elongate, the radial notch faces laterally, and the styloid process is long and contacts the proximal carpal row. The hamate is distinctive in the depth of the pit for the piso-hamate ligament and the depth and degree of twist of the triquetral groove. The metacarpal heads are palmarly broad, and pits for the collateral metacarpo-phalangeal ligaments are dorsal, almost meeting in the midline. The shafts of all digits are relatively gracile and minimally curved. The body of the thoracic vertebra is heart-shaped in proximal and distal views, and there is a discernible ventral keel anteriorly. Overall, the morphology of the body and position of the zygapophyses suggest a long, flexible vertebral column.

The new skeleton from Kipsaramon, combined with previously described specimens from other sites, demonstrates that *K. africanus* and *K. wickeri* represent two distinct genera. The description of the new genus is as follows: Order Primates Linnaeus 1758; Suborder Anthropoidea Mivart 1864; Superfamily Hominoidea Gray 1825; Genus *Equatorius* gen. nov. **Diagnosis:** Mandible with well-developed inferior transverse torus, proinclination of the sublingual planum, and robust corpora; mandibular canine low-crowned in relation to basal dimensions; mandibular molar length sequence $M_1 < M_2 < M_3$; I^1 relatively broad mesiodistally in relation to height, with a broad but low lingual tubercle and a distinct, continuous, but low-relief lingual cingulum and marginal ridges; I^2 with a highly asymmetric mesial-to-distal "spiraled" lingual cingulum; minimal expression of cingulae on both maxillary and mandibular premolars and molars; maxillary premolars buccolingually and mesiodistally expanded relative to M^1; reduction of maxillary premolar cusp heteromorphy; low broad origin of the zygomatic root off the alveolar process and expanded pneumatization of the maxillary alveolar process to include the premolar segment. The general body plan is similar to that of large Early Miocene hominoids, with a long flexible vertebral column; a humerus with a small, flattened, and posteriorly oriented head and posteriorly retroflected shaft; ulnar styloid contact with carpus; and free os centrale. It differs from *Proconsul* and *Afropithecus* in forelimb features relating to elbow and forearm mobility, including a proximal radioulnar joint facing more laterally. The femur has a high neck/shaft angle and relatively small femoral head; there is a robust, adducted hallux.

Etymology: The name reflects the proximity to the equator of all localities from which the genus has been recovered. **Type species**: *Equatorius africanus* (Leakey, 1962). **Diagnosis**: As for genus. **Holotype**: BMNH M 16649, a partial left maxilla with P^3-M^1 and roots of M^2. **Hypodigm**: Large hominoids previously referred to *K. africanus* from the Maboko Formation on Maboko Island, Ombo, Majiwa, Nyakach, and Kaloma. Also assigned to *Equatorius africanus* are large hominoids from the Aiteputh and Nachola Formations at Nachola and the Muruyur Formation in the Tugen Hills (*17*). Junior synonyms: *Proconsul africanus* MacInnes 1943; *Sivapithecus africanus* LeGros Clark and Leakey 1951; *Dryopithecus (Sivapithecus) sivalensis* Simons and Pilbeam 1965; *K. africanus* Leakey 1967; *Griphopithecus africanus* Begun 1987. **Discussion**: *Equatorius* shares a number of features with *Proconsul* and *Afropithecus* that are primitive for large hominoids. These include the morphology of the sternum, proximal humerus, distal ulna, scaphoid/centrale complex, and vertebral column. All three genera possess the primitive molar size sequence $M_1 < M_2 < M_3$ and mandibular canines that are relatively low-crowned with respect to basal crown dimensions, with roots that converge toward the midline. Features shared with *Afropithecus* alone include the lingual morphology of the maxillary central incisor, a distinct, inferior symphyseal torus on the mandible, and a robust mandibular corpus. Hindlimb bones attributable to *Equatorius* from Maboko and Nachola are similar in most respects to those of *Afropithecus* and *Proconsul*, with the exception of the proximal femur, lateral femoral condyle, distal fibula, and hallux (*5*, *18*–*20*).

Equatorius also manifests an array of derived features, which collectively distinguish it from the Early Miocene genera. Premolar and molar cingulae are much reduced (*6*). This latter feature also distinguishes *Equatorius* from *Griphopithecus*, known from the Middle Miocene of southeastern Europe (*21*). The maxillary premolars of *Equatorius*, although enlarged relative to the first molars as in *Afropithecus*, are metrically and morphologically distinct from the latter. *Equatorius* premolars from Maboko and Kipsaramon are longer relative to breadth than are those of *Afropithecus*, and cusp height is more nearly equal. The deciduous third premolar preserved in a juvenile *Equatorius* mandible from Maboko (KNM-MB 20573) possesses a distinct metaconid and lacks significant cingulum formation (*22*). Derived features in the postcranial skeleton of *Equatorius* relative to Early Miocene hominoids include (in addition to those enumerated in the diagnosis) a robust and relatively straight clavicle, reduced and posteriorly deflected humeral medial epicondyle, reduced radial fossa relative to the coronoid fossa on the distal humerus, ulna with heavily buttressed coronoid process and strongly developed supinator crest (*23*),

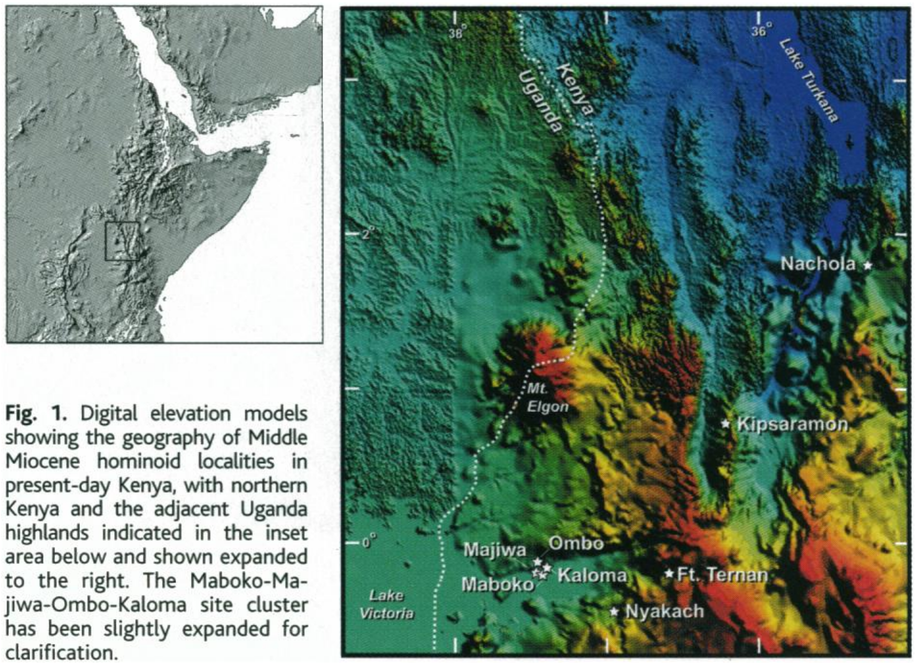

Fig. 1. Digital elevation models showing the geography of Middle Miocene hominoid localities in present-day Kenya, with northern Kenya and the adjacent Uganda highlands indicated in the inset area below and shown expanded to the right. The Maboko-Majiwa-Ombo-Kaloma site cluster has been slightly expanded for clarification.

dorsal position of metacarpo-phalangeal ligament pits, minimal to no sesamoid "fluting" on the metacarpal heads, and a femoral head that projects proximal to the greater trochanter.

Equatorius retains a number of primitive characters for which *K. wickeri* expresses a derived condition. The type maxilla of *E. africanus* differs from that of *Kenyapithecus*, KNM-FT 46, in having a lower origin of the zygomatic root off the alveolar process of the maxilla (*4*, *9*, *11*, *13*, *14*), a morphology found also in maxillae from Nachola (*24*). In addition, the maxillary sinus of BMNH M 16649 excavates the alveolar process to a greater degree and, unlike the Fort Ternan maxilla, extends into the premolar region. In these features, *Equatorius* shares with all *Proconsul* species and *Afropithecus* a similar pattern of midfacial anatomy. These differences in maxillary alveolar and zygomatic topography are important characters in defining the derived morphology of the younger Fort Ternan material with respect to earlier *Equatorius*. The new material from the Tugen Hills reinforces evidence from previous collections that these differences extend to the dentition as well.

Although there is not a uniform pattern of character polarity in the dentition as a whole, *Kenyapithecus* exhibits derived maxillary incisor and mandibular canine morphologies. The *Kenyapithecus* upper central incisor from Fort Ternan, KNM-FT 49, has a singular morphology for African Middle Miocene hominoids (Fig. 4). The lingual marginal ridges are massively inflated, to the point that they begin to envelop the more basal part of the lingual crown surface and obliterate the foveae that typically flank the lingual tubercle. Apically, the marginal ridges turn out from the lingual surface of the crown at abrupt, nearly 90° angles. This morphology contrasts with the more primitive *Equatorius* configuration, in which the lingual topography is more muted and a lingual tubercle is set off from the gradually emergent, low-relief marginal ridges by distinct foveae (*25*). There is also an upper lateral incisor from Fort Ternan, KNM-FT 3637, that lacks the spiral lingual cingulum characteristic of *Equatorius* from Maboko and Kipsaramon (Fig. 4). Instead, it has a nearly symmetrical arrangement of the lingual cingulum and a narrow, median lingual pillar. Determining character polarity in lateral incisor morphology is difficult, but a morphology similar to that of *Equatorius* is found in Early Miocene

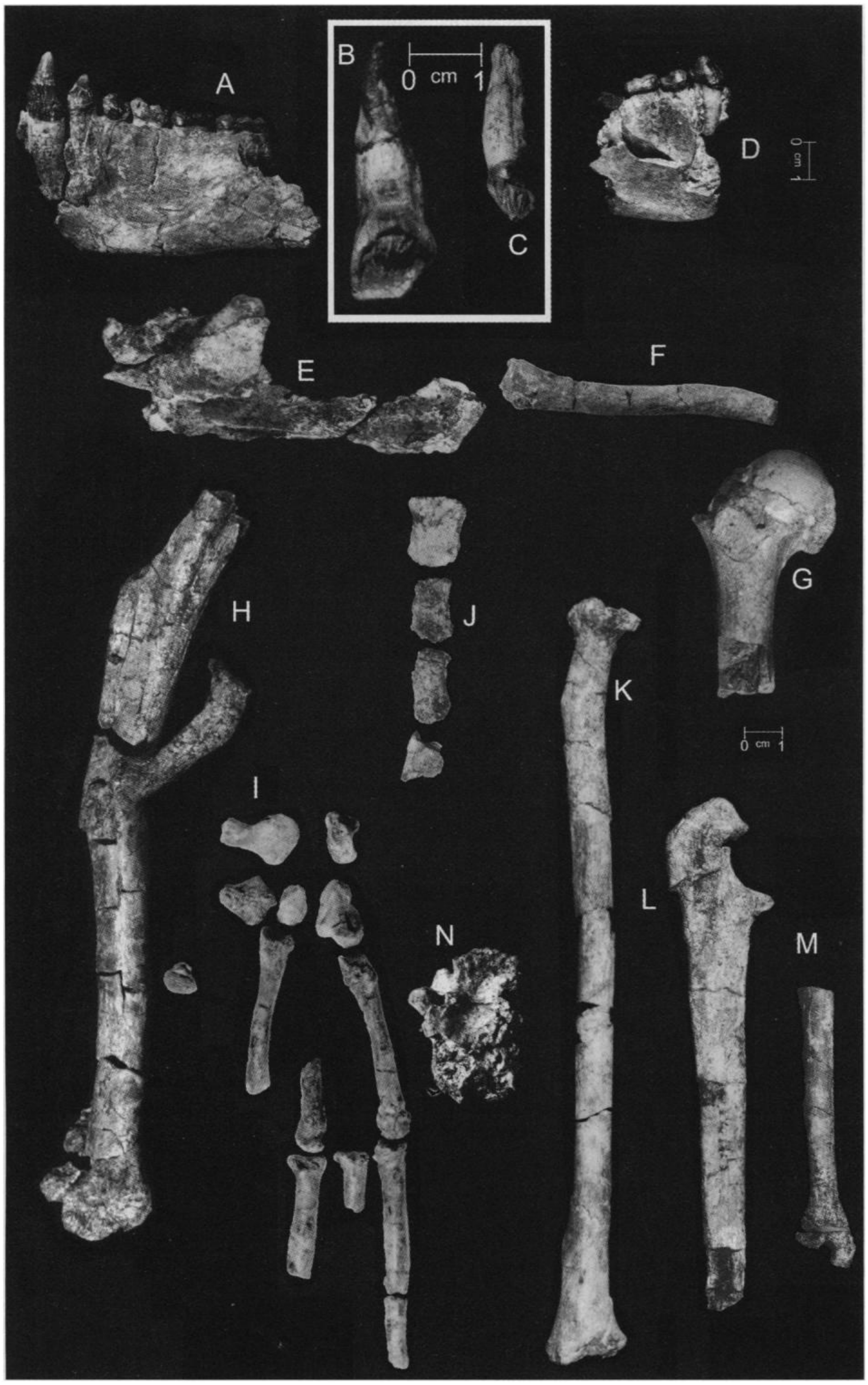

Fig. 2. KNM-TH 28860. (**A**) Left mandibular corpus. (**B**) Left maxillary central incisor. (**C**) Right maxillary lateral incisor. (**D**) Right mandibular corpus fragment. (**E**) Right scapula. (**F**) Right clavicle. (**G**) Left proximal humerus. (**H**) Right humerus with first rib attached. (**I**) Right hand (hamate; trapezium; trapezoid; scaphoid; pisiform; metacarpals II, III, and V; and phalanges). (**J**) Sternum. (**K**) Right radius. (**L**) Right proximal ulna. (**M**) Right distal ulna. (**N**) Lowest thoracic vertebra.

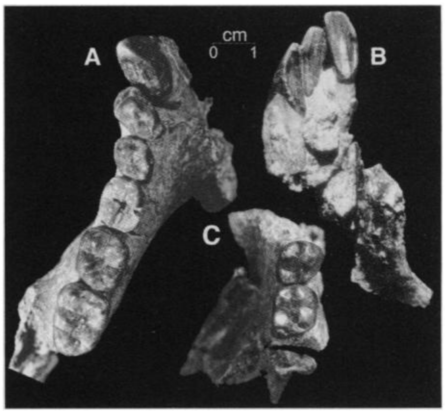

Fig. 3. Mandibular dentition of KNM-TH 28860. (**A**) Left mandibular corpus with C-M_3. (**B**) Symphyseal fragment with left I_1 and I_2 and right I_2. (**C**) Right corpus fragment with P_4 and M_1.

Proconsul major and perhaps *P. africanus*.

A male lower canine from Fort Ternan, KNM-FT 28, is high-crowned in relation to its mesiodistal length. This is an unusual morphology among Early and Middle Miocene hominoids and sets *Kenyapithecus* apart from nearly all contemporaneous and earlier genera (*26*). This morphology contrasts with the primitive, relatively blunt male canine known for *Equatorius* from Kipsaramon and Nachola (*10*) and for *Afropithecus* and *Proconsul* (Fig. 5), but it is similar to the canines of Late Miocene hominoids such as *Dryopithecus* and *Lufengpithecus* (*27*). There are no male lower canines available from Maboko. Single female upper canines are known from both Fort Ternan and Maboko, but the Maboko canine is heavily worn distally, making comparison unreliable. There is a relatively unworn male upper canine of *Kenyapithecus* (KNM-FT 39), but the few male upper canines available for *Equatorius* are all heavily worn or broken, again precluding meaningful comparison.

Lower third premolars of *Kenyapithecus* from Fort Ternan retain a distinct, continuous or nearly continuous lingual cingulum, whereas those of *Equatorius* are more derived, having only small vestiges of cingulae. An upper fourth premolar in the type maxilla of *K. wickeri* has an unusual morphology (*28*). The buccal and lingual cusps are united by a prominent crest, which divides the occlusal surface into mesial and distal foveae. The crest is divided in the middle, creating a small central fovea. Upper fourth premolars of *Equatorius* have a more or less continuous mesiodistally oriented fissure separating the two cusps. One or more crests are variably developed, but these crests never unite to obliterate completely the fissure and partition the occlusal surface into mesial and distal foveae.

A distal humerus from Fort Ternan (KNM-FT 2751) is the only postcranial specimen considered likely to be attributable to *K. wickeri*. It is derived toward the great ape condition in the depth of the olecranon fossa, well-developed lateral supracondylar crest, and in details of the capitular and trochlear anatomy, including a well-developed zona conoidea (*5*, *28*).

Most investigators have viewed the morphology preserved in the type maxilla of *E. africanus* as primitive for large hominoids and that present in the Fort Ternan maxilla as derived toward the extant great ape condition (*4*, *9*, *11*, *13*, *14*). An alternative is that the differences in the *E. africanus* and *K. wickeri* maxillae fall within an acceptable range of variation for a single genus and that the *K. wickeri* morphology is not more derived (*6*). This argument would extend to the apparently derived features of the *K. wickeri* dentition as well. Although the number of presumed derived features of *K. wickeri* is fairly large, the very small sample and consequent limited variation at Fort Ternan have made it difficult to refute the alternative view. However, the overall morphological pattern of *K. wickeri* is now also known to be present in one of the two species represented at the Middle Miocene site of Paşalar in Turkey.

The more common of the two Paşalar species has been assigned to *G. alpani*, whereas the other has not yet been named (*29*–*31*). This second species possesses the derived, high-crowned lower canine (*32*) and a variant of the highly derived upper central incisor morphology expressed by *K. wickeri* (*29*, *33*). It lacks the spiraled upper lateral incisor morphology found in *Equatorius* (*33*) and instead has an I^2 morphology resembling that of *K. wickeri*. It also shares with *K. wickeri* features of the premolar dentition (*33*) and the maxilla (*31*). The presence of the presumed autapomorphic features of *K. wickeri* in a second Middle Miocene hominoid species supports the interpretation that *Kenyapithecus* sensu stricto is derived with respect to *Equatorius* and that morphological differences between the Fort Ternan samples and the other African Middle Miocene samples are not artifacts of small sample size. Thus, *Kenyapithecus* as it has been constituted is paraphyletic. Separating *K. wickeri* and *E. africanus* at the generic level is required to maintain *Kenyapithecus* as a monophyletic taxon.

Recognition of the generic distinctiveness of *Equatorius* and *Kenyapithecus* supports the view that catarrhine diversity in the Middle Miocene was considerable (*13*). The higher taxonomic affiliations of *Equatorius* are still uncertain, but our work supports the suggestion that it is a derived member of the tribe Afropithecini (*12*), generally regarded to be stem hominoids. *Kenyapithecus* is more derived toward later Miocene hominoids and extant great

Table 1. Dental and selected postcranial measurements of KNM-TH 28860. MD, mesiodistal; BL, bucco-lingual; L, length; AP, anteroposterior; ML, mediolateral. All measurements are in millimeters. AP and ML dimensions were taken at mid-shaft.

	Maxillary teeth		
	MD		BL
I^{1R}	10.2		7.5
I^{2L}	6.5		7.1
	Mandibular teeth		
I_{1L}	5.0		6.1
I_{2L}	5.5		8.3
I_{2R}	4.9		8.2
C_L	12.4		9.5
P_{3L}	8.8		12.9
P_{3R}	8.8		12.7
P_{4L}	8.0		8.2
P_{4R}	7.5		8.5
M_{1L}	–		8.9
M_{1R}	9.9		8.5
M_{2L}	11.3		10.5
M_{3L}	13.9		11.3
M_{3R}	14.4		11.2
	Postcranials		
	L	AP	ML
Humerus*	225	18.3	13.8
Ulna†	218	10.9	13.8
Radius	193	8.5	10.7

*Humerus length was estimated by aligning the left proximal humerus with the shaft of the right humerus and correlating the position of deltopectoral crests. †Ulna length was determined by creating a composite ulna using the right and left partial ulnae and then calibrating the composite using the proximal and distal radio-ulnar articulations as landmarks.

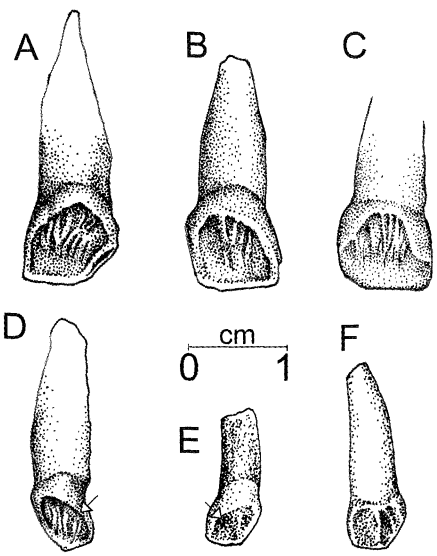

Fig. 4. Middle Miocene hominoid maxillary incisor morphology. All teeth are shown in lingual view. The upper row shows maxillary central incisors, and the lower row shows maxillary lateral incisors. (**A**) KNM-TH 28860. (**B**) KNM-MB 104. (**C**) KNM-FT 49. (**D**) KNM-TH 28860. (**E**) KNM-MB 9729. (**F**) KNM-FT 3637. (A) and (D) are from Kipsaramon; (B) and (E) are from Maboko; (C) and (F) are from Fort Ternan. Note the marked expansion of the marginal ridges on (C) and the "spiral" cingulum (arrows) on (D) and (E).

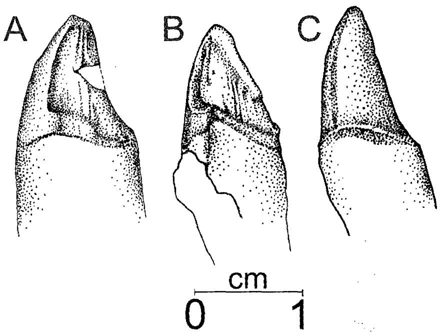

Fig. 5. Mandibular canine crowns in lingual view. (**A**) KNM-WK 17010 from Kalodirr (*Afropithecus*). (**B**) KNM-TH 28860 from Kipsaramon. (**C**) KNM-FT 28 from Fort Ternan. All teeth are unworn and are aligned on a horizontal plane that passes through their mesial and distal cervixes. (B) has been reversed to facilitate comparison with the other teeth. Note the blunter, more robust crowns and greater lingual relief in (A) and (B) when compared with (C).

apes and provides evidence of a link between African and Eurasian hominoids in the Middle Miocene (*34*).

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27. KNM-FT 28 has an index of relative canine height (crown height divided by maximum mesiodistal length) of 1.62. The value for the canine belonging to KNM-TH 28860 is 1.35. Ranges of values and sample sizes for *Proconsul* and *Afropithecus* are, respectively, 1.40 to 1.50 (9) and 1.14 to 1.18 (2); for *Dryopithecus* and *Lufengpithecus* values are 1.54 to 1.61 (3) and 1.56 to 1.85 (7).
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Fossil Plants and Global Warming at the Triassic-Jurassic Boundary

J. C. McElwain,* D. J. Beerling, F. I. Woodward

The Triassic-Jurassic boundary marks a major faunal mass extinction, but records of accompanying environmental changes are limited. Paleobotanical evidence indicates a fourfold increase in atmospheric carbon dioxide concentration and suggests an associated 3° to 4°C "greenhouse" warming across the boundary. These environmental conditions are calculated to have raised leaf temperatures above a highly conserved lethal limit, perhaps contributing to the >95 percent species-level turnover of Triassic-Jurassic megaflora.

The end-Triassic mass extinction event [205.7 ± 4 million years ago (Ma)] was the third largest in the Phanerozoic, resulting in the loss of over 30% of marine genera (*1*) and 50% of tetrapod species (*2*), >95% turnover of megafloral species (*3*, *4*), and marked microfloral turnover in Europe (*5*) and North America (*6*). Many causal mechanisms have been suggested (*7*), but because of the paucity of Triassic-Jurassic (T-J) oceanic sediments suitable for geochemical analyses (*7*–*9*), the associated environmental conditions remain poorly characterized and the causal mechanism or mechanisms equivocal. Here we provide a temporally detailed investigation of the atmospheric CO_2 and climatic conditions associated with the T-J mass extinctions, from analyses of the ecophysiological characteristics of fossil megafloras preserved in composite terrestrial T-J sections in Jameson Land, East Greenland (*10*), and Scania, southern Sweden (*11*).

Evidence from sedimentary facies (*12*), paleosols (*13*), sea-level change (*14*), and flood basalt volcanism (*15*) all indirectly suggest perturbation of the T-J global C cycle. Therefore, likely atmospheric CO_2 variations across the T-J boundary were determined from the stomatal density (SD, number of pores per unit area) and stomatal index (SI, proportion of pores expressed as a percentage of epidermal cells) of fossil leaf cuticles from 7 genera from 16 beds in Jameson Land and 11 genera from 13 beds in Scania. SD and SI are inversely related to the ambient CO_2 concentration during growth (*16*, *17*) and can be used to reconstruct geological time series of atmospheric CO_2 (*18*, *19*). The standardized SD and SI records for both localities were obtained and corrected for changes in species composition between individual beds to remove taxonomic bias (*20*) (Fig. 1).

High-resolution records of SD and SI from both sites showed reductions during the middle Rhaetian persisting into the Hettangian and then returning to preexcursion values (Fig. 1). The reductions are consistent with an increase in atmospheric CO_2 concentration across the T-J boundary, in agreement with inferences from geochemical analyses of fos-

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Department of Animal and Plant Sciences, University of Sheffield, Sheffield, S10 2TN, UK.

*To whom correspondence should be addressed. E-mail: J.McElwain@sheffield.ac.uk