

First fossil chimpanzee

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There are thousands of fossils of hominins, but no fossil chimpanzee has yet been reported. The chimpanzee (*Pan*) is the closest living relative to humans¹. Chimpanzee populations today are confined to wooded West and central Africa, whereas most hominin fossil sites occur in the semi-arid East African Rift Valley. This situation has fuelled speculation regarding causes for the divergence of the human and chimpanzee lineages five to eight million years ago. Some investigators have invoked a shift from wooded to savannah vegetation in East Africa, driven by climate change, to explain the apparent separation between chimpanzee and human ancestral populations and the origin of the unique hominin locomotor adaptation, bipedalism^{2–5}. The Rift Valley itself functions as an obstacle to chimpanzee occupation in some scenarios⁶. Here we report the first fossil chimpanzee. These fossils, from the Kapthurin Formation, Kenya, show that representatives of *Pan* were present in the East African Rift Valley during the Middle Pleistocene, where they were contemporary with an extinct species of *Homo*. Habitats suitable for both hominins and chimpanzees were clearly present there during this period, and the Rift Valley did not present an impenetrable barrier to chimpanzee occupation.

The Kapthurin Formation forms the Middle Pleistocene portion of the Tugen Hills sequence west of Lake Baringo (Figs 1 and 2). It consists of a package of fluvial, lacustrine and volcanic sediments ~125 m thick, exposed over ~150 km² (refs 7–9) that contains numerous palaeontological and archaeological sites^{9–11}. It is divided into five members informally designated K1–K5 (ref. 7), and the sequence is well calibrated by ⁴⁰Ar/³⁹Ar dating¹².

Hominin fossils attributed to *Homo erectus* or *Homo rhodesiensis* have been found in the fluvial sediments of K3 (refs 11, 13, 14). The new chimpanzee fossils were discovered at Locality (Loc.) 99 in K3', the lacustrine facies of the same geological member. Loc. 99 consists of ~80 m² of exposures at an outcrop ~1 km northeast of site GnJh-19 where hominin mandible KNM-BK (Kenya National Museum-Baringo Kapthurin) 8518 was found¹⁴. Two chimpanzee fossils, KNM-TH (Kenya National Museum-Tugen Hills) 45519 and KNM-TH 45520, were found in surface context within an area of ~12 m² within Loc. 99; additional specimens (KNM-TH 45521 and KNM-TH 45522) were recovered from sieved superficial sediments within the same restricted area. The age of the chimpanzee fossils is constrained by ⁴⁰Ar/³⁹Ar dates of 545 ± 3 kyr (thousand years) on underlying K2 and 284 ± 12 kyr on overlying K4 (ref. 12). Because they are derived from a position low in this stratigraphic interval, they are probably closer to the maximum age of 545 kyr. *Homo* fossils KNM-BK 63-67 and KNM-BK 8518 from K3 are bracketed by ⁴⁰Ar/³⁹Ar dates of 543 ± 4 kyr and 509 ± 9 kyr¹² (Fig. 2).

K3' sediments are exposed in an outcrop of ~1 km² in the eastern portion of the Kapthurin Formation. They consist of black and red zeolitized clays interbedded with sands and heavily altered volcanics. Sedimentary and geochemical features of the clays indicate that they were laid down in a shallow body of water that alternated between

fresh and intensely saline-alkaline, probably as a response to changes in outflow geometry controlled by local volcanism¹⁵. Additional intermittent sources of fresh water are suggested by localized ephemeral stream channel features and the remains of an extensive fossil spring. Loc. 99 has produced fragmentary fossils representing suids, bovids, rodents, cercopithecoid primates and catfish. Eight additional faunal collecting areas in K3' have also produced elephants, hippopotami, carnivores, crocodiles, turtles, gastropods and additional micromammals. Many K3' taxa, notably hippopotami (*Hippopotamus*), crocodiles, catfish (*Clarias*), gastropods and turtles, reflect local aquatic conditions. The bulk of K3' non-aquatic fauna, including a colobine monkey, the elephant, the bovids *Kobus*, *Tragelaphus* and specimens probably belonging to *Syncerus*, and the suids *Potamochoerus porcus* (bushpig) and the extinct *Kolpochoerus majus*¹⁶, are consistent with a closed environment. The presence of the cane rat (*Thryonomys*) indicates localized patches of moist, marshy conditions.

Remains of *Homo* (KNM-BK 63-67 and KNM-BK 8518) were recovered at sites GnJh-01 and GnJh-19 by previous workers^{11,13,14} from K3 fluvial sediments to the west that represent a system of braided streams, some of which seem to have debouched into the lake. Fluvial K3 deposits and lacustrine K3' deposits are interstratified, indicating a shoreline that shifted in position in response to alterations in lake levels. The similarity in the array of fossils encountered in K3 and K3' sediments suggests that Middle Pleistocene *Pan* and *Homo* lived, or at least died, in broadly similar environmental settings. Taken together, the evidence suggests a locally wooded habitat on the shore of an alternately fresh and saline-alkaline lake, fluctuating lake levels, ephemeral nearshore fluvial channels, a nearby freshwater spring, and a semi-arid climatic regime. These conditions are not unlike those found near the shore of Lake Baringo today, although dense human populations have eliminated much of the woodland that formerly supported chimpanzees and the faunal community of which they were a part.

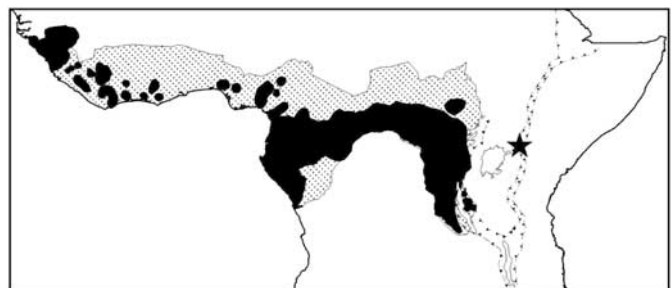


Figure 1 | Map showing current (solid black) and historical (stippled) ranges of *Pan* in equatorial Africa relative to major features of the eastern and western Rift Valleys. The Kapthurin Formation, Kenya, in the Eastern Rift Valley is marked by a star.

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The chimpanzee specimens comprise a minimum of three teeth, probably from the same individual. Two of these are right and left upper central permanent incisors (I^1 ; KNM-TH 45519 and KNM-TH 45521, respectively). They exhibit broad, spatulate and moderately worn crowns, with thin dental enamel (Fig. 3). The lingual tubercle is large and flanked at the base by deep mesial and distal foveae, characteristic of *Pan*. This feature imparts great thickness to the labiolingual profiles of the teeth, and clearly distinguishes them from known hominins. The mesial and distal marginal ridges are well formed. The distal corners of the incisal edges are slightly chipped and the labial enamel surfaces exhibit pre-mortem wear as well as slight post-mortem surface weathering. The roots have closed apices and are straight, conical and relatively short. The incisal edges and lingual tubercles exhibit dentinal exposure resulting from wear. Measurements of the specimens, with comparisons to those of extant species of *Pan*, are provided in Table 1. The upper incisors are nearly identical to those of modern *Pan* in all aspects of morphology except their shorter root length. The sub-parallel mesial and distal margins of the incisors bestow a quadrate, rather than triangular, outline to the crowns, a feature that among living chimpanzees is considered to be more common among living *P. troglodytes* than *P. paniscus*¹⁷. The enamel and cementum coverings are in good condition and the perikymata on the labial surfaces of the crowns and the periradicular striae on the lingual surfaces of the roots can be easily seen. Several of the perikymata near the cervices of the teeth are faintly incised, indicating mild enamel hypoplasia having occurred at about the age of 5 years¹⁸. The well-matched mesial interproximal wear facets of the Kapthurin Formation *Pan* incisors (KNM-TH 45519 and KNM-TH 45521), the comparable degree of wear on their incisal edges, and the continuity of the enamel hypoplasia on their crowns and the incremental markings on their roots suggest that the two teeth are antimeres.

The third tooth is a lightly worn crown of a left upper permanent molar (KNM-TH 45520) (Fig. 4). It can be problematic to dis-

tinguish first from second upper molars in *Pan*, but we identify KNM-TH 45520 as an M^1 , judging from the relatively large size of its hypocone, as this cusp is known to decrease in size from M^1 to M^3 (ref. 19). The Kapthurin Formation M^1 is an extremely low molar crown that has lost most of the enamel on its mesial and lingual faces due to breakage after fossilization. The enamel surfaces are pock-marked as a result of chemical and physical weathering. The paracone and metacone are of approximately equal heights and are separated by a sharply incised buccal groove. The hypocone is lower than either of the buccal cusps, but is relatively large and well defined. A shallow trigon basin is delimited by a weak and obliquely oriented post-protocrista (crista obliqua). A deep but short distal fovea lies between the postprotocrista and the low distal marginal ridge. Despite marring of the enamel surface, perikymata are visible on the buccal and distal faces of the paracone, but there is no evidence of enamel hypoplasia. The relative thinness of the enamel can be discerned on

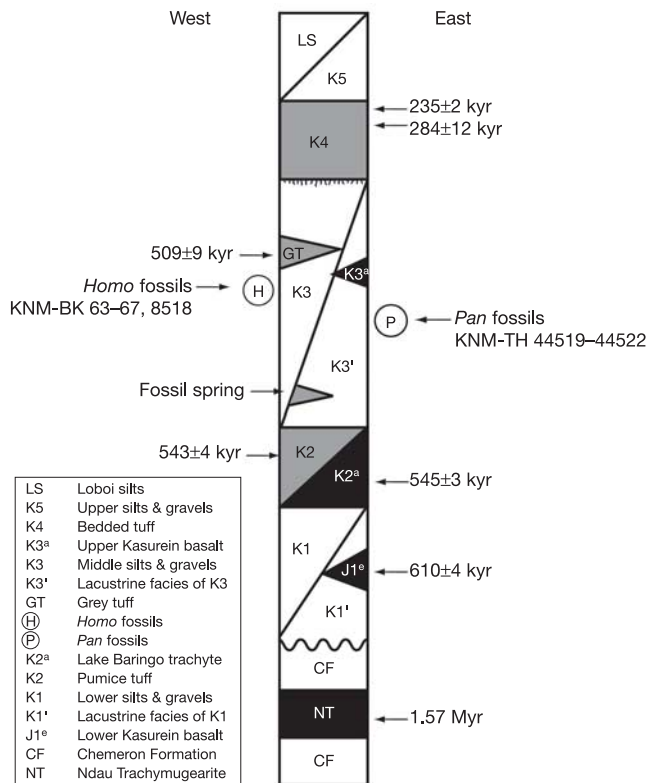


Figure 2 | Idealized stratigraphic column of the Kapthurin Formation, Kenya.



Figure 3 | Central upper incisors of *Pan* from the Kapthurin Formation, Kenya. **a**, KNM-TH 45519. From left to right: labial, lingual, mesial, distal and incisal views. **b**, KNM-TH 45521. Images are in the same sequence as for the previous specimen. **c**, Enlargement of the incisal edge of KNM-TH 45519 (left) and KNM-TH 45521 (right), showing the extreme thinness of the enamel characteristic of modern chimpanzees. **d**, Labial and lingual views of KNM-TH 45519 and KNM-TH 45521.

Table 1 | Dimensions of the Kapthurin Formation fossil chimpanzee teeth

Sample	Tooth	Mesiodistal dimension (mm)	Mesiodistal range (mm)	Buccolingual dimension (mm)	Buccolingual range (mm)
KNM-TH 45519	Right I ¹	10.46	—	9.12	—
KNM-TH 45521	Left I ¹	10.50	—	9.33	—
<i>P. troglodytes</i> (male)	I ¹	12.6 (n = 14)	10.5–13.5	10.1 (n = 15)	9.0–11.3
<i>P. troglodytes</i> (female)	I ¹	11.9 (n = 51)	10.0–13.4	9.6 (n = 50)	8.3–11.7
<i>P. paniscus</i> (male)	I ¹	10.3 (n = 15)	8.9–11.9	7.9 (n = 15)	7.2–9.2
<i>P. paniscus</i> (female)	I ¹	10.4 (n = 20)	9.0–11.5	7.6 (n = 21)	6.8–8.5
KNM-TH 45520	Left M ¹	9.7 (estimate)	—	Damage prevents measurement	—
<i>P. troglodytes</i> (male)	M ¹	10.3 (n = 19)	9.3–11.2	11.7 (n = 19)	10.7–13.2
<i>P. troglodytes</i> (female)	M ¹	10.1 (n = 51)	9.0–11.9	10.9 (n = 50)	7.0–12.8
<i>P. paniscus</i> (male)	M ¹	8.5 (n = 7)	7.9–9.4	9.5 (n = 6)	9.2–10.4
<i>P. paniscus</i> (female)	M ¹	8.3 (n = 6)	7.6–8.8	9.7 (n = 6)	9.3–10.4

Comparative dimensions are given for modern *P. troglodytes* and *P. paniscus* from ref. 19.

the broken mesial and lingual faces of the tooth. The extremely low height of the M¹ crown and the pronounced thinness of the enamel distinguish the tooth from those of known fossil or modern hominins. Among living chimpanzees, the presence of a well-expressed hypocone is more common in *P. troglodytes* than in *P. paniscus*²⁰. A fourth tooth (KNM-TH 45522), the crown and proximal roots of a tooth that may be plausibly identified as an aberrant right upper third molar (M³), will be described elsewhere and is not further discussed here.

The state of wear on the incisors and the M¹ conforms to the known sequence of dental emergence in *Pan*^{19,21}, and it is likely that they come from the same individual. If they do represent the same animal, its age at death can be estimated at approximately 7–8 years based on standards derived from captive animals²² and known dental maturation schedules for mandibular molars²³. The presence of linear enamel hypoplasia on the incisors, but not on the molars, is common in modern apes and seems to be related to nutritional stress that is experienced by the animal after weaning²⁴.

The morphology of the Kapthurin Formation teeth, especially the pronounced lingual tubercle on the incisors, the thickness of the bases of the incisors, the lowness of the molar crown, and the thinness of the enamel on all the teeth clearly supports their attribution to *Pan* rather than *Homo*. Specific diagnosis of isolated teeth within *Pan*, however, must be approached with caution, and for this reason we assign the Kapthurin Formation specimens to *Pan* sp. indet. Non-metric characters that have been suggested as diagnostic criteria for *P. troglodytes*, such as a more quadrilateral outline shape to the upper central incisor crowns¹⁷ and a better expressed hypocone on the maxillary molars^{19,20}, seem to suggest more similarity for the Kapthurin Formation fossils to *P. troglodytes* than to *P. paniscus*, but these features are variably expressed among the living species and

subspecies of *Pan*^{19,25}. Although mean tooth size is known to be significantly smaller in *P. paniscus* than in *P. troglodytes*^{17,25,26}, size ranges overlap (Table 1). Furthermore, apart from the present specimens, we lack a fossil record for the Pliocene and Pleistocene from which to assess past variability within the genus, and it is feasible that the Kapthurin Formation fossils represent members of an extinct lineage within the genus *Pan*.

The Kapthurin Formation fossils represent the first unequivocal evidence of *Pan* in the fossil record, and they demonstrate the presence of chimpanzees in the eastern Rift Valley of Kenya, ~600 km east of the limit of their current range (Fig. 1). The Rift Valley clearly did not pose a physiographical or ecological barrier to chimpanzee occupation. Chimpanzee habitat is now highly fragmented, in part by human activities, but in historic times chimpanzees ranged over a wide belt of equatorial Africa from southern Senegal to western Uganda and Tanzania (Fig. 1). Although much of this region is rainforest, chimpanzees currently also occupy dry forest, woodland and dry savannah, particularly near the eastern edge of their range^{27–29}. The modern Baringo region ecosystem is a mosaic of semi-arid *Acacia* bushland and riverine woodland, with a significant substratum of perennial and annual grasses³⁰. The Tugen Hills palaeosol carbon isotope record indicates that the woodland and grassland components of the vegetation have been present there from 16 Myr³⁰. Representatives of both *Homo* and *Pan* are present in the same stratigraphic interval of the Kapthurin Formation at sites only ~1 km apart, and faunal data suggest that they occupied broadly similar environments in the Middle Pleistocene. This evidence shows that in the past chimpanzees occupied regions in which the only hominoid inhabitants were thought to have been members of the human lineage. Now that chimpanzees are known to form a component of the Middle Pleistocene fauna in the Rift Valley, it is quite

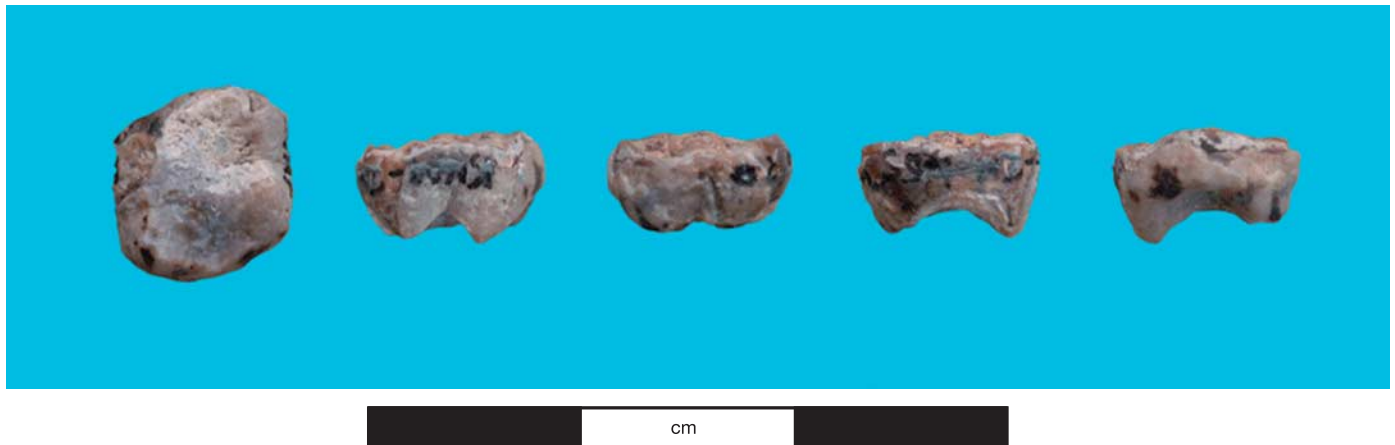


Figure 4 | Upper left first molar (KNM-TH 45520). From left to right: occlusal, labial, lingual, mesial and distal views. Note the thinness of the enamel on the broken mesial face of the paracone in the mesial view.

possible that they remain to be recognized in other portions of the fossil record there, and that chimpanzees and hominins have been sympatric since the time of their divergence.

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