



RESEARCH ARTICLE SUMMARY

PALEOECOLOGY

The evolution of hominoid locomotor versatility: Evidence from Moroto, a 21 Ma site in Uganda

Laura M. MacLatchy*, Susanne M. Cote, Alan L. Deino, Robert M. Kityo, Amon A. T. Mugume, James B. Rossie, William J. Sanders, Miranda N. Cosman, Steven G. Driese, David L. Fox, April J. Freeman, Rutger J. W. Jansma, Kirsten E. H. Jenkins, Rahab N. Kinyanjui, William E. Lukens, Kieran P. McNulty, Alice Novello, Daniel J. Peppe, Caroline A. E. Strömberg, Kevin T. Uno, Alisa J. Winkler, John D. Kingston

INTRODUCTION: Inherent in traditional views of ape origins is the idea that, like living apes, early large-bodied apes lived in tropical forests. In response to constraints related to locomoting in forest canopies, it has been proposed that early apes evolved their quintessential upright torsos and acrobatic climbing and suspensory abilities, enhancing their locomotor versatility, to distribute their weight among small supports and thus reach ripe fruit in the terminal branches. This feeding and locomotor transition from a quadruped with a horizontal torso is thought to have occurred in the Middle Miocene due to an increasingly seasonal climate and feeding competition from evolving

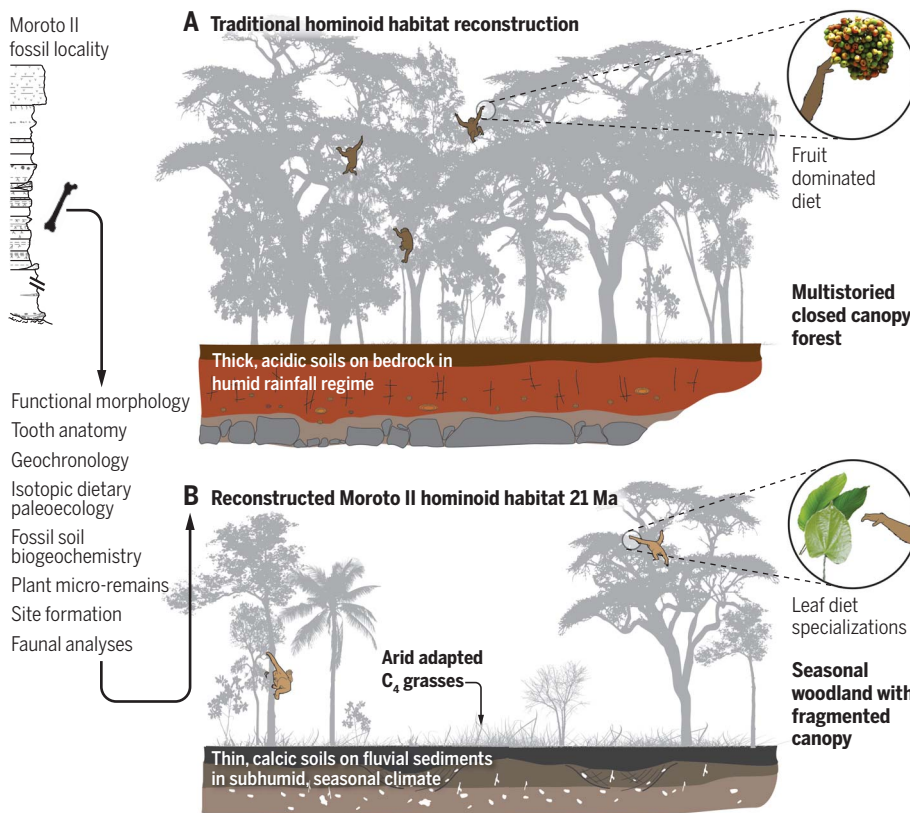
monkeys. Although ecological and behavioral comparisons among living apes and monkeys provide evidence for versions of terminal branch forest frugivory hypotheses, corroboration from the early ape fossil record has been lacking, as have detailed reconstructions of the habitats where the first apes evolved.

RATIONALE: The Early Miocene fossil site of Moroto II in Uganda provides a unique opportunity to test the predictions of terminal branch forest frugivory hypotheses. Moroto II documents the oldest [21 million years ago (Ma)] well-established paleontological record of ape teeth and postcranial bones from a single lo-

cality and preserves paleoecological pro to reconstruct the environment. The following lines of evidence from Moroto II were analyzed: (i) the functional anatomy of femora and a vertebra attributed to the ape *Morotopithecus*; (ii) dental traits, including molar shape and isotopic profiles of *Morotopithecus* enamel; (iii) isotopic dietary paleoecology of associated fossil mammals; (iv) biogeochemical signals from paleosols (ancient soils) that reflect local relative proportions of C₃ (trees and shrubs) and C₄ (tropical grasses and sedges that can endure water stress) vegetation as well as rainfall; and (v) assemblages of phytoliths, microscopic plant-derived silica bodies that reflect past plant communities.

RESULTS: A short, strong femur biomechanically favorable to vertical climbing and a vertebra indicating a dorsostable lower back confirm that ape fossils from Moroto II shared locomotor traits with living apes. Both *Morotopithecus* and a smaller ape from the site have elongated molars with well-developed crests for shearing leaves. Carbon isotopic signatures of the enamel of these apes and of other fossil mammals indicate that some mammals consistently fed on water-stressed C₃ plants, and possibly also C₄ vegetation, in a woodland setting. Carbon isotope values of pedogenic carbonates, paleosol organic matter, and plant waxes all point to substantial C₄ grass biomass on the landscape. Analysis of paleosols also indicates subhumid, strongly seasonal rainfall, and phytolith assemblages include forms from both arid-adapted C₄ grasses and forest-indicator plants.

CONCLUSION: The ancient co-occurrence of dental specializations for leaf eating, rather than ripe fruit consumption, along with ape-like locomotor abilities counters the predictions of the terminal branch forest frugivory hypotheses. The combined paleoecological evidence situates *Morotopithecus* in a woodland with a broken canopy and substantial grass understory including C₄ species. These findings call for a new paradigm for the evolutionary origins of early apes. We propose that seasonal, wooded environments may have exerted previously unrecognized selective pressures in the evolution of arboreal apes. For example, some apes may have needed to access leaves in the higher canopy in times of low fruit availability and to be adept at ascending and descending from trees that lacked a continuous canopy. ■



Hominoid habitat comparisons. Shown are reconstructions of a traditionally conceived hominoid habitat (A) and the 21 Ma Moroto II, Uganda, habitat (B).

The list of author affiliations is available in the full article online.

*Corresponding author. Email: maclatch@umich.edu
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The evolution of hominoid locomotor versatility: Evidence from Moroto, a 21 Ma site in Uganda

Laura M. MacLatchy^{1,2*}, Susanne M. Cote³, Alan L. Deino⁴, Robert M. Kityo⁵, Amon A. T. Mugume^{5,6}, James B. Rossie⁷, William J. Sanders^{1,2}, Miranda N. Cosman¹, Steven G. Driese⁸, David L. Fox⁹, April J. Freeman⁸, Rutger J. W. Jansma¹⁰, Kirsten E. H. Jenkins¹¹, Rahab N. Kinyanjui^{12,13,14}, William E. Lukens¹⁵, Kieran P. McNulty¹⁶, Alice Novello^{17,18}, Daniel J. Peppe⁸, Caroline A. E. Strömberg¹⁸, Kevin T. Uno¹⁹, Alisa J. Winkler^{20,21}, John D. Kingston¹

Living hominoids are distinguished by upright torsos and versatile locomotion. It is hypothesized that these features evolved for feeding on fruit from terminal branches in forests. To investigate the evolutionary context of hominoid adaptive origins, we analyzed multiple paleoenvironmental proxies in conjunction with hominoid fossils from the Moroto II site in Uganda. The data indicate seasonally dry woodlands with the earliest evidence of abundant C₄ grasses in Africa based on a confirmed age of 21 million years ago (Ma). We demonstrate that the leaf-eating hominoid *Morotopithecus* consumed water-stressed vegetation, and postcrania from the site indicate ape-like locomotor adaptations. These findings suggest that the origin of hominoid locomotor versatility is associated with foraging on leaves in heterogeneous, open woodlands rather than forests.

Living nonhuman hominoids are distinguished from most other primates by postcranial adaptations that facilitate arboreal positional behaviors in which the torso is upright (orthograde) and the fore- and hindlimbs often have wide excursions and are oriented in different directions. Most hypotheses seeking to explain the adapt-

ive significance of these versatile behaviors propose that they help medium- and large-bodied primates forage for ripe fruit in the terminal branches or the upper canopy of forests, where small, flexible branches must be navigated [e.g., (1–4)]. Such terminal branch forest frugivory hypotheses predict that versatile positional behaviors (including both postures and locomotion) would have first appeared in hominoids that were committed frugivores and were foraging in tropical forest habitats.

The Moroto II Miocene fossil site in Uganda (Fig. 1) provides a unique opportunity to test these predictions because it documents the oldest well-established paleontological record of hominoid teeth and postcranial bones from a single locality. Here, we report on new radiometric dates, data on fossil hominoid diet and locomotion, and multiple paleoecological proxies from Moroto II that allow us to elucidate the evolutionary context and refine the nature and timing of key aspects of early hominoid adaptive origins.

Background

Terminal branch forest frugivory hypotheses

Hominoid arboreal positional behavior is particularly versatile because it involves transitions among a range of postural and locomotor modes and across a range of substrates. This versatile behavior fundamentally stems from having a dorsostable, orthograde torso, which in turn facilitates differential limb use and the ability to have limbs aligned differently while serving a weight-bearing function. Although this use of the term “versatile” is not established in the literature, which has an accepted positional behavioral terminology that that both

consolidates and simplifies nomenclature (4–7), we use it as shorthand to refer to behaviors such as vertical climbing on substrates oriented $\geq 45^\circ$; arboreal travel during which multiple limbs are propulsive but oriented differently, and suspension (below-branch behaviors) (movies S1 to S3). Versatile behavior thus represents an alternative to quadrupedalism, in which the torso is roughly horizontal (pronograde), limbs are generally below the body, and joint excursions are more modest (4). Versatile behaviors are thought to be especially important when moving in the trees with a large body size and have been linked to hominoid-specific anatomical specializations, including dorsoventrally shallow but mediolaterally broad torsos; dorsally placed scapulae; relatively short, dorsostable lumbar regions; relatively long forelimbs paired with relatively short hindlimbs; mobile limb joints; manual and pedal specializations for grasping; and tail loss (8, 9).

In attempting to explain the evolutionary origins of the unique hominoid body plan, researchers have focused on particular versatile behaviors, including suspension (10, 11), quadrumanous climbing (12), and vertical climbing (13, 14), all of which normally incorporate the use of limbs outside of the parasagittal plane. These capabilities also rely on an upright, stable torso, so it has been further suggested that it is the capacity for orthogrady that may be largely responsible for hominoid positional behavioral distinctiveness (6, 15).

Several influential hypotheses have been advanced to explain the adaptive significance of the acquisition of versatile positional behaviors in hominoids and are here grouped under a single umbrella as the terminal branch forest frugivory hypotheses. The earlier forms of these hypotheses focused on substrate. It was proposed that versatile behaviors contribute to the fitness of medium- and large-bodied apes by allowing them to use multiple supports to distribute their weight and thereby successfully forage either in the terminal branches generally or in the middle and upper canopy of forests [e.g., (1, 2, 16, 17)]. Enhanced competition with cercopithecoid monkeys and/or increasing seasonality were invoked (2, 10, 18) to explain the increase in body size. Such models of hominoid-cercopithecoid divergence also typically situate cercopithecoids in more open habitats [e.g., (3, 18, 19)].

Forests figure prominently in these models of hominoid divergence. They are generally defined as distinct from woodlands in having greater structural complexity and taxonomic richness, usually including taller trees with multistoried, intermingling crowns, with the highest level of foliage (the canopy) more closed (20, 21). By contrast, woodlands in tropical and subtropical Africa tend to have a single-story broken canopy, extensive ground

¹Department of Anthropology, University of Michigan, Ann Arbor, MI 48109, USA. ²Museum of Paleontology, University of Michigan, Ann Arbor, MI 48109, USA. ³Department of Anthropology and Archaeology, University of Calgary, Calgary, Alberta T2N 1N4, Canada. ⁴Berkeley Geochronology Center, Berkeley, CA 94709, USA. ⁵Department of Zoology, Entomology and Fisheries Sciences, Makerere University, Kampala, Uganda. ⁶Uganda National Museum, Department of Museums and Monuments, Ministry of Tourism, Wildlife and Antiquities, Kampala, Uganda. ⁷Department of Anthropology, Stony Brook University, Stony Brook, NY 11794, USA. ⁸Department of Geosciences, Baylor University, Waco, TX 76798, USA. ⁹Department of Earth & Environmental Sciences, University of Minnesota, Minneapolis, MN 55455, USA. ¹⁰Institute of Human Origins, School of Human Evolution and Social Change, Arizona State University, Tempe, AZ 85281, USA. ¹¹Department of Social Sciences, Tacoma Community College, Tacoma, WA 98466, USA. ¹²Earth Sciences Department, National Museums of Kenya, Nairobi, Kenya. ¹³Max Planck Institute for Geoanthropology, Jena D-07743, Germany. ¹⁴Human Origins Program, National Museum of Natural History, Smithsonian Institution, Washington, DC 20013, USA. ¹⁵Department of Geology & Environmental Science, James Madison University, Harrisonburg, VA 22807, USA. ¹⁶Department of Anthropology, University of Minnesota, Minneapolis, MN 55455, USA. ¹⁷CEREGE, Aix-Marseille Université, CNRS, IRD, Collège de France, INRAE, Aix en Provence, France. ¹⁸Department of Biology & Burke Museum of Natural History and Culture, University of Washington, Seattle, WA 98195, USA. ¹⁹Division of Biology and Paleo Environment, Lamont-Doherty Earth Observatory of Columbia University, Palisades, NY 10964, USA. ²⁰Roy M. Huffington Department of Earth Sciences, Southern Methodist University, Dallas, TX 75275, USA. ²¹Section of Anatomy, Department of Surgery, University of Texas Southwestern Medical Center, Dallas, TX 75390, USA. *Corresponding author. Email: maclatch@umich.edu

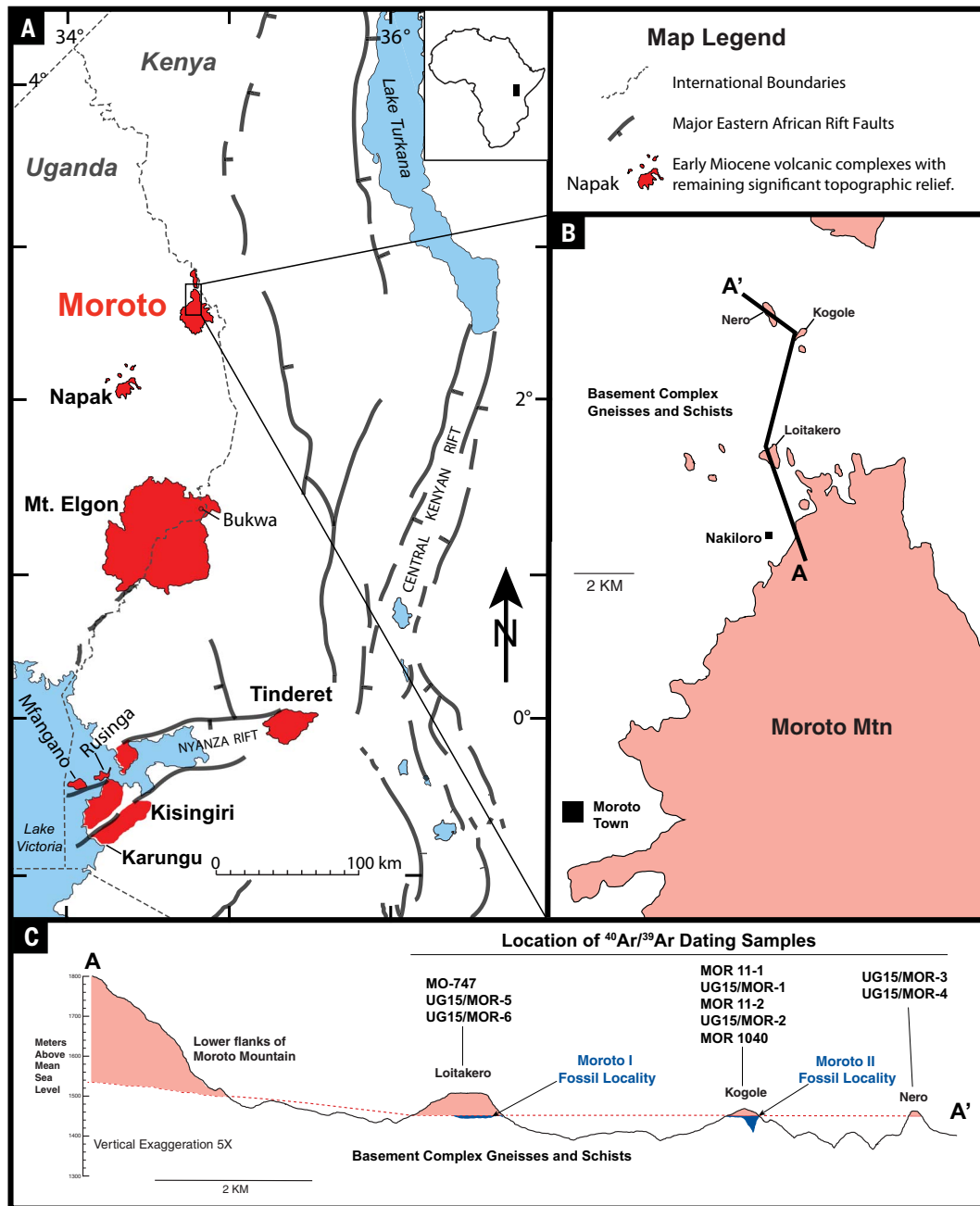


Fig. 1. Location maps and cross sections of the Moroto region. (A) Regional map of the Uganda-Kenya rift system depicting major Early Miocene fossil site complexes (in red). (B) Inset of current Moroto volcanic edifice and environs, including the location of Moroto II at Kogole and Moroto I at Loitakero (volcanics

are shown in pink and the metamorphic basement in white). (C) Topographic cross-sectional profile [depicted in (B)] showing the intersection with the hills of Loitakero, Kogole, and Nero overlying the fossil sites (in blue). Locations of $^{40}\text{Ar}/^{39}\text{Ar}$ dating samples from lavas capping three topographic highs are shown.

cover including grasses, and distinctive dry-wet seasons. Consequently, forests have greater connectivity between adjacent trees, as well as more shade and moisture. Ripley (18) proposed that terminal branch feeding on fruit would have occurred in evergreen forests. Temerin and Cant (3) also postulated that hominoid divergence occurred within a forest environment. These primatologists, along with paleontologists [e.g., (19)], speculated that the

development of nonforested habitats occurred in the Middle Miocene (~15 Ma), with ancestral cercopithecoids exploiting the woodlands or savannas and hominoids remaining in tropical forests (19, 22).

Frugivory was emphasized in most detail by Temerin and Cant's (3) insightful model of hominoid origins, which held that versatility evolved to increase speed and decrease the path length of arboreal travel in forest habitats

under conditions of decreased fruit availability. These authors postulated that suspension- and forelimb-dominated climbing allowed apes to outcompete monkeys (as well as arboreal squirrels, bats, and birds) for rare, small, and/or dispersed high-quality fruit patches, whereas monkeys, which are restricted to longer, above-branch pathways and must frequently return to the core of a tree, exploited abundant ripe and nonripe fruit and leaves. Temerin and Cant

(3) proposed that a reduction in fruit availability, driven by a cooler and drier climate, was the selection pressure leading to the ecological divergence of hominoids and cercopithecoids. A more recent synthesis by Hunt (4) also invoked competition with cercopithecoids, in which small size, bilophodonty, and greater tolerance for the chemical defenses of plants allowed them to more successfully exploit unripe or small patches of fruit and leaves in the center of tree crowns. Apes, in turn, evolved postcranial specializations to feed on fruit in the terminal branches (4).

Although most reconstructions of hominoid foraging ecology focus on fruit, Sarmiento (23) proposed that the slow movements found in larger forms of select mammals, including hominoids, lorises, colobines, the fossil lemur *Paleopropithecus*, and sloths, are correlated with folivory, although no causal links to an ecological context were proposed. The importance of terminal branch resources has been strengthened by research documenting that at least some fruits are larger, more abundant, denser, and most nutritionally valuable in the upper canopy (24); and leaves in the upper canopy may have higher protein (25), with young leaves having relatively higher protein than mature leaves (26). The higher quality and/or quantity of food in the upper canopies is thus a potential driver of versatile positional behaviors among hominoids.

There remains a prevailing and persistent perception that early hominoid evolution played out in a forested context and that frugivory was an important component. This relates to a number of long-held observations and interpretations, including: (i) all modern hominoids (and several fossil taxa) exhibit and are defined by arboreal adaptations for which behavioral versatility (as we define it) is key; (ii) the preferred habitats of modern hominoids are forests, so forest dwelling could be construed as a synapomorphy of the hominoid clade; (iii) the preferred diet of modern hominoids is largely focused on fruit; and (iv) the Early Miocene is viewed as consisting of a pan-equatorial African forest [see (27), which presents an expansive, regional interpretation of the vegetation of the Early Miocene]. The terminal branch forest frugivory hypotheses represent a formal distillation of these concepts, and we invoke them as representative of broad perceptions that persist today.

The Moroto II locality

As described by Bishop and Whyte (28), fossils in Moroto District were first found just north of Moroto Mountain (Moroto I) in 1959 by J. G. Wilson. The site of Moroto II was subsequently discovered in 1962 (28). The sites were prospected by Bishop and colleagues between 1961 and 1965 (28–30), resulting in the William Bishop fossil collection. Ongoing research at

Moroto II by our team has produced fossil collections from the years 1994 to 2017.

Initial K/Ar dates for the capping basaltic lavas at the fossil sites in the 1960s yielded ages of 12.5 and 14.3 Ma (31), but more recent $^{40}\text{Ar}/^{39}\text{Ar}$ incremental dating techniques resulted in an age of 20 to 20.6 Ma (32). Although this date has been questioned and an age of 17.5 Ma advocated on the basis of qualitative biostratigraphic interpretations (33–35), the more comprehensive geochronologic strategy described below unequivocally supports an age of 21 Ma for the Moroto fossil localities.

The hominoids of Moroto II

Morotopithecus bishopi is one of at least two large-bodied primates from the Early Miocene fossil site of Moroto II in Uganda (32, 36). Its status as one of the oldest fossil hominoids, coupled with derived postcranial traits, including a dorsostable lower back, has placed it in a unique position among its Miocene contemporaries (37–39), because other Early Miocene (e.g., *Proconsul* and *Ekembo*) and even Middle Miocene (e.g., *Equatorius* and *Kenyapithecus*) African taxa retain ancestral, monkey-like body plans (37–39). Although the distinctiveness of *M. bishopi* from *Afropithecus turkanensis* (40, 41) and the composition of the *Morotopithecus* hypodigm (42, 43) have been questioned, recent (36) and current analyses support our assignments of functionally informative dental and postcranial specimens recovered at Moroto II to *Morotopithecus*.

The distinctiveness of the holotype maxilla and partial face UMP 62-11 described by Allbrook and Bishop (29), as well as the fragmentary mandibular remains UMP 62-10 and UMP 66-01 described by Pilbeam (44), were recently reassessed by MacLatchy *et al.* (36) after the discovery of another partial mandible (UMP MORII 03'551) and an isolated *Proconsul*-like tooth (UMP MORII 03'559) at Moroto II. Comparisons of taxonomically, developmentally, and functionally diagnostic characteristics, including tooth crown morphology and tooth row proportions, relative enamel thickness, enamel-dentine junction morphology, long-period line periodicity, and dental wear patterns, clearly discriminate among *Afropithecus*, *Morotopithecus*, and the *Proconsul* clade and support genus-level distinctiveness for all three (36). In addition, it was concluded, given the similarity in the tooth row proportions between the holotype UMP 62-11 and the mandible UMP MORII 03'551 and the complementary morphology between mandibles MORII 03'551, UMP 66-01, and UMP 62-10 (including having a long tooth row and vertical planum alveolare), that all of these specimens were best assigned to *M. bishopi* (36).

The functional assessments of these dental specimens provide evidence for specialized leaf eating (36) rather than the more generalized fruit-based diet reconstructed for primitive

catarrhines (45, 46). Both the upper and lower molars are mesiodistally elongated, and an unworn M_2 has conspicuous, well-developed shearing crests (36), a characteristic long accepted as being reflective of folivory (45, 46). The presence of features for specialized leaf eating in both the upper and lower dentition further supports the attribution of all of these specimens to *Morotopithecus* (36). Although incipient signals of folivory have been documented in some smaller-bodied Early Miocene catarrhines (45), this combination of features was previously unknown for any great apes (>30 kg) catarrhine before the Late Miocene. A folivorous diet is corroborated by thin occlusal enamel (23, 36), which, although not necessarily diagnostic for leaf eating, rules out the hard-object feeding inferred for other fossil taxa, including *Afropithecus* (47).

Two hominoid postcranial remains from Moroto II attributed to *M. bishopi* represent the oldest clear evidence of derived locomotor adaptations in hominoids: a lumbar vertebra [UMP 67-28; originally described by Walker and Rose (48)] indicative of a dorsoventrally stable lumbar spine consistent with orthogrady (37, 49, 50) and associated partial femora [UMP MORII 94'80; first described by Gebo *et al.* (32)] reflective of vertical climbing and slow forms of orthograde or pronograde clamber (15, 50, 51). These are core derived behaviors of the hominoid clade emphasized in the terminal branch forest frugivory hypotheses. The right femur is now complete and new functional implications are described below.

The precise location within Moroto II where the hominoid vertebra UMP 67-28 and some dental remains (UMP 66-01, UMP 62-10, and the holotype UMP 62-11) were found ~50 years ago is not documented, so there will always be ambiguity about their association. However, the mandible bearing the lightly worn M_2 with well-developed shearing crests (UMP MORII 03'551) and the right and left femora (UMP MORII 94'80) were found by our team within a single stratigraphic level (Fig. 2A) (36) from a restricted spatial distribution (see geologic setting below) and are the only hominoid fossils known from this level. As noted above, we believe that the holotype UMP 62-11 and mandible UMP MORII 03'551 belong in the same taxon because of their complementary morphology and specialized features for folivory. Likewise, the vertebra UMP 67-28 and the femora UMP MORII 94'80 share adaptive characteristics (see below). The co-occurrence of hominoid folivory and ape-like climbing abilities (regardless of taxonomic attribution) at a single, constrained stratigraphic level counters the predictions of the terminal branch forest frugivory hypotheses and makes reconstructing the environment and age of Moroto II highly relevant for developing adaptive explanations for the early stages of the hominoid lineage.

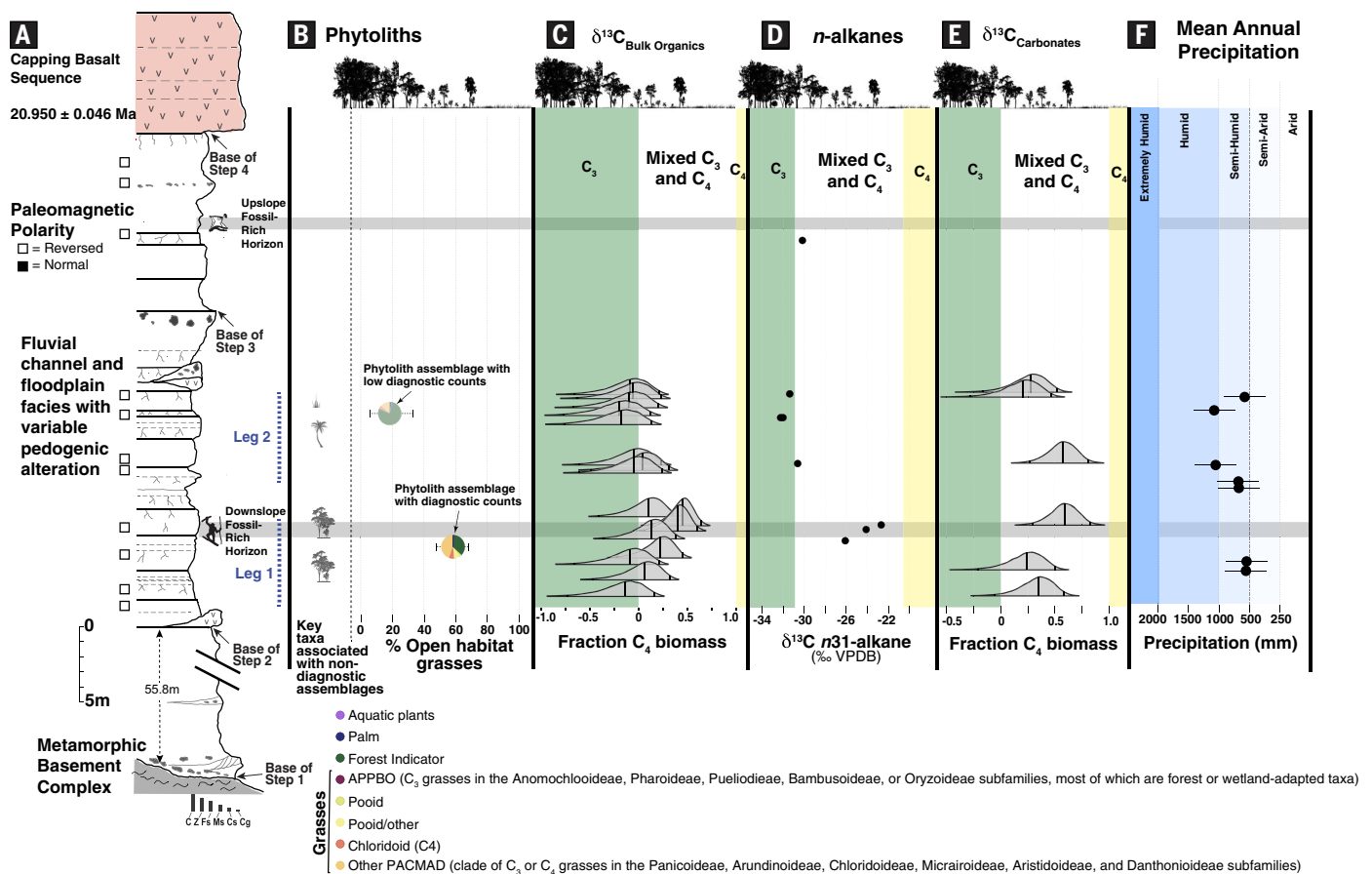


Fig. 2. Moroto II paleoenvironmental proxies in stratigraphic context.

(A) Composite stratigraphic section at Moroto II depicting generalized sedimentary lithofacies, relationship to overlying basalt sequence, magnetostratigraphy, and fossil-rich horizons. (B) Percentage of open habitat grasses on the basis of phytolith assemblages, with the dark pie chart representing diagnostic assemblage data; the faded pie chart assemblage representing low diagnostic counts; and the grass, forest, and palm images

representing key taxa associated with nondiagnostic assemblages. (C) Fraction of C_4 biomass on the basis of $\delta^{13}C_{\text{Bulk Organics}}$ ($\delta^{13}C_{\text{OM}}$). Fractions of <0 and >1 result from Monte Carlo resamples less than and greater than median plant $\delta^{13}C$ reference values, respectively (52). (D) $C_{31}n$ -alkane homolog. (E) Fraction of C_4 biomass on the basis of $\delta^{13}C_{\text{Carbonates}}$ ($\delta^{13}C_{\text{PC}}$) components (52). (F) MAP estimates on the basis of the random forest (RF)-MAP machine learning model (89) with uncertainty ranges.

Results

Geologic and taphonomic setting

Fossiliferous sediments exposed at the site of Moroto II represent a fluvial system with deposition in a deeply incised channel eroded directly in the underlying Precambrian metamorphic basement complex and are directly overlain by a basaltic lava sequence. Deposits exposed at Moroto II consist almost exclusively of fluvial facies with minor fine-grained lacustrine or ponding facies, perhaps within the paleochannel(s) or floodplains. Sediments have been overprinted by pedogenic processes to varying degrees, suggesting that the channel and associated floodplains were intermittently inactive or meandered laterally. The site is currently ~11 km north of Mount Moroto, a volcanic complex that formed along the tectonically active west margin of the eastern branch of the East African Rift System during the Early Miocene, in conjunction with a series of eruptive centers extending north to the Turkana Basin and south into western Kenya (Fig. 1A). A lack

of volcanoclastic debris in the sedimentary sequence indicates deposition on the basement complex that was independent of any input from the Moroto volcano. These observations suggest that although the site was formed adjacent to a developing eruptive center, the fossil assemblage more likely sampled ecosystems associated with the basement penneplain rather than the flanks of a volcano.

Fossils were recovered from multiple fluvial channels in fine- to coarse-grained sediments. Occasionally, elements from multiple taxa have been recovered together in small pockets within floodplain or overbank deposits, but most of the specimens derive mainly from two concentrations within the succession (Fig. 2A). The spatial proximity of the specimens recovered at each of these two stratigraphic levels (confined to an $\sim 10 \times 10$ m area) indicates that fossils are generally associated. Taphonomic analysis (52) indicates that fossil assemblages likely represent time-averaged streamside accumulations in an open environment without

a dominant biogenic accumulating process. Weathering patterns reveal that remains were often exposed to sunlight or frequent wetting and drying, which may suggest a more open environment (53). Attritional death assemblages such as Moroto II may be faithful indicators of broader ancient living assemblages (54, 55), with the exception of small taxa that are underrepresented in our collections.

Chronology

The basaltic sequence overlying the fossiliferous sediments represents the initial input of volcanic material in the vicinity of the fossil localities. This overlying lava flow is in direct superposition with a paleosol surface in the Moroto II succession, indicating relatively rapid replacement of the lavas within and over the active channel system without a protracted temporal hiatus (Figs. 1C and 2A). There are currently a number of topographic highs immediately northwest of the main Moroto volcanic edifice capped by erosional

remnants of the same sequence of lavas (Fig. 1C). Ten basalt samples were dated by $^{40}\text{Ar}/^{39}\text{Ar}$ laser incremental heating [Fig. 1C, figs. S1 to S3, and tables S1 to S3 (52)] from outcrops at multiple levels within the lava sequence at Moroto II (Kogole Hill and the nearby hills of Loitakero, which overlies the Moroto I fossil site) and Nero (52) (Fig. 1 and figs. S1 to S3). Ages are consistent within error, yielding a mean of 20.950 ± 0.046 Ma, corroborating previous radiometric ages of 20.6 Ma for the Loitakero basalt and ~20 Ma for the Kogole basalt (32).

On the basis of the reversed polarity of all samples at Moroto II, coupled with a representative age for the Moroto capping lavas of 20.950 ± 0.046 Ma and the stratigraphic relationship of the lava flows to the Moroto II sediments, our preferred correlation to the Geomagnetic Polarity Time Scale (GPTS) is to C6Ar, which occurred from 21.204 to 21.130 Ma (± 0.037 Ma) (56). Given that all samples are reversed, if the section sampled the entire chron, then the maximum duration of deposition of Moroto II was 365 ± 36.9 thousand years. On the basis of the sedimentological and paleosol features of the deposits, the site was likely deposited over a much shorter duration (52) (figs. S4 and S5 and tables S4 and S5).

This geochronology is entirely consistent with biostratigraphic data from the mammalian assemblage at Moroto II. There is a long sequence of Early Miocene fossil sites in Uganda and western Kenya that document faunal change in eastern Africa [e.g., (57, 58)]. A major aspect of this faunal change is the gradual transition from the afrotherian-dominated assemblages characteristic of the Paleogene to assemblages that are dominated by laurasiatherian immigrants by the onset of the Middle Miocene. Our detailed comparisons of the identifiable mammal fossils ($n = 146$) (table S6) provide strong support for the radiometric date, because some common laurasiatherian taxa are completely absent. By 20 Ma, and documented at sites such as Songhor and Rusinga, eastern African faunas incorporate additional laurasiatherian immigrants such as suids, tragulids, or perissodactyls and additional rodent lineages [e.g., (57, 59–61)]. By contrast, at Moroto II, there are no suids or tragulids, no perissodactyls, and hyracoids are relatively abundant (table S6), suggesting that this assemblage is older than 20 Ma.

The radiometric age is further supported by the proboscideans, which are the best-known mammals in the Moroto II assemblage. *Eozygodon*, in particular, has a limited stratigraphic range in Africa and is only known from sites ~20 to 19 Ma and older (62). In eastern Africa, *Eozygodon* is only found at Moroto II and Meswa Bridge [22.5 Ma (63)]. The Moroto II material displays more derived dental features (table S6), supporting a biostratigraphic framework in

which Meswa Bridge is older than Moroto. In addition, at younger sites in eastern Africa, such as Rusinga, *Eozygodon* is replaced by the more derived *Zygodon*, and a second proboscidean genus at Moroto II, *Progomphotherium*, is succeeded by *Archaeobelodon* (62). Therefore, these two proboscidean taxa also support an age of >20 Ma. Overall, biostratigraphy provides strong support that Moroto II is older than the well-sampled ~20 Ma site complexes of Napak and Tinderet, but younger than the ~28- to 23 Ma Late Oligocene faunas from eastern Africa (62).

Hominoid and other catarrhine fossils Femur

New catarrhine fossils from Moroto II include additional fragments of the right femur UMP MORII 94'80 attributed to *Morotopithecus* (32, 50), which complete the previously partial shaft for a total length of 240.7 mm (data S1). Very few complete femora from large-bodied Miocene hominoids exist. Relative to the mid-shaft, femoral head, and bicondylar breadths, UMP MORII 94'80 is very short (52) (Fig. 3), like the femora of extant great apes and unlike those of large cercopithecoids and the large-bodied Miocene hominoid *Ekembo nyanzae* (51), which is considered to be a generalized pronograde quadruped (38) (Figs. 3 and 4A). The cortical bone of UMP MORII 94'80 is thick, as in living great apes (50, 51), with a ratio of cortical area divided by subperiosteal area (CA/PA) of 0.83 at about midshaft (52) (fig. S6). This is greater than the CA/PA ratio of the Early Miocene ape *Ekembo heseloni* [0.67 for KNM-RU 2036 (50)]. Both CA (282 mm^2) and strength (J) (18117.49 mm^4) at about midshaft are high relative to shaft length (fig. S7) and resemble proportions found in *Pongo* (52). This heavy reinforcement of cortical bone in *Pongo* has been interpreted to reflect an emphasis on axial loading, and may be associated with static postures (64) and slow movement with prolonged muscular recruitment (50). The finding that the hominoid represented by UMP MORII 94'80 had very short but strong legs is also consistent with the biomechanical expectation for large-bodied vertical climbers, in which the ability to remain on vertical supports (especially large ones) requires differentiated limb use involving (i) sustained muscular contractions, (ii) leaning away from the substrate using relatively long forelimbs, and (iii) having relatively short hindlimbs that flex at the hip and knee (65) (Fig. 4B). In combination, the short legs and large body size of *Morotopithecus* also suggest that its vertical climbing kinematics may have been more similar to those of great apes than to those of hylobatids. Isler (14) has shown that compared with the smaller gibbons (who have longer hindlimbs for their body size; Fig. 3), great apes position the body closer to the substrate, climb more slowly, and

use shorter strides with a more extended thigh and abducted hip.

As noted previously (50), UMP MORII 94'80 has a broad bicondylar breadth; a well-developed popliteal groove; a wide, shallow patella groove; and a medial condyle that is broader than the lateral condyle (50). These features are correlated with ape-like capacities in the knee for rotation and hindlimb abduction (50, 66, 67). Proximally, the femoral head is somewhat small compared with extant hominoids, as reflected in the smaller body mass estimates that were calculated by Ruff (51) on the basis of femoral head breadth (29.5 kg) versus bicondylar breadth (37.3 kg) using a combined catarrhine sample. However, the relative femoral head surface area falls between those of African apes and monkeys, implying at least moderate hip mobility, and is broadly consistent with locomotion that included vertical climbing and with locomotor inferences stemming from the femoral shaft and distal femur (68).

Vertebra

Lumbar vertebra UMP 67-28 from Moroto II shares anatomical features with hominoids that are absent in cercopithecoid monkeys (37, 48, 49). For example, transverse processes arise from the base of robust pedicles and are oriented dorsally (49), increasing the moment arm of the muscles iliocostalis and longissimus dorsi to resist ventroflexion (69). Also, the vertebra lacks anapophyses (tailed catarrhines have anapophyses as insertions for caudal vertebral extensors), has reduced ventral keeling, and exhibits a caudally inclined spinous process (which is associated with reduced dorsoventral mobility) (37, 49). New cleaning and preparation of this vertebra in 2016 revealed the presence of salient ligamentous pits medial to the postzygapophyses; these had been filled with sediment and had not previously been obvious (data S2). The pits represent insertions for the ligamentum flavum, intervertebral ligaments positioned between laminae of adjacent vertebrae in mammals. Their primary function in the lumbar column is to limit ventroflexion and stabilize lumbar vertebrae on one another. The depth of these ligamentous pits in UMP 67-28 suggests ligaments of substantial strength. With the features mentioned above, these ligaments can be interpreted to help maintain orthograde and lumbar stability, as opposed to increasing spinal mobility. These features differ from those found in the lumbar vertebrae of *Ekembo*, which were interpreted as being associated with monkey-like flexion and extension of the spine during quadrupedal locomotion (37).

Dental specimens

In addition to *Morotopithecus*, at least three smaller, non-cercopithecoid catarrhine taxa are represented in the 1994–2017 fossils collected

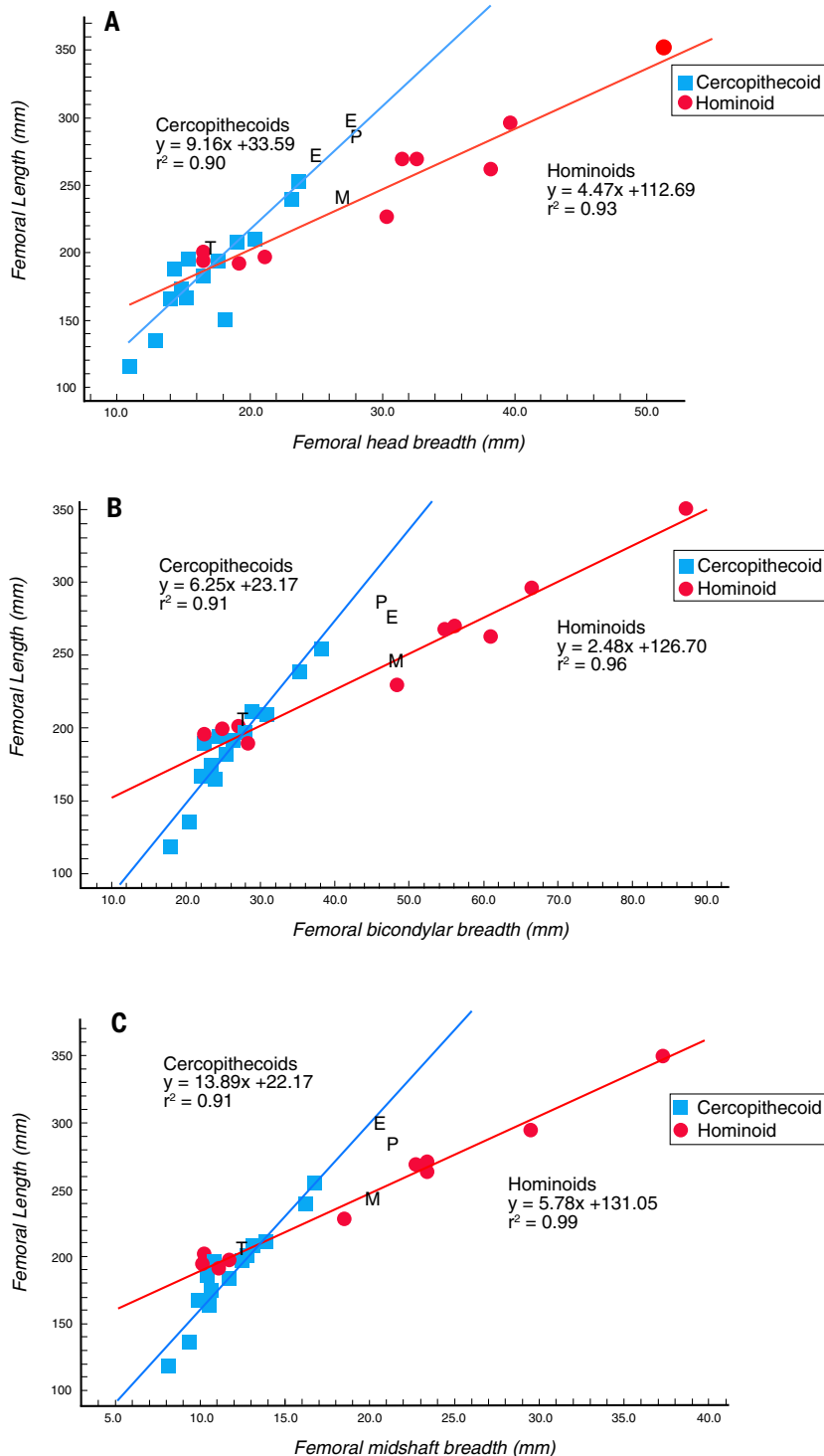


Fig. 3. Catarrhine femoral proportions. (A to C) Bivariate plots of mean femur length for extant hominoids and cercopithecoidea regressed on mean femur bicondylar breadth (A), mean femur head superoinferior breadth (B), and mean femur midshaft breadth (C). Extant values are from (51) [see also (52)]. Fossil taxa are plotted and are from the following specimens: *Morotopithecus* (M) is from UMP MORII 94'80; *Paracolobus* (P) is from BC3; *Ekembo* (E) are from KNM-RU 5527 [(A) and (B)] and KNM-MW 13142 [(B) and (C)]; and *Turkanapithecus* (T) is from KNM WT 16950. Note that hylobatids and cercopithecoidea cannot be distinguished on the basis of femoral proportions, and that femur length is only a diagnostic trait at larger body size.

by our team (table S6): a proconsulid (UMP MORII 03'559), aff. *Rangwapithecus* (UMP MOR II 11'1938; figs. S8 and S9 and table S7), and a small-bodied non-cercopithecoidea catarrhine (UMP MORII 02'352) that is represented only by a lower canine that does not fit in the hypodigm of any known small catarrhine genus (fig. S10).

The lower third molar (UMP MOR II 11'1938) attributable to aff. *Rangwapithecus* is the first record of the genus outside of Kenya, and the oldest. We describe it in brief because *Rangwapithecus* has very well developed shearing crests compared with other Early Miocene catarrhines (45) and microwear denotive of folivory (46), indicating that another, smaller catarrhine with this dietary specialization was present at Moroto II. The specimen compares favorably to *R. gordonii* from Songhor and shares with it several traits, including a large and elongate crown, peripherally positioned conical cusps linked by rounded crests, and delicate secondary enamel crenulations (42, 70). However, there are some features suggesting that it is more primitive and/or unique, including a narrower mesial buccal notch and less discrete buccal cusp outlines. Traits such as the well-developed mesostylid and lack of a crest between the hypocondylar and entocondylar are reminiscent of traits found in the older nyanzapithecine from the Late Oligocene, *Rukwapithecus* (71). On balance, we find the specimen to have strong affinities to *Rangwapithecus*, with the differences likely reflecting the ancestral nyanzapithecine condition, which is compatible with its greater antiquity.

Stable isotopes of enamel

Dietary carbon isotopic signatures of molars from *Morotopithecus*, aff. *Rangwapithecus*, and the proconsulid reveal that all three taxa had ^{13}C -enriched diets relative to modern hominoids (Fig. 5B and table S8), indicating dietary niches and habitat preferences distinct from those of living apes (52). Specifically, the carbon isotopic signals of the enamel ($\delta^{13}\text{C}_{\text{enamel}}$) of the Moroto hominoids are consistent with water-stressed C_3 dietary vegetation, encroaching on the isotopic range of modern catarrhines that forage in more open habitats, such as *Papio* or some of the earliest hominins (Fig. 5B). Although the $\delta^{18}\text{O}_{\text{enamel}}$ value of *Morotopithecus* is within the isotopic range of associated large-bodied terrestrial fossil herbivores at Moroto II (e.g., proboscideans and anthracotheres), it is ^{18}O enriched relative to the other catarrhines (figs. S11B and S12 and table S8). As a taxon with derived orthograde and climbing capabilities, this suggests that *Morotopithecus* may have (despite its large size) more easily foraged in peripheral or higher parts of the canopy, where evapotranspiration and irradiance were higher and vegetation was more water stressed (72).

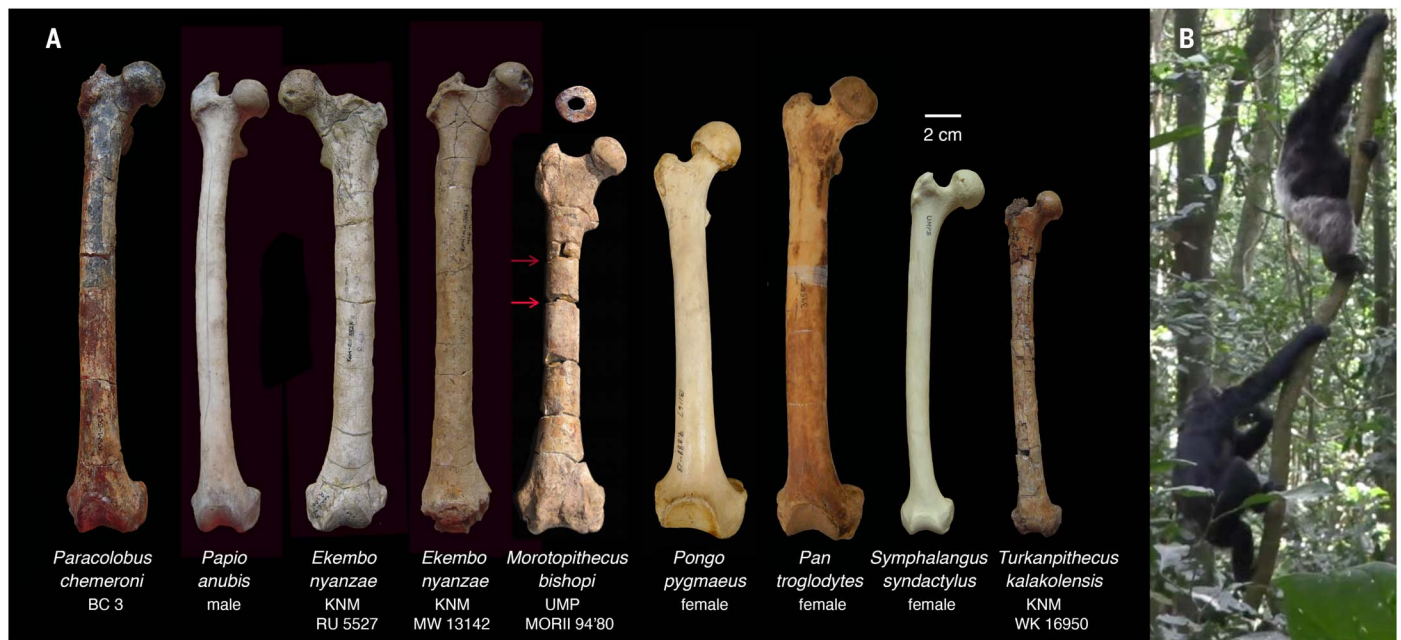


Fig. 4. Catarrhine femora. (A) Catarrhine femora, anterior view. The Pliocene cercopithecoïd *Paracolobus* [mass ~36 kg based on regressions in (51)] and *Papio* [male mass ~25 kg (103)] have proportionately longer shafts than extant hominoids. *Ekembo* (~36 kg) and *Morotopithecus* (~35 kg) have similar femoral midshaft and joint dimensions and inferred body sizes (51), but the *Morotopithecus* femur is shorter. *Turkanpithecus* [~10 kg based on regressions in (51)] is Early Miocene in age and is the size of extant *Symphalangus* [~12 kg (51)]. The larger fossil taxa are about the same size as female *Pongo* [mass ~36 kg (103)], but smaller than female *Pan* [mass ~46 kg (103)].

Pan, *Pongo*, and *Morotopithecus* have shorter femora for their size than do cercopithecoïds and *Ekembo*. The top red arrow adjacent to the *Morotopithecus* femur denotes where cortical bone was exposed and analyzed (50) when this fragment was hypothesized to be midshaft. The bottom arrow indicates the break exposing the cortical bone analyzed in this study, with its cross section pictured above. (B) Short femora and hindlimbs are biomechanically advantageous for vertical climbing. Shown are Jackson (adult male, top) and Sarah (adult female), chimpanzees from Kibale Forest in Uganda, vertically climbing a liana.

Paleoecology

Paleoecological reconstructions of fossil catarrhine and hominoid sites in eastern Africa have suggested a primitive phyloecological context for hominoid origins characterized by a complex canopy structure(s) associated with forested habitats [e.g., (73–76)]. However, evidence and interpretations from fossil sites in eastern Africa have also yielded empirical data implicating more heterogeneous habitats that include woodland and even wooded grassland components [e.g., (27, 77, 78)]. Overall, the fossil record leading up to the Early Miocene in eastern Africa has revealed variable ecosystems, although the general distribution and relevance of any particular habitat(s) for hominoid evolution remains unknown. Given this difficulty, it is important to situate the evolution of hominoids and their vertebrate communities specifically within local and regional paleoecological frameworks.

To assess the paleoecological context of the Moroto II fossil assemblage, several independent approaches were used, including (i) isotopic dietary ecology of fossil herbivore guilds; (ii) biogeochemical analyses of paleosol bulk organics, *n*-alkanes, and pedogenic carbonate; (iii) elemental characterization of paleosols to

estimate mean annual precipitation (MAP); and (iv) analyses of phytolith assemblages. These approaches provide a composite perspective on the physiognomy and physiology of the vegetation but also reflect climatic factors such as seasonality and precipitation. Cumulatively, these data have relevance for constraining aspects of the canopy architecture and resource distribution that are critical for determining the adaptive significance of early hominoid locomotor and foraging behaviors.

Stable carbon isotopes of fossil enamel

Isotopic paleodietary ecology has figured prominently in discussions of the evolution of eastern African terrestrial communities, particularly in using $\delta^{13}\text{C}$ proxies to establish the relative significance of C_4 grasses in past ecosystems [e.g., (79, 80)]. However, $\delta^{13}\text{C}_{\text{enamel}}$ datasets are comparatively rare from sites older than ~9 Ma. This is in part because Early and Middle Miocene sites were presumed to predate significant C_4 biomass in eastern Africa. Thus, enamel samples were not analyzed because the paleoecological reconstructive potential of isotopes based only on C_3 plant variation is limited. This study provides one of the first applications of this technique to the

Early Miocene of eastern Africa, thereby filling a crucial data gap.

The application of enamel isotopic analyses for differentiating dietary guilds within C_3 -dominated biomes or among C_3 browsers and grazers currently remains coarse. Although there is no strict relationship between canopy cover or architecture and $\delta^{13}\text{C}_{\text{enamel}}$ values, general trends related to water stress, irradiance, and canopy density have been established [e.g., (81, 82)], providing guidelines for reconstructing general aspects of past landscapes and habitats. A framework generated for interpreting the isotopic signatures of fossil enamel at Moroto II [Fig. 5 (52)] is based on analysis of a compilation of $\delta^{13}\text{C}$ values of modern and fossil vegetation and herbivore enamel in both C_3 -dominated habitats and mixed C_3/C_4 ecosystems.

$\delta^{13}\text{C}_{\text{enamel}}$ values of fossil enamel from 25 fossil herbivores at Moroto II, representing nine genera from seven families, range from -6.8‰ to -15.3‰, with ~85% of the values falling between -12‰ and -8‰ (Fig. 5B and table S8). This dietary range is most consistent with foraging in mesic to arid woodland ecosystems, as depicted in Fig. 5, with limited evidence of closed canopy forest or open woodland and

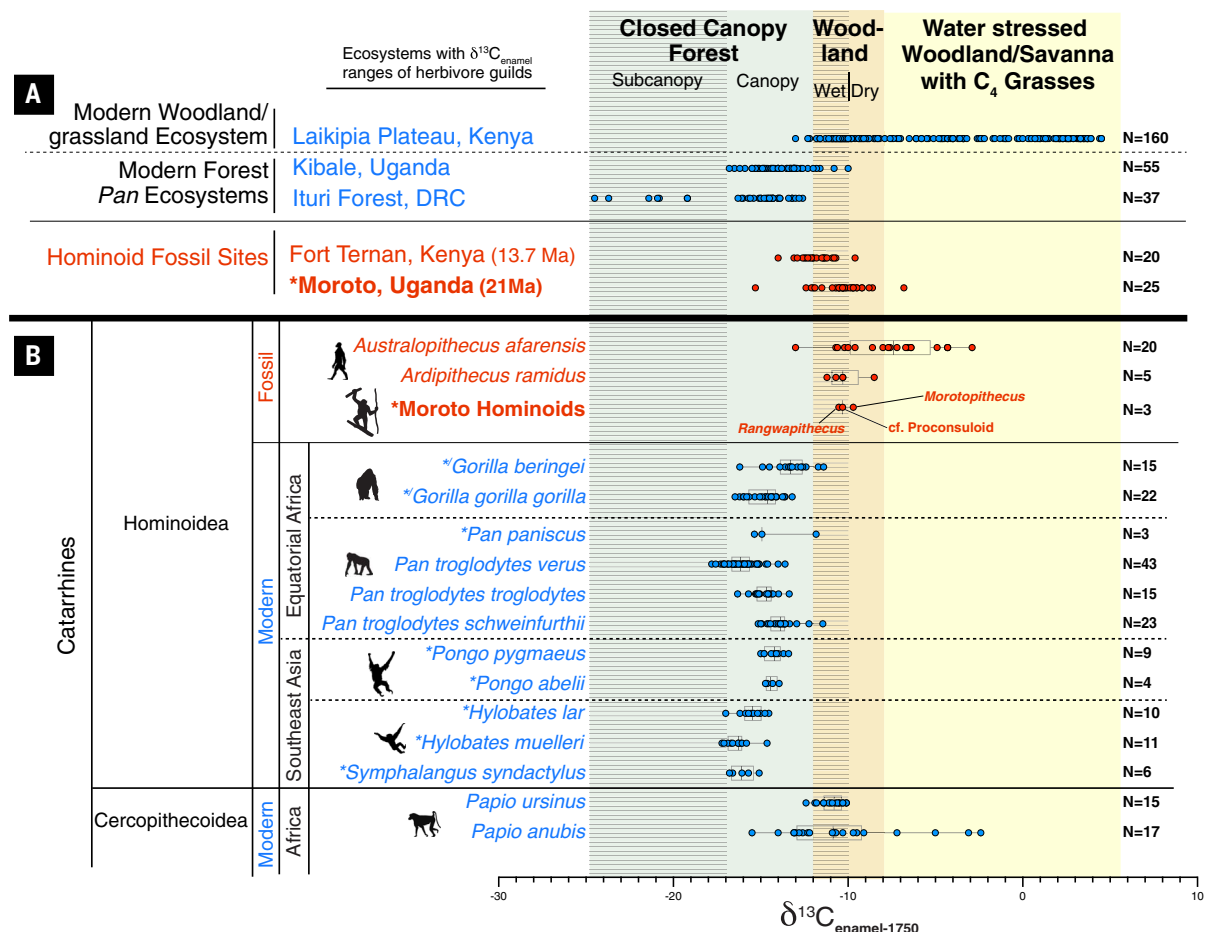


Fig. 5. Dietary $\delta^{13}\text{C}_{\text{enamel}}$ values from modern and fossil ecosystems and taxa.

(A) An isotopic ecological framework (52) relating foraging strategy to habitat type applied to $\delta^{13}\text{C}_{\text{enamel}}$ dietary signatures from a range of herbivores collected from three modern ecosystems in equatorial Africa (79, 104, 105). Isotopic dietary ranges of fossil herbivores analyzed from Fort Ternan (106) and the Moroto sites I and II (this study) are shown. Extant taxa are shown in blue and fossil taxa in red.

(B) Comparative isotopic dietary signals of fossil hominins (107, 108), three Moroto hominoids (this study), and extant catarrhines used to constrain foraging habitats. Modern catarrhine values include gorillas [(109); this study, $n = 21$], chimpanzees [(110) and references therein; this study, $n = 3$], orangutans (this study, $n = 13$), gibbons (this study, $n = 27$), and baboons (109). *, Data from this study; */, data from this study and previous research; all other data are from previous studies.

savanna microhabitats. The more positive dietary values ($\sim -9\%$) indicate feeding on ^{13}C -enriched C_3 vegetation (typically associated with water-stressed modern habitats) and possibly including minor C_4 (or CAM) dietary components (i.e., largely arid-adapted grasses and/or succulents in the tropics). The Moroto II isotopic fossil dietary range differs from modern herbivores feeding in tropical forest and woodland and grassland ecosystems in equatorial Africa (Fig. 5A), with no clear modern analogs yet established isotopically. Isotopic variation of fossil herbivores at Moroto II is also distinguished from the more closed, forested profile established for the Middle Miocene fossil site of Fort Ternan (Fig. 5A).

Paleosol carbon isotopes

Multiple environmental indicators were also assessed on the basis of analyses of paleosols throughout the sequence (52), including the

interval associated with the *Morotopithecus* mandible and femora (Fig. 2A). These indicators are biogeochemical proxies, primarily reflecting local relative proportions of C_3 and C_4 vegetation. The carbon isotope values of bulk organic matter ($\delta^{13}\text{C}_{\text{OM}}$; $n = 16$) from Moroto II range from -29.9% to -20.1% [relative to the Vienna PeeDee Belemnite (VPDB)] (Fig. 2C), and pedogenic carbonate values ($\delta^{13}\text{C}_{\text{PC}}$; $n = 6$) range from -7.7% to -2.5% (VPDB) (Fig. 2E). Although some paleosol samples at Moroto II are consistent with entirely C_3 vegetation, paleosols stratigraphically adjacent to the *Morotopithecus* fossil-bearing interval had the largest proportion of reconstructed C_4 vegetation, with up to 59% C_4 [95% confidence interval (CI) = 29 to 83%; $\delta^{13}\text{C}_{\text{PC}} = -2.5\%$] based on micritic pedogenic carbonates and up to 45% (95% CI = 13 to 64%; $\delta^{13}\text{C}_{\text{OM}} = -20.1\%$) based on paleosol organic matter (Fig. 2C and tables S9 and S10). Overall,

the $\delta^{13}\text{C}_{\text{PC}}$ and $\delta^{13}\text{C}_{\text{OM}}$ datasets suggest that C_3 vegetation was interspersed with either water-stressed C_3 plants or C_4 grasses throughout the stratigraphic succession.

Paleosol n -alkanes

n -Alkanes are plant leaf wax-derived biomarkers found in paleosols that can be used to reconstruct vegetation. Biomarker concentrations and molecular distributions indicate excellent preservation of n -alkanes in the Moroto II paleosols and support the interpretation that isotope data reflect the Early Miocene plant community (table S11). The carbon isotope values of $\text{C}_{31}n$ -alkanes range from -31.4% to -22.7% (Fig. 2D), which represent a range of C_3 - to C_4 -dominated ecosystems, respectively. Carbon isotope values from other plant-derived n -alkanes are presented in table S12. The $\delta^{13}\text{C}$ values of the $\text{C}_{35}n$ -alkanes for three samples range from -24.1% to -20.7% , which indicate

high abundances of C_4 vegetation on the landscape. The C_{35} homolog has been shown to be a highly sensitive indicator of C_4 vegetation in other Miocene samples from Africa (83, 84) and from the Siwalik sequence in Pakistan and India (85). Several studies have shown that C_4 grasses, especially from Africa, produce much higher abundances of long-chain n -alkanes (i.e., C_{33} and C_{35}) than do C_3 plants (86, 87). Samples with $\delta^{13}C$ values associated with C_4 vegetation from Moroto II also have relatively high concentrations of C_{33} and C_{35} homologs and together provide compelling isotopic and molecular evidence for C_4 grasses at Moroto II.

Seven samples from Moroto II have paired carbon isotope data for both bulk organic matter and n -alkanes. The $\delta^{13}C$ values of bulk organic matter for these samples are strongly and significantly correlated with the $\delta^{13}C$ values of C_{31} alkanes ($r = 0.98$, $P < 0.001$) and C_{35} alkanes ($r = 0.94$, $P = 0.002$), corroborating the reliability of the bulk organic carbon isotope results. Only two sampling levels at Moroto II included analyses of both pedogenic carbonate and n -alkanes, because the sample sizes from other levels were too small for meaningful comparisons.

Paleosols and hydroclimate

Paleosols at Moroto II typically formed on the finer-grained fluvial deposits and include gleyed Vertisols, calcic and noncalcic Inceptisols, and Alfisols (figs. S12 and S13). Qualitatively, these features are consistent with a seasonally varying hydroclimate that requires water deficit and surplus for Vertisol development and seasonal dewatering for pedogenic carbonate formation with a potential maximum MAP of ~1000 mm given the rarity of modern calcic soils above this threshold (88). Paleo-MAP was estimated using three proxies that use the bulk elemental composition of the uppermost subsoil (B) horizon as input data (52, 89). The samples from the Moroto II sequence (Fig. 2F, figs. S13 and S14, and tables S13 to S15) yielded MAP values of 626 to 1313 mm/year, indicative of a subhumid paleoclimate within the range of modern woodlands in Africa (90, 91). Further, none of the results from Moroto II supports MAP values in excess of 1500 to 2000 mm regardless of wet season length or fire regime, conditions that currently characterize closed canopy forests in equatorial Africa [e.g., (91)].

Phytoliths

Phytoliths are microscopic silica bodies precipitated in living plant cells and cell walls that remain in soils or sediments when plants die and decay. Preserved phytolith assemblages allow reconstruction of vegetation structure and type on a relatively local scale, especially in tropical and subtropical ecosystems (92–94). The six variably preserved phytolith assemblages from Moroto II confirm inferences from isotopic data of habitat heterogeneity, either spatially or temporally (52) (Fig. 2B and tables S16 to S18). The best-preserved assemblage, sampled from the *Morotopithecus* interval, is dominated by grass phytoliths (63.1% of diagnostic morphotypes) that are mainly from PACMAD grasses (C_3 or C_4 taxa in the Panicoideae, Arundinoideae, Chloridoideae, Micrairoideae, Aristidoideae, or Danthonioideae subfamilies), and includes phytoliths of the arid-adapted, C_4 Chloridoideae PACMAD subfamily. This assemblage also contains forest-indicator phytoliths, including rare evidence of palms, indicating spatial heterogeneity in the vegetation. Compositionally, this assemblage has affinities with modern phytolith assemblages from wooded grasslands, but it is also consistent with open forests containing a substantial grass understory (e.g., riparian forest in a savanna landscape, dry forest, or forest openings) (27).

Discussion

Context of the hominoid remains from Moroto

Moroto II records not only the earliest evidence of clearly derived hominoid postcrania and the first record of folivory for a large-bodied hominoid, but also the oldest known African ecosystem with C_4 grasses. Compilation of lithostratigraphic, pedogenic, biogeochemical, phytolith assemblage, and taphonomic data from Moroto II indicate a seasonal, mixed C_3/C_4 environment with broken canopy forest or woodland habitats. Evidence of water-stressed C_3 woodland-based diets for the catarrhines and associated fauna, as well as pedogenic proxies documenting a major C_4 component, are congruent with habitats characterized by a fragmentary canopy cover. These reconstructions provide empirical evidence supporting the concept that Early Miocene apes may have been broadly associated with heterogeneous, woodland habitats (27, 77).

Discussion

Context of the hominoid remains from Moroto

These data call into question previous assumptions regarding hominoid dietary and locomotor coevolution because, in combination, they fail to support prevailing terminal branch forest frugivory hypotheses that orthograde locomotor versatility evolved to facilitate feeding on fruit in a tropical forest. Instead, the earliest known appearance of enhanced orthograde and shortened hindlimbs occurred in a seasonal woodland and wooded grassland context, where soft, ripe fruit would be periodically limited. Indeed, the morphology of dental remains reveals that leaves were an important component of the diet of at least two Moroto hominoids, *Morotopithecus* (36) and the nyanzapithecine aff. *Rangwapithecus*.

Positional behavioral versatility and its anatomical correlates may have evolved multiple times in large-bodied catarrhines. There is no evidence to indicate, for example, that *Morotopithecus* is closely related to the Eurasian taxa

Pierolapithecus (~12 Ma) or *Hispanopithecus* (~10 Ma), the next-oldest hominoids inferred to have had dorsostable lumbar spines (95, 96). These hominoids have been associated with forested environments (97, 98), but because they are so much younger, their adaptive and phylogenetic significance reflects more the evolution of crown hominoids (i.e., that are closely related to the living hominoids) (99) than hominoid origins in Africa.

In the absence of additional fossils such as hand bones, it is not possible to judge whether suspension (10, 11), quadrumanous climbing (12), and vertical climbing (13, 14) were more or less associated with hominoid adaptive origins (39). However, the record from Moroto II supports the hypothesis that orthograde is key to hominoid distinctiveness (6, 15) because it is among the first identifiable steps in the evolution of anatomical features associated with the modern-type hominoid adaptive niche.

Furthermore, in this first recorded instance, locomotor and postural innovation seem to have evolved in hominoids for effective arboreal feeding on leaves and fruit situated in higher and/or peripheral aspects of tree crowns in seasonal woodland habitats characterized by gaps in the canopy. Such environments may exert hitherto unrecognized selective pressures on the evolution of arboreal apes, such as the need, in times of seasonal low fruit availability, to access young leaves with relatively high protein (26) in the terminal or higher aspects of the canopy. Although some breaks in the canopy could be bridged through enhanced climbing adaptations, larger gaps would have necessitated repeated descent and ascent of tree trunks and/or lianas, which is consistent with the locomotor behavior indicated by the femoral and vertebral morphology of the hominoid fossils of Moroto II.

Hominoid adaptive evolution in eastern Africa

Documenting the early stages of hominoid evolution as the lineage diverged from other catarrhines is critical for interpreting the adaptive significance of traits that ultimately define modern hominoids, including humans. Although high catarrhine taxonomic and phylogenetic diversity in the Early Miocene have been recognized for some time (42), a schema is now emerging of high adaptive diversity among these primates (100), as well as high environmental variability (27, 73, 78), a perspective reinforced by reconstructions of hominoid behavior and ecology at Moroto II. These findings suggest that early hominoid morphologies and environments do not match classic ideas about the origins of the group, revealing a complexity yet to be studied and understood. The traditional paradigm for interpreting the origin of the hominoid lineage has involved forested habitats, but the data described herein

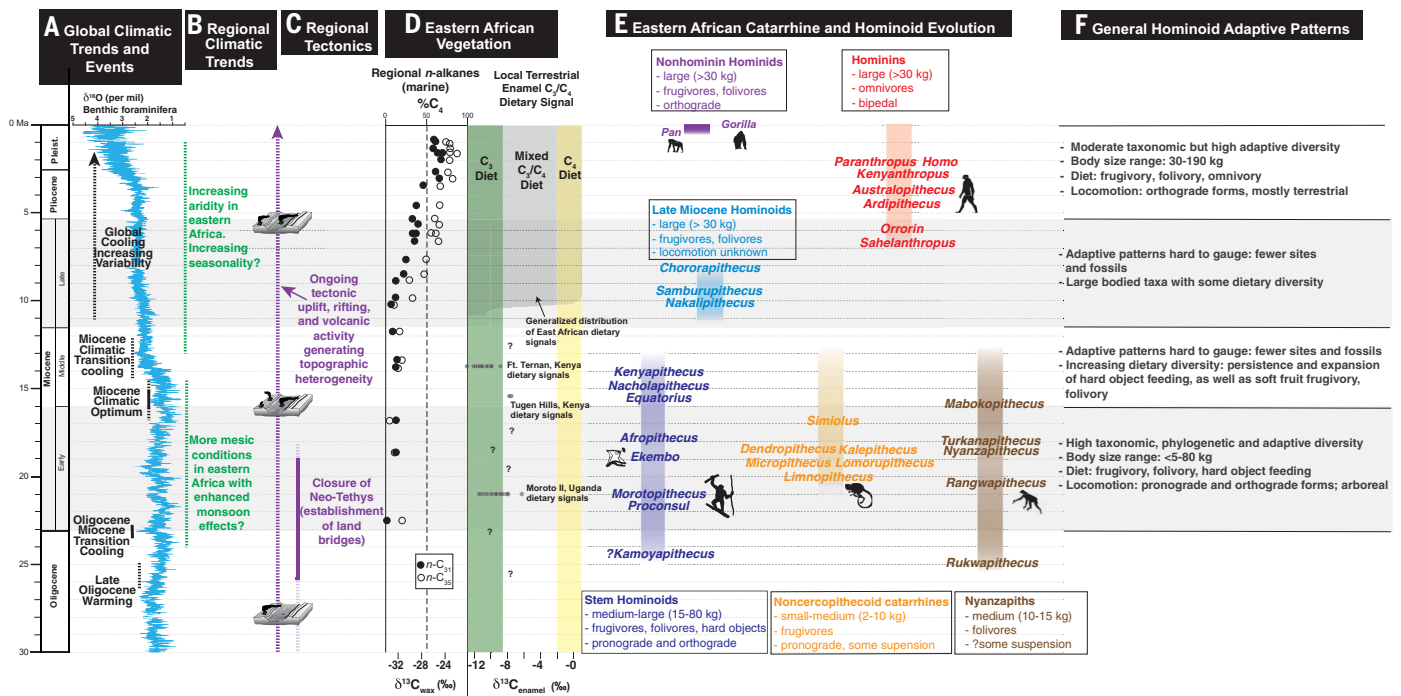


Fig. 6. Environments and catarrhine adaptive evolution. (A) Global climatic trends and events (111–115). Benthic foraminifera $\delta^{18}\text{O}$ are shown in blue (115). (B) Regional climatic trends (seasonality and variability) [e.g., (116, 117)]. (C) Regional tectonic events and trends in eastern Africa (118, 119). (D) Regional n -alkane record of terrestrial vegetation (83, 120) and eastern Africa fossil dietary record (this study) (121, 122). The gray area depicts reported herbivore dietary isotopic signals that include a range of C_3 and C_4 dietary components and an apparent increase in C_4 dietary biomass after ~10 Ma ago (84, 100, 120). (E) African catarrhines grouped using biogeography, chronology, and adaptive inferences, not strict phylogeny. The group “stem hominoids” is well supported

(99), but including *Kamoyapithecus*, although plausible (123), is not typical [e.g., (71)] and is informed by size and inferred adaptive similarity (8). Nyanzapithinae (e.g., *Rangwapithecus* and *Rukwapithecus*) are folivorous and considered a monophyletic group (124). “Noncercopithecoid catarrhines” are poorly known and [with possible exceptions (125)] unlikely to be hominoids (42). Late Miocene hominoids, related by biogeography and age, remain enigmatic (42, 126–129). *Pan* and *Gorilla* share adaptive similarity (130), but *Pan* is more related to hominins. Hominin adaptations, including canine reduction (131) and bipedality (108, 132), are often linked to habitat heterogeneity. (F) Chronologically informed adaptive patterns.

reveal that in the Early Miocene, hominoid adaptive diversity may have been influenced by environmental heterogeneity (Fig. 6), as has already been documented in the Late Miocene/Pliocene and invoked in scenarios of hominin origins (101, 102). This requires more careful consideration of the nature of habitat heterogeneity in the past and a reevaluation of how it may be linked to features (e.g., bipedality and dental and foraging specializations) associated with early hominin expansion into more open microhabitats within diverse ecosystems.

Materials and methods summary

Material and methods for all techniques are available in the supplementary materials. This includes radiometric, paleomagnetic, and biostratigraphic dating methods; morphological, taphonomic, and faunal analyses; paleosol biogeochemical approaches (carbon isotopic analysis from both bulk organic and carbonate samples, n -alkane analysis, and paleosol-based hydroclimate analysis); and paleoecological analyses including isotopic dietary paleoecology and phytolith analyses.

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SUPPLEMENTARY MATERIALS

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The evolution of hominoid locomotor versatility: Evidence from Moroto, a 21 Ma site in Uganda

Laura M. MacLatchy, Susanne M. Cote, Alan L. Deino, Robert M. Kityo, Amon A. T. Mugume, James B. Rossie, William J. Sanders, Miranda N. Cosman, Steven G. Driese, David L. Fox, April J. Freeman, Rutger J. W. Jansma, Kirsten E. H. Jenkins, Rahab N. Kinyanjui, William E. Lukens, Kieran P. McNulty, Alice Novello, Daniel J. Peppe, Caroline A. E. Strmberg, Kevin T. Uno, Alisa J. Winkler, and John D. Kingston

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A new habitat for hominoid emergence?

The hominoid lineage underwent a major morphological change in the Miocene, acquiring strong hind legs and a more upright posture. The prevailing hypothesis pertaining to these changes has been that they were adaptive for foraging on fruit in the terminal branches of tropical forest trees. A pair of papers now argue that, instead, such changes may have been driven by adaptation to feeding on leaves in seasonally dry and open forests. Peppe *et al.* used new data from fossil mammal study sites and found that the expansion of grassy biomes dominated by grasses with the C4 photosynthetic pathway in eastern Africa likely occurred more than 10 million years earlier than prior estimates. MacLatchy *et al.* looked at fossils of the earliest ape in this region at this time, *Morotopithecus*, and found isotope evidence of the consumption of water-stressed vegetation and postcranial morphology indicative of strong hind limbs similar to modern apes. Together, these papers suggest that early hominoids emerged in a dryer and more irregular environment than was previously believed. —BEL and SNV

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