and high-temperature x-ray diffraction was performed on wiggler beam line 10-2 at the Stanford Synchrotron Radiation Laboratory with a photon energy of 20 keV. We collected diffraction patterns in the angle-dispersive mode using image plates; these patterns were angle-integrated to obtain the data shown here [J. H. Nguyen and R. Jeanloz, *ibid.* **64**, 3456 (1993)]. In all cases the instrument resolution was far greater than the intrinsic diffraction linewidths because of the small crystallite size. We collected optical absorption spectra using a scanning ultraviolet-visible spectrometer with 2-nm resolution in 6 to 7 min. Optical transitions in wurtzite nanocrystals are electronically allowed, and the absorption consists of a series of discrete features in the visible region. Rock-salt nanocrystals have a band gap in the near-infrared, and the transitions are electronically forbidden but phonon-assisted, as in the bulk material [S. H. Tolbert, A. B. Herhold, C. S. Johnson, A. P. Alivisatos, *Phys. Rev. Lett.* **73**, 3266 (1994)], resulting in a featureless absorption spectrum. We observed an abrupt change in the electronic absorption, a clear signature of the phase transition.

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A Hominoid Genus from the Early Miocene of Uganda

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Fossils from a large-bodied hominoid from early Miocene sediments of Uganda, along with material recovered in the 1960s, show features of the shoulder and vertebral column that are significantly similar to those of living apes and humans. The large-bodied hominoid from Uganda dates to at least 20.6 million years ago and thus represents the oldest known hominoid sharing these derived characters with living apes and humans.

Between 1961 and 1965, W. Bishop and colleagues recovered facial, dental, and vertebral remains of a large-bodied hominoid from the Moroto II locality in Uganda (*1*, *2*). Although the dental and facial remains have been interpreted as being primitive [(*1*, *3–7*) but see (*8*, *9*)], the lumbar vertebrae have been considered to be morphologically derived and similar to those of living hominoids, suggesting stiff-backed, orthograde positional behavior like that of living apes and humans (*2*, *10–12*). Thus, the Moroto fossils have remained rather enigmatic, and researchers have been reluctant to associate the primitive teeth and face of the Moroto palate with the derived lumbars, even though all of the elements indicate that the body sizes are similar. In 1994 and 1995, we revisited the East African fossil localities known as Moroto I and II in northeastern Uganda and recovered new hominoid postcranial fossils. These provide additional information about the taxonomy, phylogeny, and functional morphology of the Moroto hominoid.

The fossil-bearing sedimentary rocks at Moroto I and II consist of fluvial and lacustrine sedimentary rocks lying unconformably on Precambrian metamorphic gneisses and capped by a basalt flow. At Moroto II, intercalated coarse- to fine-grained sandstone, conglomerate, siltstone, and mudstone indicate that the depositional environment alternated between fluvial and ponding conditions. Fossils have been found at a number of horizons and are typically associated with medium-grained sandstone and siltstone. Poorly developed paleosols in the sequence suggest that sedimentation was intermittently interrupted. The sequence at Moroto II is up to 38 m thick and is overlain by a fine-grained basalt that presumably flowed down an ancient channel. The sedimentary section at Moroto I is less extensive and consists of a 2.5-m thick section deposited directly on basement and overlain by a basalt. A conglomerate at the base of the exposed section grades up into fine-grained clay, reflecting lacustrine conditions. A paleosol is evident near the top. Fossils are found in both the coarse- and fine-grained deposits.

Assuming that the contact between the basalt and underlying sediments at the two localities defines the same plane, analogous stratigraphic relationships, and similar petrography, it is likely that the basalts represent the same flow. The capping basaltic lavas at Moroto I and II have conventional K/Ar ages of 12.5 ± 0.4 and 14.3 ± 0.3 million years ago (Ma), respectively (*13*). Using faunal correlations, Pickford estimated that the age of Moroto I and II was 14.5 to 16.5 Ma (*14*) and later revised this estimate to older than 17.5 Ma (*15*). To provide firmer dates, we used the $^{40}Ar/^{39}Ar$ incremental heating technique (*16*). Ages were determined with the use of Fish Canyon Tuff sanidine as the neutron flux monitor (age of 27.84 Ma) (*17*, *18*). The lava from Moroto I gave an internally defined isochron age of 20.61 ± 0.05 Ma (the mean of two experiments). The step-heating spectra for the lava from Moroto II, although demonstrating isotopic disturbance, indicate an emplacement age of more than 20 Ma (Fig. 1).

The fossils from Moroto II [MUZM 80 (MUZM, Makerere University Zoology Museum) (Fig. 2 and Table 1)] consist of several pieces of the right and left femurs of a single large hominoid. We estimate that the length of the femur was 270 mm (*19*, *20*). Several primitive features are present. The

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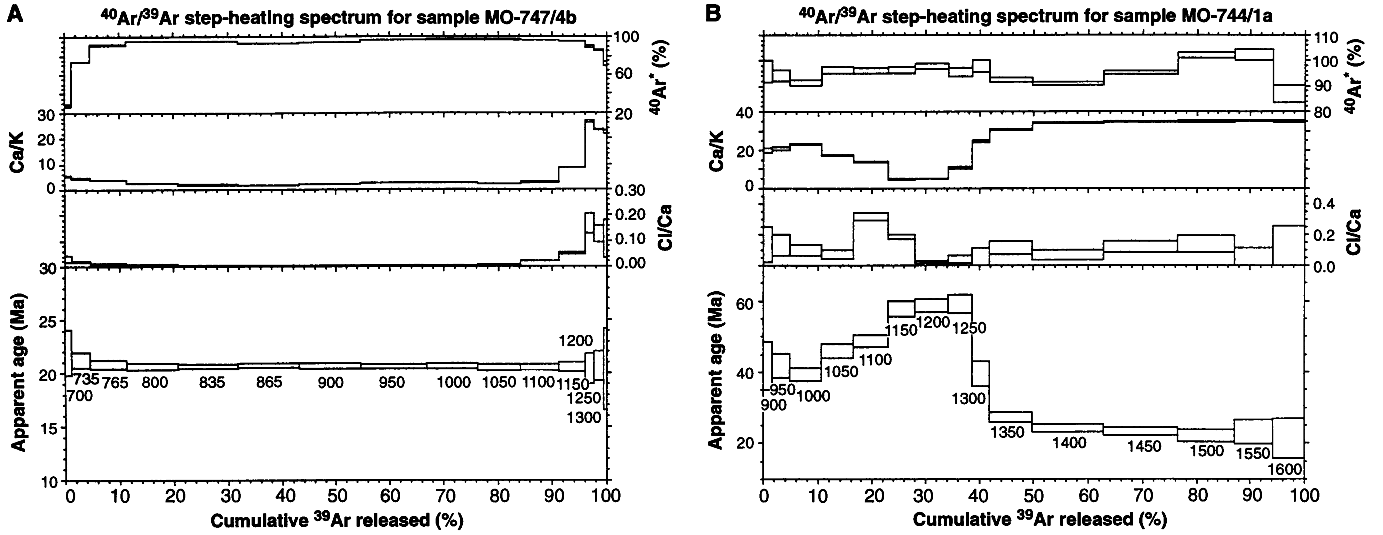

Fig. 1. $^{40}Ar/^{39}Ar$ step-heating spectra for lavas from Moroto I (**A**) (sample MO-747/4b, intergrown plagioclase-pyroxene microphenocrysts) and Moroto II (**B**) (sample MO-744/1a, plagioclase concentrate). The Moroto I lava is characterized by a single apparent age plateau across the entire gas release, with a high percentage of radiogenic ^{40}Ar relative to total argon and stable Ca/K and Cl/Ca compositional parameters. The Moroto II lava has undergone more extensive weathering and reveals disturbed argon systematics in the initial steps but settles to a plateau-like release with an age of about 20 Ma in the second half of the incremental heating experiment. $^{40}Ar^*$, radiogenic argon.

femoral head is small relative to those of living apes and is more similar to those of other Miocene hominoids (*21*). The articular surface of the femoral head is asymmetrical and has greater anterior extension like that of monkeys rather than a more evenly distributed articular surface like that of chimpanzees (*22*). Posteriorly, a large trochanteric crest is prominent, as is a large and open greater trochanteric fossa. These last two features are common among other Miocene hominoids but are rare in living apes and humans. Overall, proximal femoral anatomy is primitive and unlike that of all extant hominoids.

The shaft is extremely robust, and the ratio of cortical area to periosteal area is similar to that of bipedal hominids (*23*). Large cortical areas have also been reported for orangutans and lorises (*24*, *25*), primates that engage in cautious climbing, a functional pattern that we therefore infer for this hominoid. The intercondyloid notch is well buttressed, particularly the lateral wall of the medial condyle (inferior view), a condition similar to that in great apes; and distally, the knee is broad, as is the patellar region. These two features are similar to those in a variety of living and extinct hominoids and atelines but unlike those in cercopithecines. MUZM 80 also shares a deep popliteal groove and a buttressed intercondylar notch with the great apes, as well as a large body size (the weight for this specimen is estimated to have been approximately 40 to 50 kg) (*26*–*28*). These femoral features are not shared with *Proconsul* or hylobatids.

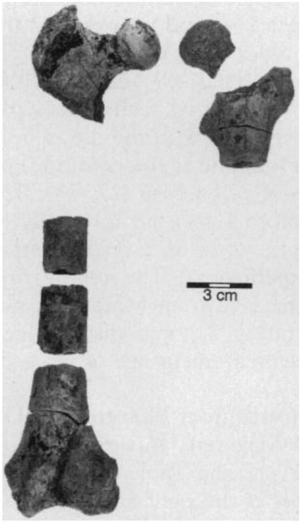

Fig. 2. Moroto II femurs (MUZM 80, right and left partial femurs).

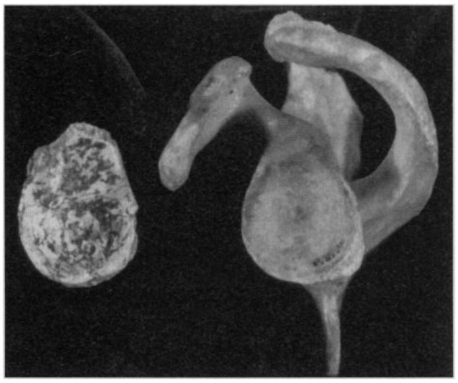

Fig. 3. The glenoid region (MUZM 60, left) of a left scapula (recovered from Moroto I) compared to that of a chimpanzee (right).

We also found the glenoid region of a scapula at the Moroto I site (MUZM 60) (Fig. 3 and Table 1). The widened superior half of the glenoid articular surface, as well as its smooth craniocaudal curvature (*29*), are similar to those of living apes, hominids, and some atelines, in contrast to those of other primates. This morphology indicates enhanced shoulder mobility (*29*) and is found in primates that brachiate or arm-hang, a functional interpretation we postulate for MUZM 60. A locomotor repertoire with a significant forelimb component is compatible with the locomotion inferred from the lumbar vertebrae, which imply a shorter and stiffer back (*2*, *10*–*12*) and (probably) a mediolaterally broader torso than in pronograde catarrhines (*11*). Thus, we interpret the Moroto hominoid material to represent an arboreal primate that moved using climbing, a slow to moderate speed of brachiation, and quadrupedalism, and utilized an arm-hanging posture.

We suggest that the new and old mate-

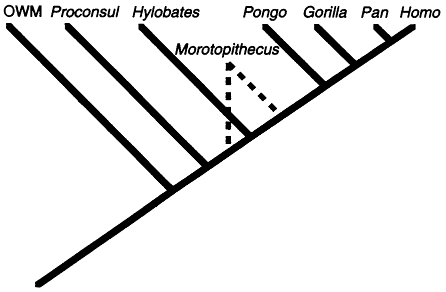

Fig. 4. A cladogram showing the two most likely phylogenetic positions for *Morotopithecus*. OWM, Old World monkey.

rial should be allocated to the same species. First, although Miocene sites in Kenya have produced a number of hominoid taxa of varying sizes at a single site, remains of only two primates have ever been recovered at the Moroto II site, representing a large-bodied hominoid (*1–3*) and a small galagine (*14*). Size estimates for the large-bodied hominoid range from 62 kg [for M^2 UMP 62-11 (*30*)] and 61 kg [for M_1 UMP 62-10 (*31*)], to 38 kg [from the vertebra (*12*)], to 51 to 54 kg (using only femoral cortical area or epicondylar breadth). In view of the variation in within-species estimates made from teeth and body parts (*32, 33*), these numbers are close. When we compare the Moroto palate and postcranial elements with those of living apes, we find no reason to exclude one from the other on the basis of size. Furthermore, none of the East African sites (Buluk, Koru, Rusinga, or Songhor) possess more than a single hominoid in this size range, and no evidence exists among the dental remains to suggest that there is more than one large-bodied hominoid at Moroto. We believe it unlikely that two large-bodied hominoids are represented—one represented only by teeth and the other by the postcranium.

Table 1. Femur and glenoid measurements. ML, mediolateral; AP, anteroposterior.

Femur	
Right femoral head height	25.9 mm
Anteroposterior width	27.0 mm
Depth	22.6 mm (approximate)
Left femoral head height	25.8 mm
Anteroposterior width	27.0 mm
Depth	23.3 mm
Femoral head and neck length	41.0 mm
Femoral neck length	22.0 mm
Greater trochanter width	26.8 mm
Greater trochanter height	43.3 mm
Lesser trochanter width	14.8 mm
Lesser trochanter height	21.2 mm
Proximal shaft breadth	23.4 mm
Anteroposterior depth	18.4 mm
Short shaft piece	
Length	28.2 mm
Width (ML)	21.1 mm
Depth (AP)	18.8 mm
Long shaft piece	
Length	32.8 mm
Width (ML)	22.6 mm
Depth (AP)	19.6 mm
Distal shaft	
Width (ML)	30.9 mm
Depth (AP)	20.2 mm
Distal femur width	54.2 mm
Bicondylar width	48.1 mm
Distal femur height	35.8 mm
Patellar width (max.)	30.1 mm
Patellar length (max.)	26.0 mm
Medial condyle width	18.5 mm
Lateral condyle width	14.4 mm
Angle of femoral head and neck	45°
Angle of lesser trochanter	30°
Glenoid	
Maximum height	32.2 mm
Maximum width	24.7 mm

Previous taxonomic assessments of the large-bodied hominoid material from Moroto link it with primitive Miocene hominoids (such as *Proconsul* or *Afropithecus* sp.) (*1, 3–5*) on the basis of dental and facial anatomy. In view of the important new postcranial material available for *Proconsul* and *Afropithecus* (*5, 11, 34–37*) and the derived scapular and lumbar anatomy of the Moroto specimens as compared with the more primitive postcranial remains now attributed to these other species, we propose a new genus and species name for the Moroto hominoid (*38*): *Morotopithecus bishopi*.

The body design of *Morotopithecus* is unlike that of other penecontemporary Miocene hominoids (such as *Proconsul*), which share very few derived postcranial characters with the living ape clade (*11, 34–36, 39, 40*). Only late Miocene *Oreopithecus* [8 to 11 Ma (*41*)] and *Dryopithecus* [9.5 Ma (*42*)] are postcranially more derived (*43, 44*). However, several dental, facial, and proximal femoral features are primitive compared to those of living hylobatids. These features, such as molar cingulum, a less expanded maxillary sinus, small femoral head size, and the open trochanteric fossa, raise questions about the phylogenetic position of *Morotopithecus* (Fig. 4). *Morotopithecus* may be a primitive great ape (*8, 9, 12*), in which case the facial, dental, and proximal femoral similarities of hylobatids and large extant hominoids are homoplasies. We believe rather that it is the sister taxon of all living hominoids. Given the age of *Morotopithecus*, a position after the split of hylobatids would raise problems for the overall timing of the primate radiations (*45*).

In either case, *Morotopithecus* represents the earliest evidence for a significantly apelike body plan in the primate fossil record. If *Morotopithecus* represents a lineage that is sister to all living hominoids, its body size raises questions about the view that the ancestors of all living apes were gibbon-sized (*45–47*). Rather, a body size of 20 to 40 kg, intermediate between small and large hominoids, may be the ancestral condition for all (*45–47*). This also raises issues concerning the phyletic relationships of *Graecopithecus* (*48*), *Otavipithecus* (*49*), *Afropithecus*, and *Kenyapithecus* (*9*). These species possess either poorly known or primitive postcrania, and their purported proximity to the living hominoids has rested almost entirely on dental and facial characters (*45, 50*). At present, we believe these species to be less closely related to extant hominoids than is *Morotopithecus*.

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38. Order Primates Linnaeus 1758; suborder Anthropoidea Mivart 1864; infraorder Catarrhini Geoffroy, 1812; superfamily Hominoidea Gray 1825; family not assigned. Genus *Morotopithecus* gen. nov. **Generic diagnosis:** Large hominoid, male weight around 40 to 50 kg, most comparable in facial and dental morphology to *Proconsul* and *Afropithecus*. Differs from later Miocene and extant apes in having a longer midface and has less alveolar prognathism than extant large apes. Differs from *Afropithecus,* later Miocene hominoids, and extant apes in the greater degree of cingular development on cheek teeth, especially molars. Differs from *Afropithecus* and *Proconsul* in having a narrower interorbital region and larger premolars relative to M1; differs from *Proconsul* in a smaller M2 and M3 relative to M1. Differs from *Afropithecus* in possessing a shorter premaxilla, a higher face, a broader nasal aperture (*5*), a P^3 that is much broader buccally and in which the paracone is situated closer to the protocone, buccal wrinkling on the side of the molars, and a larger M^3. Judging from worn occusal surfaces, the enamel was intermediate thin as in *P. major* (*51*). Further, computed tomography scans on the skull of *Afropithecus* reveal a thick palate with a small incisive canal (*52*), an anatomical condition that is distinctly different from the large canal of the Moroto palate (*53*). The glenoid is rounder in shape and more like that of extant apes and atelines than can be inferred for Miocene hominoids other than *Oreopithecus* and possibly *Dryopithecus* (*42*). Lumbar morphology differs from that of *Proconsul* and resembles that of *Oreopithecus*, possibly *Dryopithecus*, and extant large apes and siamangs in transverse process position. Proximal femoral morphology resembles that of cercopithecines and primitive hominoids such as *Proconsul*, differing from that of extant apes. Distal femoral anatomy resembles that of *Proconsul*, *Kenyapithecus,* and extant apes in mediolateral breadth but differs from hylobatids, *Proconsul*, and *Kenyapithecus* in the buttressing of the intercondylar notch. In 1962, L. S. B. Leakey referred the Moroto palate to *Pseudogorilla* (*54*) but did so without any species diagnosis. *Pseudogorilla* was created by Elliot in 1912 for ape specimens from the "Upper Congo" (*55*), now referred to *Gorilla*. Regardless of the validity of *Pseudogorilla*, the Moroto fossil is clearly different from any extant ape. **Type species:** *Morotopithecus bishopi* sp. nov. **Etymology:** Moroto, after Moroto township in Karamoja District in Uganda, and *pithekos* from the Greek for ape; and after the late W. W. Bishop. **Type specimen:** UMP 62-11 (UMP, Ugandan Museum of Paleontology), a palatofacial specimen with all teeth. **Type locality:** Moroto II. **Distribution:** Early Miocene, Karamoja District, NE Uganda. **Hypodigm:** Type and UMP 62-10 and UMP 66-01, which are probably associated mandibular fragments; UMP 62-12, left upper canine; UMP 67-28, middle lumbar vertebra; UMP 68-05, middle lumbar vertebral body; UMP 68-06, a last thoracic vertebra; UMP 68-07, the lamina and base of a spine of a lumbar vertebra; MUZM 80, right and left femoral pieces (all from the Moroto II locality); and MUZM 60, scapular fragment with glenoid (Moroto I locality). **Specific diagnosis:** As for genus.
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Positional Cloning of the Gene for Multiple Endocrine Neoplasia–Type 1

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Multiple endocrine neoplasia–type 1 (MEN1) is an autosomal dominant familial cancer syndrome characterized by tumors in parathyroids, enteropancreatic endocrine tissues, and the anterior pituitary. DNA sequencing from a previously identified minimal interval on chromosome 11q13 identified several candidate genes, one of which contained 12 different frameshift, nonsense, missense, and in-frame deletion mutations in 14 probands from 15 families. The *MEN1* gene contains 10 exons and encodes a ubiquitously expressed 2.8-kilobase transcript. The predicted 610–amino acid protein product, termed menin, exhibits no apparent similarities to any previously known proteins. The identification of *MEN1* will enable improved understanding of the mechanism of endocrine tumorigenesis and should facilitate early diagnosis.

Familial cancer syndromes have attracted widespread interest over the past decade, in part because of their potential to shed light on the general mechanisms of carcinogenesis. Positional cloning methods have led to the precise identification of the responsible gene for more than a dozen such disorders (*1*). In keeping with the hypothesis originally articulated by Knudson for retinoblastoma (*2*), most of the responsible genes are of the tumor suppressor type. In such a circumstance, affected individuals have inherited one altered copy of the responsible gene from an affected parent, but the tumors have lost the remaining copy (the wild-type allele) as a somatic event. Thus, the inheritance pattern is dominant, but the mechanism of tumorigenesis is recessive. The importance of gene discovery often extends beyond affected pedigrees, as the same tumor suppressor gene is often found to play a role (by mutation of both alleles) in sporadic cases of the same neoplasm.

Multiple endocrine neoplasia–type 1 (MEN1) (OMIM *131100) appears to be a compelling example of this paradigm, with prevalence estimates ranging from 1 in 10,000 to 1 in 100,000 (*3*, *4*). Affected individuals develop varying combinations of tumors of parathyroids, pancreatic islets, duodenal endocrine cells, and the anterior pituitary, with 94% penetrance by age 50 (*4*). Less commonly associated tumors include foregut carcinoids, lipomas, angiofibromas, thyroid adenomas, adrenocortical adenomas, angiomyolipomas, and spinal cord ependymomas. Except for gastrinomas, most of the tumors are nonmetastasizing,