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A new species of great ape from the late Miocene epoch in Ethiopia

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With the discovery of *Ardipithecus*, *Orrorin* and *Sahelanthropus*[1–7], our knowledge of hominid evolution before the emergence of Pliocene species of *Australopithecus*[8,9] has significantly increased, extending the hominid fossil record back to at least 6 million years (Myr) ago. However, because of the dearth of fossil hominoid remains in sub-Saharan Africa spanning the period 12–7 Myr ago, nothing is known of the actual timing and mode of divergence of the African ape and hominid lineages. Most genomic-based studies suggest a late divergence date—5–6 Myr ago and 6–8 Myr ago for the human–chimp and human–gorilla splits, respectively[10–14]—and some palaeontological and molecular analyses hypothesize a Eurasian origin of the African ape and hominid clade[15,16]. We report here the discovery and recognition of a new species of great ape, *Chororapithecus abyssinicus*, from the 10–10.5-Myr-old deposits of the Chorora Formation at the southern margin of the Afar rift. To the best of our knowledge, these are the first fossils of a large-bodied Miocene ape from the African continent north of Kenya. They exhibit a gorilla-sized dentition that combines distinct shearing crests with thick enamel on its 'functional' side cusps. Visualization of the enamel–dentine junction by micro-computed tomography reveals shearing crest features that partly resemble the modern gorilla condition. These features represent genetically based structural modifications probably associated with an initial adaptation to a comparatively fibrous diet. The relatively flat cuspal enamel–dentine junction and thick enamel, however, suggest a concurrent adaptation to hard and/or abrasive food items. The combined evidence suggests that *Chororapithecus* may be a basal member of the gorilla clade, and that the latter exhibited some amount of adaptive and phyletic diversity at around 10–11 Myr ago.

The Chorora Formation represents the earliest known record of sedimentation within the Afar rift of Ethiopia[17]. Perilacustrine sediments and their palaeontological contents were first reported in the 1970s (ref. 18) and estimated to be between 10 and 11 Myr old[19,20]. More recent re-evaluations have confirmed this chronology from both radioisotopic dating and biochronological considerations[17,21]. Before now, the Chorora Formation large mammal fauna was known from a fragmentary fossil assemblage recovered from a single locality, the 'type site', and included a primitive *Stegotetrabelodon* proboscidean, a large giraffid, a primitive hippopotamid, and a hipparionine equid[17,18]. The latter is the most abundant taxon represented, and is considered the earliest known record of an equid in Africa with a best age-estimate of 10.7–10.1 Myr old[21].

The Chorora fossils have been seen as a key assemblage for addressing both within-African and intercontinental mammalian evolutionary patterns[21]. This is because of Chorora's intermediate geographic position between sub-Saharan Africa and Eurasia, as well as the paucity of African fauna spanning the time periods 12–7 Myr ago. Despite such expectations, the fragmentary assemblages hitherto known have not realized the site's potential.

We report here the first primate fossils recovered from the Chorora Formation. These were discovered during newly initiated systematic surveys from 2005 through to 2007 that aimed to locate palaeontological localities other than the relatively well-researched Chorora Formation type site. Primate remains were recovered at the Beticha locality, 3 km from the type site exposures, and include a macaque-sized cercopithecoid monkey (represented by a partial phalanx) and teeth of a large bodied hominoid primate. The primate fossils derive from the upper portions of the Chorora Formation, higher in the section than the type site assemblage. Their age is best considered as approximately 10.0 to 10.5 Myr old (Fig. 1, and Supplementary Information).

The large-bodied ape is represented by a canine and eight partial molars from at least three, and perhaps six or more, individuals (Fig. 1, and Supplementary Information). These teeth are collectively indistinguishable from modern gorilla subspecies in dental size and represented proportions (Supplementary Information). This modest sample nevertheless exhibits substantial size variation, with molars at both the largest and smallest end of the modern gorilla ranges of variation. The species also exhibits a suite of subtle but derived characteristic molar features that are shared with modern gorillas (see below). Functionally, they indicate incipient morphological specialization towards a relatively fibrous diet. Phylogenetically, these fossils represent the first Miocene ape species to be recognized as a strong candidate for membership in the modern gorilla clade.

Order Primates
Superfamily Hominoidea Gray, 1825
Chororapithecus gen. nov.
Chororapithecus abyssinicus sp. nov.

Etymology. The genus name is taken after Chorora, the name of the geological formation from which the fossils are derived; Chorora is the name of a local village approximately 8 km south of the Beticha locality. The species name is taken from Abyssinia, the former name of Ethiopia, in light of the geographical location of discovery at the junction area of the Main Ethiopian and Afar rift systems.

Holotype. CHO-BT 4 right upper M^2 (second molar).

Paratype. CHO-BT 3, left lower canine; CHO-BT 5, right upper M^3; CHO-BT 6, right upper M^3; CHO-BT 7, left lower M_3; CHO-BT 8, left lower M_1; CHO-BT 9, left lower molar fragment; CHO-BT 10, right lower molar fragment; and CHO-BT 11, right upper M^3.

Diagnosis. A hominoid primate with molars of equivalent size to those of *Gorilla gorilla* subspecies that combine a tendency for enhanced shearing structures (relatively long mesial protocone crest of the upper molars and high trigonid crest of the lower molars) and

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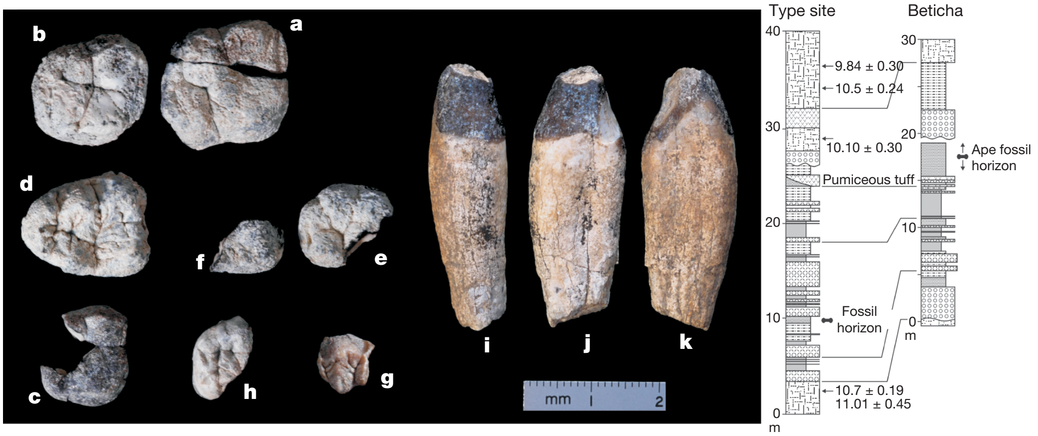

Figure 1 | *Chororapithecus abyssinicus* fossils and schematic stratigraphy. **a**, CHO-BT 4, mesiodistal dimension 19.1 mm, buccolingual dimension 18.0 mm. **b**, CHO-BT 5, mesiodistal dimension 16.9 mm, buccolingual dimension 17.5 mm. **c**, CHO-BT 6, mesiodistal dimension 13.2 mm, buccolingual dimension 15.0 mm. **d**, CHO-BT 7, mesiodistal dimension 19.1 mm, buccolingual dimension 15.9 mm. **e**, CHO-BT 8, buccolingual dimension 13.2 mm. **f**, CHO-BT 9. **g**, CHO-BT 10. **h**, CHO-BT 11. **i**–**k**, CHO-BT 3 buccal, distal and mesial views, respectively, maximum diameter 13.9 mm, perpendicular diameter 10.7 mm. All dimensions except for those of CHO-BT 3 are estimated values corrected for minor damage. Simplified stratigraphy (type site section after ref. 20, radioisotopic age determinations from refs 17 and 20; see Supplementary Information for details).

relatively low cuspal topography with thick enamel at the 'functional' side cusps (lingual in upper and buccal in lower molars). The upper molars tend to be buccolingually narrow and mesiodistally elongate in shape, with a mesiobuccally extending mesial protocone crest. The epicrista is thin and buccolingually straight, creating a narrow mesial fovea located buccally. The high and continuous trigonid crest of the lower molars is situated distinctly above the level of a low mesial marginal ridge. The metaconid is moderately tall, forming a deep lingual notch in comparison with other large-bodied Miocene hominoids. In both upper and lower molars, cusp tips are relatively peripherally placed and cingular expressions are weak.

Differential diagnosis. *Chororapithecus abyssinicus* differs from *Gorilla gorilla* subspecies by having molar crown and cusps lower in height and with thicker enamel; upper molars with less distinct crista obliqua; and lower molars lacking buccolingual infolding of the buccal occlusal margin (that is, a lack of extremely enlongated shearing crests). *C. abyssinicus* differs from all known modern and fossil hominoids (including the nearly contemporaneous African genus *Samburupithecus*), with the exception of *Gorilla*, *Rangwapithecus*, *Nyanzapithecus* and *Oreopithecus,* in enhanced shear between the mesial protocone crest and the distal occlusal slope of the metaconid. Furthermore, *C. abyssinicus* is different from *Samburupithecus*

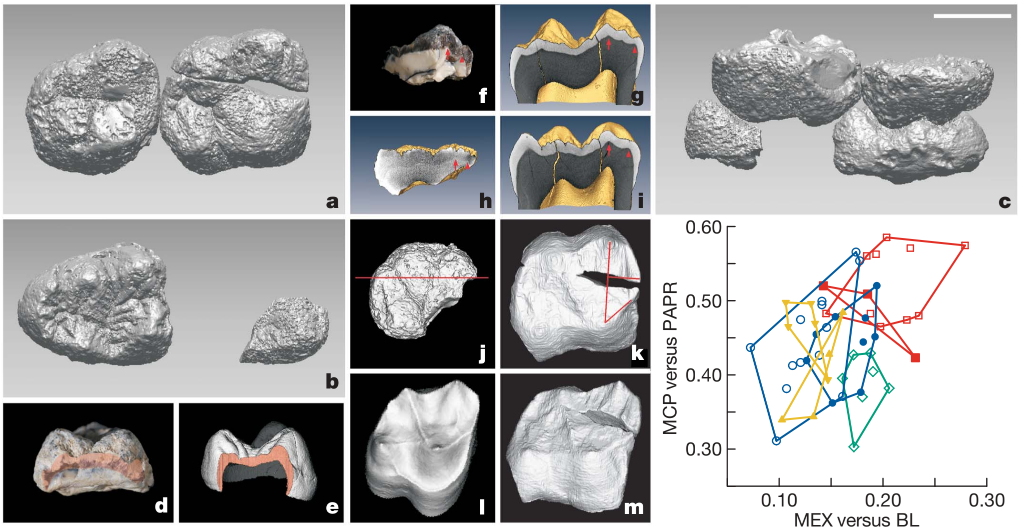

Figure 2 | Micro-CT-based morphological evaluations of the outer enamel surface and enamel–dentine junction. Three-dimensional rendered views of right upper M^2 and M^3 (**a**), and left lower M_2 and M_3 (**b**). **c**, Lower molars mirror-imaged and placed in an occlusal relationship with the upper molars; lingual view, mesial to the left. Note the shearing relationship between mesiolingual protocone and the distal slope of the metaconid. Mesial view of *Chororapithecus* (**d**) and *Gorilla* (**e**) lower M_3s, with the mesial marginal ridge broken or cut off, showing a prominent trigonid crest. Natural section of *Chororapithecus* lower M_2 metaconid break (mirror-imaged, **f**), and equivalent micro-CT section of a *Gorilla* molar (**g**). **h**, *Chororapithecus* lower M_1 longitudinal section at mid-protoconid, its position as indicated in **j**, and equivalent section of a *Gorilla* molar (**i**). Note the prominent trigonid crest of the EDJ (left arrows) located distinctly above the level of the mesial marginal ridge (right arrowheads). Micro-CT visualization of EDJ surfaces of *Chororapithecus* (**k**, **m**) and *Gorilla* (**l**) upper M^2s. Occlusal view of *Chororapithecus* upper M^2 EDJ (**k**), showing the metrics evaluated in the right lower scatter plot. MCP-versus-PAPR is the distance between protocone tip and protoconule (or equivalent point) divided by paracone–protocone cusp tip distance, both measured on the EDJ. MEX-versus-BL is the projected length of the mesial fovea (measured from the paracone–protocone plane) divided by buccolingual crown breadth. Filled red squares, *Chororapithecus*; open squares, *Gorilla*; open diamonds, *Pongo*; open circles, *P. troglodytes*; filled circles, *P. paniscus*; filled triangles, *Australopithecus africanus* (pointing up) and *Australopithecus robustus* (pointing down). See the Supplementary Information for methodological details and comparative sample compositions. Note the linear to slightly concave mesial protocone crest of CHO-BT 4 resembling the *Gorilla* condition but with lower crown and cusp topography. Scale bar, 1 cm (common to all images).

because it has molars with a more open occlusal basin, weak expression of the anterolingual cingular complex, and a continuous crista obliqua (of M^2), as opposed to a crest incised by the longitudinal groove. *C. abyssinicus* differs from *Proconsul major*, *P. nyanzae* and '*Ugandapithecus*' *gitongai*[22] in its larger size, buccolingually narrower upper molars, more peripherally located molar cusps, resulting in a more open occlusal basin, thin and weak cingular expressions, and lack of tendency for a strong expression of the protoconule. Also, *C. abyssinicus* differs from *Ouranopithecus* in having a larger upper M^2 with a more mesiodistally elongate shape, better developed occlusal crests, and lack of lower M_3 posterior cusp development (hypoconulid and cusp 6 regions small); from *Ankarapithecus* and *Sivapithecus parvada* in its larger size, buccolingually narrower upper molars, and lack of tendency for a strong expression of the protoconule; and from *Gigantopithecus* in being smaller in size and possessing lower crowned molars, buccolingually narrow upper molars, better developed occlusal crests, and a lower canine with interlocking relationship with the upper canine. Other comparative remarks are given below and in the Supplementary Information.

The most distinctive features of the *Chororapithecus* dentition are the derived shearing structures seen in portions of its molars (Fig. 2), despite a generally low cuspal topography (the latter is apparently a primitive retention).

Examination of internal morphology by micro-computed tomography (micro-CT) demonstrates that these occlusal features were underlain by distinct enamel–dentine junction (EDJ) structure (Fig. 2). In particular, the straight to weakly concave mesial protocone crest seen in the EDJ of CHO-BT 4, -BT 5 and -BT 6 is gorilla-like, and is formed by a mesiobucally located junction of the mesial protocone crest and mesial marginal ridge. Such spatial placements are best considered to be regulated by enamel-knot-related signalling patterns during early morphogenesis[23,24], and may be one of the underlying causes of the mesiodistally elongate upper molar shape generally characteristic of folivorous primate species. In the lower molars, the most distinctive EDJ topography occurs at the trigonid crest, the structural counterpart that occludes with the upper molar mesial protocone crest. The high trigonid EDJ crest is continuous between the metaconid and protoconid cusp tips (Fig. 2). Because recent experimental and quantitative genetic studies suggest significant degrees of morphogenetic independence between corresponding upper and lower molar structures[25,26], the presence of a functionally integral inter-jaw pattern of morphological expression, as seen in the *Chororapithecus* molars, suggests adaptation by natural selection, as opposed to chance emergence of neutral morphological minutia.

For the features in which *Chororapithecus* differs from gorillas, the gorilla condition is clearly the more derived towards advanced molar shear. In particular, *Chororapithecus* exhibits a much lower cusp relief and thicker molar enamel (Fig. 3). Maximum radial lateral thickness of the 'functional' side cusps (which form the main occlusal areas for crushing and grinding) of *Chororapithecus* appears to scale isometrically to that of *Australopithecus*, whereas enamel thickness of the opposite side cusps is equivalent to the intermediate conditions of *Pongo* and *Ardipithecus*. Enamel thickness is thought to probably have a significant developmental component directly related to steepness of EDJ topography[27]. Scaled by basal crown area, enamel volume of *Chororapithecus* is intermediate between the *Gorilla* and *Australopithecus* conditions (Fig. 3). Thus, the higher crown and larger EDJ surface area of the gorilla molar would in part explain its thinner enamel coverage. Although the gorilla condition could potentially be attained from a thicker-enamelled ancestor, it is difficult to evaluate whether *Chororapithecus* itself could represent such an ancestral condition. This is because descriptions of EDJ topography and enamel thickness patterns among Miocene hominoids are limited. However, the thick enamel of the *Chororapithecus* 'functional' side cusps, and the extremely low EDJ topography seen in one of the upper molars (CHO-BT 4) indicate that *Chororapithecus* itself is probably too specialized to represent a direct ancestral condition of the modern gorilla.

Thus, we consider *Chororapithecus* to exhibit a derived molar morphology indicative of incipient adaptation to a comparatively fibrous diet, as indicated by the emphasis of shear between the mesial protocone crest and the distal slope of the metaconid. At the same time, the low relief of the 'functional' side cusps endowed with thick enamel enable prolonged retention of an occlusal platform of rigid enamel (without exposing the more compliant dentine). This is reminiscent of three-dimensional enamel distribution patterns seen in *Pongo* and may be an adaptation for consuming hard and brittle food items[28]. With such a unique combination of molar structures, the shearing crests of *Chororapithecus* may have functioned in the folding and pulverizing of fibrous foodstuff, rather than the actual cutting of fibrous materials by sharp, shearing crests, as in advanced folivores with higher cusps. So far, among the diversity of known African and Eurasian middle- to large-bodied Miocene apes, with the exception of *Oreopithecus* (which is even more uniquely specialized), we are not

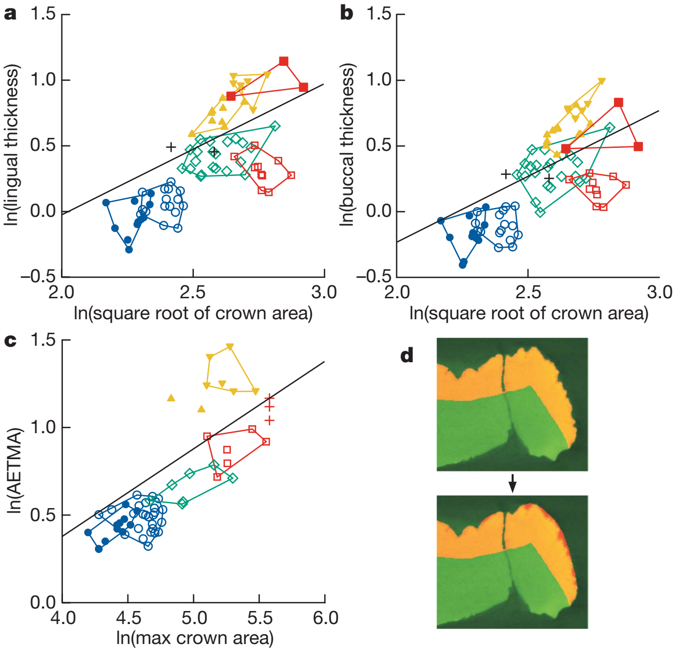

Figure 3 | Micro-CT-based evaluations of upper molar enamel thickness. Bivariate plots of ln(maximum radial enamel thickness) of the lateral crown faces of lingual 'functional' side cusps (**a**), and buccal 'non-functional' side cusps (**b**) by ln(crown area). The isometric line going through the mid-point of the *Ardipithecus ramidus* molars[1] ($n = 2$, crosses) is drawn for reference. Other symbols are as in Fig. 2. Reliable micro-CT-based estimates were obtained for three *Chororapithecus* upper molars as follows. CHO-BT 4: paracone, 1.64 mm; protocone, 2.53 mm; hypocone, 2.62 mm; CHO-BT 5: paracone, 2.32 mm; metacone, 2.28 mm; protocone, 3.28 mm; hypocone, 3.00 mm; CHO-BT 6: paracone, 1.62 mm, protocone, 2.41 mm. *Chororapithecus* shows a unique combination of thick enamel on the 'functional' side cusps, and intermediate thickness on the 'non-functional' side cusps. **c**, Log bivariate plot of AETMA (enamel volume/crown area) by crown area. Isometric line through the CHO-BT 4 estimate is shown for reference. The three crosses for CHO-BT 4 indicate the raw uncorrected enamel volume (lowest cross), correction for macro-damage (middle cross), and an additional 5% increase estimated for weathering and minor wear loss (upper cross). The degree of this correction in a representative section is depicted in **d**. Yellow, enamel; red, restored enamel crown. Other symbols are as in the previous plots. Note that with this measure of average enamel thickness, gorillas have enamel as 'thick' as the other apes; that is, despite the thinner enamel of the gorilla, total enamel volume available per crown area is comparable with other modern ape species, indicating broad equivalence in durability against abrasion. Note that *Chororapithecus* is intermediate between apes and *Australopithecus*. See Supplementary Information for the details of methodology and sample compositions.

aware of a single instance of a coherent set of derived features shared with the modern gorilla like those seen in *Chororapithecus*.

The similarities seen between the two genera raise the possibility that *Chororapithecus* is a Miocene member of the *Gorilla* clade. Alternatively, with its combination of thick enamel and distinct molar cresting pattern, *Chororapithecus* may represent a unique adaptation that is convergent with gorillas in molar structure and function. Although the evidence for phylogenetic affinity between *Chororapithecus* and *Gorilla* is inconclusive, it may be that the basal members of the gorilla clade shared large tooth size and incipiently enhanced molar shear as a part of an herbivorous diet that accompanied (presumed) larger body size. *Chororapithecus* may then represent one example of adaptational (and perhaps phyletic) differentiation within that clade.

Acceptance of *Chororapithecus* as a basal member of the gorilla clade would push back the gorilla species split to $>$10.5 Myr ago. Because this is a minimum date established from a meagre fossil record, the actual divergence would have predated this by an unknown time gap. From the currently available evidence, we consider that a species split of $\sim$20 Myr ago for *Pongo*, 12 Myr ago for *Gorilla*, and 9 Myr ago for *Pan* are all probable estimates (see Supplementary Information). We consider that the early divergence hypothesis is congruent with both fossil and molecular data, and should be further evaluated using both sides of the evidence.

At Chorora, previous systematic field research at the type site has yielded a '*Hipparion*'-dominated fauna, which was considered to indicate a significant representation of open habitats in possibly a mosaic environment[17], an interpretation corroborated by recent isotopic and wear studies of '*Hipparion*' teeth[21]. To the contrary, the Beticha locality is poorly fossiliferous, dominated by primates, and almost lacking in '*Hipparion*' (Supplementary Information). The Beticha fossils occur at a higher stratigraphic level, within sediments formed by a braided river system with intermittent palaeosol formation (Supplementary Information). We hypothesize that this indicates a mosaic that includes a forested lake margin environment formed towards the end of sedimentation of the Chorora Formation palaeobasin, while episodic rifting was locally ceasing. Although the evidence is so far limited, this suggests that, in the changing landscape of the African middle to late Miocene, ape species were actually present in both what are now Kenya[29,30] and Ethiopia. The available contextual evidence suggests that they predominantly occupied the more forested environments, and that the modern African ape and hominid clades probably emerged from a late Miocene African diversity of apes, which is only starting to be revealed. Palaeontologically, our results indicate that more focus is needed on comparatively poorly fossiliferous sediments that sample the habitats that were preferred by the Miocene apes.

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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