A new Late Miocene great ape from Kenya and its implications for the origins of African great apes and humans

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Extant African great apes and humans are thought to have diverged from each other in the Late Miocene. However, few hominoid fossils are known from Africa during this period. Here we describe a new genus of great ape (*Nakalipithecus nakayamai* gen. et sp. nov.) recently discovered from the early Late Miocene of Nakali, Kenya. The new genus resembles *Ouranopithecus macedoniensis* (9.6–8.7 Ma, Greece) in size and some features but retains less specialized characters, such as less inflated cusps and better-developed cingula on cheek teeth, and it was recovered from a slightly older age (9.9–9.8 Ma). Although the affinity of *Ouranopithecus* to the extant African apes and humans has often been inferred, the former is known only from southeastern Europe. The discovery of *N. nakayamai* in East Africa, therefore, provides new evidence on the origins of African great apes and humans. *N. nakayamai* could be close to the last common ancestor of the extant African apes and humans. In addition, the associated primate fauna from Nakali shows that hominoids and other non-cercopithecoid catarrhines retained higher diversity into the early Late Miocene in East Africa than previously recognized.

hominoid evolution

Recent molecular studies suggest that the divergence between humans and chimpanzees occurred at 7–5 Ma and that the divergence of gorillas occurred at 9–8 Ma (1–4). Consequently, the Late Miocene (11–5 Ma) is the crucial period for understanding the origins of African great apes and humans, but unfortunately the African hominoid fossil record is extremely poor after 13 Ma (5, 6). A rare exception is *Samburupithecus kiptalami* (9.6 Ma), discovered from Samburu Hills, northern Kenya (7, 8). However, its dental morphology is so specialized that its phyletic position is unclear. Although there is a variety of Late Miocene hominoids in Eurasia, the majority of them are likely to belong to the *Pongo* clade (9, 10). *Ouranopithecus macedoniensis* has often been considered to resemble African great apes (11, 12), but it is known only from the Late Miocene of Greece, and its phyletic relationships are not yet agreed on (13). Because of the poor nature of the hominoid fossil record in Africa, some authors have suggested that a Eurasian Miocene hominoid returned to Africa in the Late Miocene to become the last common ancestor of the African great apes and humans (11, 14). Our recent fieldwork, however, has recovered a diverse primate fauna, including large-bodied hominoids, from the early Late Miocene of Nakali, Kenya (15). Here we report a new genus of great ape from Nakali and provide information on its geological, geochronological, and paleontological context. Among the known fossil hominoids, this great ape resembles *Ouranopithecus*, from the Late Miocene (9.6–8.7 Ma) of Greece

(16, 17), in size and some morphological features, but a number of differences lead us to assign the Nakali material to a different new genus. *Nakalipithecus nakayamai* and the associated primate fauna provide important new evidence for understanding the origins of the extant African ape and human clades, as well as catarrhine evolution in general in the Middle to Late Miocene Africa. [Since our article was submitted, Suwa *et al.* (18) published an article on *Chororapithecus abyssinicus* from Chorora, Ethiopia (10.7–10.1 Ma). We do not yet know how *N. nakayamai* relates to *C. abyssinicus*.]

Systematics

Order Primates Linnaeus, 1758; suborder Anthropoidea Mivart, 1864; infraorder Catarrhini Geoffroy, 1812; superfamily Hominoidea Gray, 1825; genus *Nakalipithecus* gen. nov. Type species: *N. nakayamai* gen. et sp. nov. Etymology: Nakali, the area where the fossils were discovered, and *pithekos*, ape in Greek. Generic diagnosis: as for the species *N. nakayamai* gen. et sp. nov. Holotype: KNM-NA46400, a right mandibular fragment with M_1–M_3 (Fig. 1). The repository is the National Museums of Kenya. Hypodigm: the type specimen; left I^1 (KNM-NA47592); right C* (KNM-NA47594); right P^3 (KNM-NA46431); left P^4 (KNM-NA46430); right M^1 (KNM-NA47591); right I_2 (KNM-NA46425); left P_3 (KNM-NA46423); right P_4 (KNM-NA46424); right M_3 (KNM-NA46429); left M_3 (KNM-NA46436); left dp_4 (KNM-NA46435) (Figs. 2 and 3 and Table 1). Locality: Nakali, 40 km west of Maralal, along the eastern edge of the Rift Valley, Kenya. Horizon: Upper Member of the Nakali Formation. Age: early Late Miocene (9.9–9.8 Ma). Etymology: After the late Katsuhiro Nakayama, who contributed much to the geological aspects of the expedition.

Specific Diagnosis. *N. nakayamai* is a large hominoid similar in dental size to female gorillas and orangutans. The mandible has a well developed inferior transverse torus that extends posteriorly to mid-M_1. The thickness/height index of the mandibular body is ≈45% at M_1. M_1 is relatively large compared with M_2.
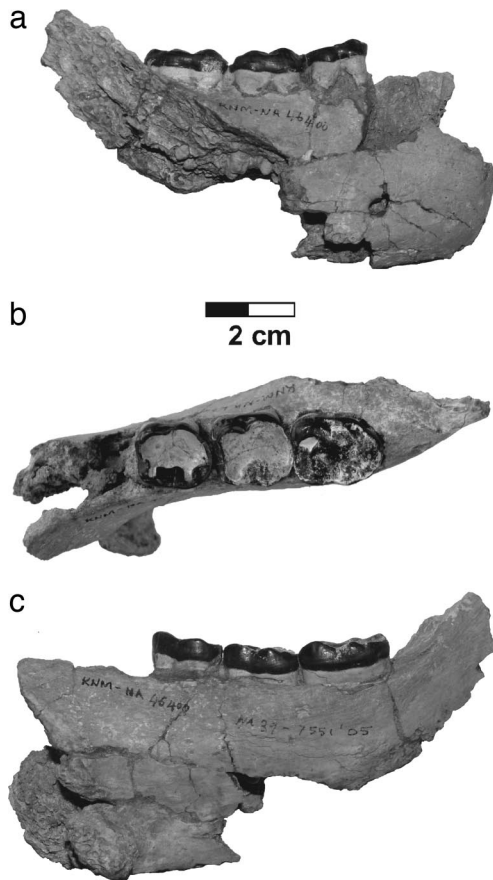
Fig. 1. Type specimen of *N. nakayamai* (KNM-NA46400, right mandible with M_1–M_3). Buccal (*a*), occlusal (*b*), and lingual (*c*) views are shown.

M_3 is considerably larger than M_2 and mesiodistally elongated relative to the buccolingual breadth. Molars have thick enamel, relatively flat dentine/enamel junction, peripherally positioned and voluminous cusps, and reduced but still marked cingula. I_2 is mesiodistally narrow and buccolingually thick with a tall, slender crown relative to the mesiodistal dimension. P_3 has weak bilateral compression, being semitriangular in occlusal outline with a lingual crest lingually oriented and a wide distal fovea. P_4 is broad with voluminous cusps being peripherally positioned. M^1 is relatively elongated [mesiodistal length (MD)/buccolingual breadth (BL) = 92.5%] with a short but marked cingular
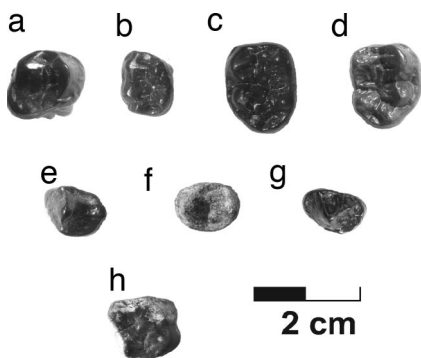

Fig. 2. Isolated cheek teeth of *N. nakayamai*. (*a*) KNM-NA46424, right P_4. (*b*) KNM-NA46435, left dp_4. (*c*) KNM-NA46436, left M_3. (*d*) KNM-NA46429, right M_3. (*e*) KNM-NA46431, right P^3. (*f*) KNM-NA46430, left P^4. (*e*) KNM-NA46423, right P_3. (*h*) KNM-NA47591, right M^1.
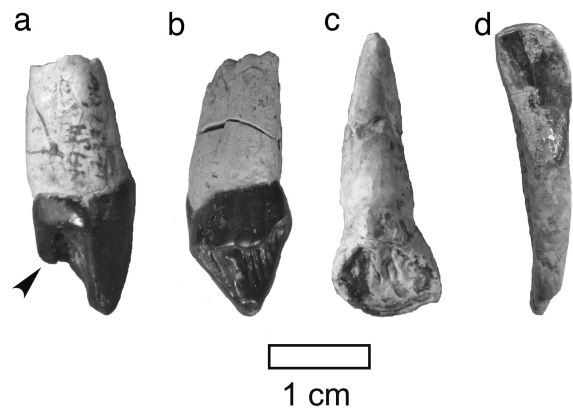
Fig. 3. Isolated canine and incisors of *N. nakayamai*. (*a*) Distal view. (*b–d*) Lingual view. (*a* and *b*) KNM-NA47594, right C*. The arrowhead in *a* indicates the well developed lingual cusplet. (*c*) KNM-NA47592, left I^1. (*d*) KNM-NA46425, right I_2.

remnant on the mesiolingual corner of the protocone. I^1 is low-crowned and mesiodistally wide with the strongly curved distal margin, relatively elevated lingual cingulum, and the lingual surface featured by a thick, rounded crest running from the cingulum toward the incisive edge, and a few other vertical wrinkles. The upper canine is low-crowned and buccolingually as broad as mesiodistally long, showing a continuous and prominent lingual cingulum that is elevated with a remarkably well developed lingual cusplet. Upper premolars are elongated, having peripherally positioned and voluminous cusps with weak heteromorphy.

Differential Diagnosis. *N. nakayamai* differs from the other known Miocene and extant hominoids in having an upper canine (presumed female) that is low-crowned and as broad as long and is bordered basally by a highly elevated and clearly differentiated, continuous lingual cingulum that develops an extremely large lingual cusplet. *N. nakayamai* is distinguished from *Proconsul*, *Ugandapithecus*, *Afropithecus*, and *Nacholapithecus* by its large size, mesiodistally elongated upper premolars with reduced cusp heteromorphy, reduced cingulum on upper molar, bilaterally less compressed P_3, and low-crowned I^1. *N. nakayamai* differs from *Kenyapithecus wickeri* and *Equatorius africanus* in its

Table 1. Dental measurements (in millimeters) of *N. nakayamai*

Accession no.	Tooth type	Length	Breadth
		Max	Perp
KNM-NA46423	Left P_3	12.4	8.2
		MD	BL
KNM-NA46425	Right I_2	6.5	9.1
KNM-NA46424	Right P_4	10.4	14.0
KNM-NA46400	Right M_1	15.6	14.0
	Right M_2	16.2	15.8
	Right M_3	19.5	15.1
KNM-NA46429	Right M_3	15.8	13.2
KNM-NA46436	Left M_3	16.0	12.7
KNM-NA46435	Left dp_4	11.4	9.4
KNM-NA47592	Left I^1	10.8	8.6
KNM-NA47594	Right C*	10.7	10.5
KNM-NA46431	Right P^3	9.3	11.1
KNM-NA46430	Left P^4	9.5	11.9
KNM-NA47591	Right M^1	12.4	13.4

Max, maximum; Perp, perpendicular; MD, mesiodistal; BL, buccolingual.

large size, mesiodistally elongated upper premolars, relatively higher mandibular body, and less compressed P₃. *N. nakayamai* is distinguished from *Samburupithecus* by less inflated molar cusps, which are positioned more peripherally, more spacious occlusal foveae and basins, and reduced upper molar cingulum. *N. nakayamai* differs from *Ouranopithecus* in the following features: upper canine (presumed female) slightly higher-crowned with a higher position of the mesial shoulder; molars having less thick enamel and less inflated cusps that result in more spacious occlusal basins and foveae; better developed molar cingula; P₃ with more marked buccal and lingual cingula and slightly longer mesiobuccal slope [compared with similar-sized (presumed female) P₃s of *O. macedoniensis*]; upper premolars more elongated; P³ having more marked buccal cingula and styles and a better developed mesial transverse crest; P⁴ cusps less inflated; and dp₄ having a mesiodistally shorter mesial fovea, a larger distal fovea, more rounded distobuccal margin of the crown (straight and oblique in *Ouranopithecus*), and more buccally placed hypoconulid. *N. nakayamai* is distinguished from *Ankarapithecus*, *Sivapithecus*, and *Khoratpithecus* by its large size (excluding *Sivapithecus parvada*), more gracile mandibular body, better developed molar cingula (excluding *Khoratpithecus*), more peripherally positioned molar cusps, and weaker bilateral compression of P₃. *N. nakayamai* is different from *Dryopithecus* in its large size, thick molar enamel with flatter dentine/enamel junction, and upper premolars mesiodistally elongated relative to the buccolingual breadth.

Geology and Geochronology of Nakali

The Nakali Formation is divided into the Upper, Middle, and Lower Members. Hominoid fossils were recovered from the volcanic mud flow (lahar) deposits of the Upper Member at two sites [supporting information (SI) *Text* and SI Figs. 4 and 5]. Multistory fluvial channel fill deposits are rarely found in the Upper Member, and no soil intervals are present. These features suggest a rapid sediment accumulation during deposition of the upper Nakali Formation. ⁴⁰Ar-³⁹Ar ages of anorthoclase from pumices in the uppermost part of the Lower Member are 9.82 ± 0.09 and 9.90 ± 0.09 Ma, whereas one grain from pyroclastic flow deposits from the Middle Member is 10.10 ± 0.12 Ma (SI Figs. 4, 6, and 7 and SI Table 2). The uppermost level of the Lower Member and the lowest level of the Upper Member document a reversed magnetic polarity (SI Figs. 4, 8, and 9). This reversed polarity interval, combined with the ⁴⁰Ar-³⁹Ar ages, can be reasonably correlated with Chron C5n.1r, dated at 9.88–9.92 Ma (19). Consequently, the hominoid bed is located within the C5n.1n chronozone [9.74–9.88 Ma (19)]. Given the rapid sediment accumulation, the age of the hominoid bed is most probably 9.80–9.88 Ma.

Description

The type specimen (KNM-NA46400) is a right mandibular fragment with M₁–M₃ (Fig. 1). It is of female gorilla size, and, among the presently known Miocene hominoids, it is as large as *Samburupithecus*, *Ouranopithecus*, and *S. parvada*, all of which are known from the early Late Miocene. The alveolar plane slopes down posteriorly to the P₃/P₄ level and makes a moderate superior transverse torus. The inferior transverse torus is very well developed. It is thick and robust and extends posteriorly to the mid-M₁ level. The body height can be estimated as ≈44 mm at the M₁ level. The body thickness is 19.8 mm at the same level. The lateral aspect of the body is vertical below M₁, and there is a single mental foramen two-thirds of the body height down from the alveolar margin below P₄/M₁. The molars are heavily worn. In M₁ and M₂ the buccal cusps are completely worn away, leaving a very large and hollowed area of dentine exposure. The lingual cusps are also worn, but they still retain some occlusal relief. M₃ preserves the occlusal morphology better than the anterior

molars. The cusps appear to be low and voluminous. The crown is mesiodistally elongated relative to the buccolingual breadth and tapers slightly near the distal margin. The buccal cingulum is relatively reduced on the lower molars, but there are weak cingular remnant on the mesiobuccal aspect of the protoconid and marked remnants between the buccal cusps. M₁ is relatively large [M₁/M₂ ratio in area (MD × BL) = 85%]. M₃ is considerably larger than M₂ (M₃/M₂ ratio = 115%).

There are five isolated permanent lower teeth assigned to *N. nakayamai* (Figs. 2 and 3). A right (KNM-NA46429) and a left (KNM-NA46436) M₃ are slightly worn and are considerably smaller than the M₃ in the type mandible. They are ≈70% of the latter in crown area, suggesting the presence of high levels of intraspecific variation (possibly sexual dimorphism) in *N. nakayamai*. Otherwise, they exhibit a similar morphological pattern to the larger M₃. The cusps are massive and rather peripherally positioned. The occlusal foveae and basin are moderately spacious. The enamel is thick with a low dentine/enamel relief (SI Figs. 10 and 11). The crown tapers slightly near the distal end. The buccal cingulum is interrupted on the buccal aspect of the protoconid but is prominent distally, surrounding the buccal aspect of the hypoconid. KNM-NA46424 is a right P₄ that matches in size the lower molars of the type mandible. The occlusal outline is asymmetrical with a protruding distolingual corner. The two main cusps are massive and peripherally located. The distal fovea is much larger than the mesial fovea. The buccal surface of the crown is decorated basally with a discontinuous but prominent cingulum. KNM-NA46423 is a left P₃. It is relatively small and corresponds in size to the smaller M₃s. The crown is short and broad with a semitriangular occlusal outline. The mesiobuccal slope is short and is decorated with short, marked cingula both mesially and distally. The lingual crest of the protoconid runs down lingually, forming an approximately right angle with the distal crest of the protoconid. Consequently, the distal fovea is quite wide. The basal portion of the lingual crest is slightly swollen, from which a short crest runs distally. The lingual cingulum is prominent and is continuous along the whole lingual aspect. KNM-NA46425 is a right I₂. The crown is high and mesiodistally narrow. In lingual view, the mesial margin is nearly straight, whereas the distal margin is strongly convex distally. The marginal crests are weak, and there is no distinct lingual cingulum at the base of the lingual aspect.

Five permanent upper teeth are assigned to *N. nakayamai* (Figs. 2 and 3). KNM-NA47591 is a right M¹ crown. This molar is relatively elongated mesiodistally and is low-crowned with low and massive cusps. The cusps are peripherally positioned as in the lower molars. There is a very short but distinct cingular remnant on the mesiolingual corner of the protocone. Two upper premolars, a right P³ (KNM-NA46431) and a left P⁴ (KNM-NA46430), are buccolingually narrow and mesiodistally elongated. The cusps are peripherally located. The cusp heteromorphy is not extensive. In the P³ the buccal moiety is slightly longer than the lingual moiety. The paracone is moderately higher than the protocone. The mesial transverse crest is developed, but the distal transverse crest is obscure. Styles are developed at the base of the mesial and distal crests of the paracone. The buccal cingula are discontinuous but prominent. There is a shallow, short groove at the distal end of the lingual aspect of the crown. The P⁴ is oval in occlusal outline. The paracone is only slightly higher than the protocone. The mesial transverse crest is continuous, but the distal transverse crest is interrupted by a longitudinal groove. KNM-NA47592 is a left I¹. The crown is low and is mesiodistally wide and buccolingually thick. The lingual aspect is bordered basally by a high lingual cingulum that becomes continuous with the mesial and distal marginal crests. The lingual surface is crenulated with a thick, rounded crest rising from the lingual cingulum and a few other vertical wrinkles. The distal margin of the crown is markedly curved and

meets the incisive edge at a blunt angle. KNM-NA47594 is a right upper canine. The crown is low and is as long as broad, having short mesial crest and groove. The lingual cingulum is elevated to a very high position ($\approx$40% of the lingual crown height) and prominently differentiated, being continuous along the lingual aspect of the crown. An extremely large tubercle is developed on the lingual cingulum. Light wear facets are observed at the basal part of the mesial crest, at the apex, along the distal crest, and on the lingual cingulum distal to the lingual tubercle apex.

In addition to the permanent teeth, there is one left dp_4 (KNM-NA46435). The mesial end of the crown is slightly narrowed buccolingually. The buccal cingulum is strongly reduced to form a short and weak groove on the mesiobuccal face of the protoconid and very faint depressions at the bases of the buccal grooves. The five main cusps are massive and low. The protoconid is positioned slightly mesially relative to the metaconid. The protoconid and metaconid are linked by a thick mesial transverse crest, which runs slightly obliquely. The hypoconulid is smaller than the hypoconid and is positioned close to the latter. The entoconid is as small as the hypoconulid, and these two cusps are connected to each other by a low distal transverse crest. The distal fovea is relatively broad and is only slightly oblique. The talonid basin, coarsely crenulated with several wrinkles, is long and narrow and is incised with fine intercuspal grooves.

Comparisons with Other Hominoids

N. nakayamai is distinguished from the East African Early Miocene hominoids such as *Proconsul*, *Ugandapithecus*, and *Afropithecus* in its much larger dental size and having mesiodistally elongated upper premolars with reduced cusp heteromorphy, bilaterally less compressed P_3, and low-crowned I^1. In *Proconsul* and *Ugandapithecus*, whereas the superior transverse torus is developed, the inferior transverse torus is absent or very weak in contrast to the well developed inferior transverse torus of *N. nakayamai*, and the molar cingula are better-developed in these Early Miocene taxa, especially on the upper molars, differing from the reduced and discontinuous condition in *N. nakayamai*. *Afropithecus* has an inferior transverse torus better-developed than the superior one, but not to the extent observed in *N. nakayamai*. In addition, compared with the molar size, the mandibular body of *Afropithecus* is relatively taller than that of *N. nakayamai*.

The early Middle Miocene East African hominoids such as *Kenyapithecus*, *Equatorius*, and *Nacholapithecus* are baboon-sized animals (20, 21), somewhat smaller than *N. nakayamai*. They differ from *N. nakayamai* in having bilaterally compressed P_3 crowns and broader upper premolars. *Nacholapithecus* differs from *N. nakayamai* in having stronger cusp heteromorphy of upper premolars (21). *Kenyapithecus* and *Equatorius* are distinguished from *N. nakayamai* in having a lower and thicker mandibular body.

A few isolated teeth of hominoids are known from the Ngorora Formation ($\approx$12.5 Ma) in Tugen Hills, $\approx$80 km southwest of Nakali (5). The Ngorora premolar (P_4) is assigned to *Proconsul* sp. Compared with the Nakali P_4 (KNM-NA46424), the crown is considerably smaller, and the cusps are relatively higher and more crystalline and are more centrally located. The Ngorora molar (M^1 or M^2) is the size of those of female gorillas. Hill and Ward (5) considered that the best match is with modern chimpanzee second molars, although the Ngorora molar is larger. In our observation the cusp configuration also appears reminiscent of that of modern gorillas, but the cusps are lower. The occlusal foveae and basin are more spacious than those of the Nakali upper molar. In addition, micro-computed tomography scanning has revealed that the enamel of the Ngorora molar is not as thick as in *N. nakayamai* (Y.K., unpublished data). Recently, Pickford and Senut (22) reported a lower molar of a chimpanzee-sized hominoid from Ngorora. Its phylogenetic

relationship is still uncertain, but it is too small to belong to the same taxon with *N. nakayamai*.

Among the African Miocene hominoids, *N. nakayamai* is nearly contemporaneous with *S. kiptalami*, known from Samburu Hills, $\approx$70 km north of Nakali. The type maxilla of *S. kiptalami* (KNM-SH 8531) and the type mandible of *N. nakayamai* are of similar dental size and are as large as those of female gorillas. The upper premolars of *Samburupithecus* resemble those of *N. nakayamai* in being elongated mesiodistally, but the cusps are more inflated and positioned more centrally. In the upper molars of *Samburupithecus* the cusps are quite strongly inflated and positioned centrally so that the occlusal foveae and basins are extremely restricted (7). In these features, *Samburupithecus* seems to be strongly specialized compared with other Miocene and extant apes. There is an upper molar included in the present hypodigm of *N. nakayamai*, which has less inflated and more peripherally positioned cusps and more spacious foveae and basins. In addition, the dentine/enamel junction of *Samburupithecus* shows a higher relief relative to the flatter dentine/enamel junction of *N. nakayamai*. These features clearly distinguish *N. nakayamai* from *Samburupithecus*.

The other contemporaneous Miocene hominoids are all known from Eurasia: *Dryopithecus* from western and central Europe, *Ankarapithecus* from Turkey, *Sivapithecus* from South Asia, *Lufengpithecus* from southwestern China, and *Khoratpithecus* from Thailand (23). They are smaller than *N. nakayamai*, except for *Ouranopithecus* (24, 25) and *S. parvada* (26). Among the Late Miocene Eurasian hominoids, *Ankarapithecus*, *Sivapithecus*, *Lufengpithecus*, and *Khoratpithecus* are broadly considered to belong to the *Pongo* clade (9, 10). Although the specimens of *Lufengpithecus* are heavily deformed, *Ankarapithecus*, *Sivapithecus*, and *Khoratpithecus* have more robust mandibular bodies, which become very thick posteriorly and form a very wide extramolar sulcus between the M_3 and ascending ramus. The remaining part of the body of the Nakali mandible (KNM-NA46400) shows that it is not as robust as in these Eurasian Miocene hominoids. In this aspect, it is more similar to the condition in *Ouranopithecus*. In fact, the body height, thickness, and height/thickness index at M_1 in the Nakali mandible are very close to those in the larger mandibles of *Ouranopithecus*. In *N. nakayamai*, M_1 is relatively large with the M_1/M_2 ratios in area (MD $\times$ BL) being 85%. A relatively enlarged M_1 is characteristic of extant great apes, *Australopithecus*, and some Middle to Late Miocene Eurasian hominoids such as *Ouranopithecus* (24, 25) and *Dryopithecus* (27), whereas the relative M_1 size is considerably smaller in the Early and Middle Miocene hominoids of East Africa. *Ankarapithecus*, *Lufengpithecus*, *Khoratpithecus*, and *Sivapithecus* are intermediate in this feature ([SI Table 3]). *N. nakayamai* has a M_3 considerably larger than M_2 ($M_3/M_2 =$ 115%). In this feature it is similar to *Ouranopithecus* (24, 25) ([SI Fig. 12]) and geologically older *Sivapithecus* (*Sivapithecus indicus*) from Chinji (12.7–11.2 Ma) and *S. parvada* ($\approx$10 Ma) (28). Geologically younger *Sivapithecus* (*Sivapithecus sivalensis*), *Dryopithecus*, *Lufengpithecus*, and possibly *Ankarapithecus* have a less enlarged M_3 (27, 29). *Khoratpithecus piriyai* is quite different from *N. nakayamai* and other hominoids, both extinct and extant, in having M_3 exceptionally larger than M_2 [RIN765, $M_3/M_2 =$ 147% (10)], even exceeding those of the Early and Middle Miocene hominoids that show M_3/M_2 ratios as large as or even larger than in *N. nakayamai* ([SI Table 3]). In *Ankarapithecus* and *Sivapithecus* the buccal cingulum of the lower molars is absent, as in extant *Pongo*. In *N. nakayamai* the buccal cingulum is reduced and discontinuous, compared with Early Miocene taxa like *Proconsul*, but the cingular remnants are rather marked on the mesiobuccal aspect of the protoconid and between buccal cusps. In *Ouranopithecus* the buccal cingulum is more reduced, although weak remnants are still observed.

ANTHROPOLOGY

As in the case for the Early to early Middle Miocene African hominoids, the P_3 morphology distinguishes *N. nakayamai* from the majority of the Middle to Late Miocene Eurasian hominoids, whose P_3s are more compressed bilaterally and have a more distally oriented lingual crest of the protoconid, resulting in a much narrower distal fovea. In contrast, *Ouranopithecus* and *N. nakayamai* share P_3s that are less compressed and semitriangular in occlusal outline with a low main cusp, from which the lingual crest runs almost directly lingually and delimits a very broad distal basin. The P_3 of *N. nakayamai*, however, develops the lingual and buccal cingula more strongly than in *Ouranopithecus*, and the mesiobuccal slope is slightly less vertical relative to similar-sized (presumed female) P_3s of *Ouranopithecus*. Some *Sivapithecus* specimens from stratigraphically younger localities are reported to have relatively broad P_3s (27), but, compared with P_3s of *N. nakayamai* and *Ouranopithecus*, their crowns are still more compressed bilaterally with a narrow distal basin. *Dryopithecus* from younger localities are said to have very short, sometimes triangular P_3s (27), but *Dryopithecus* is clearly different from *N. nakayamai* in its smaller size and thinly enameled molars with high dentine penetration (23). The upper premolars, which are buccolingually broad relative to the mesiodistal length, are different from the relatively long and narrow upper premolars of *N. nakayamai*. Although the molar cingula are rather prominent in the older species of *Dryopithecus* (*Dryopithecus fontani*), they are reduced in younger species such as *Dryopithecus brancoi* (23), which are contemporaneous with *N. nakayamai*.

Although female upper canines of Miocene hominoids are low-crowned and have a well developed lingual cingulum in general, the upper canine of *N. nakayamai* is distinguished from them by the combination of the following features: crown as broad as long, a well differentiated and elevated lingual cingulum, and an extremely large lingual cusplet on the cingulum, showing a tendency for premolarization. In the mesiodistal and buccolingual dimensions, the upper canine of *N. nakayamai* is similar to the smaller (presumably female) canines of *Ouranopithecus*. In *N. nakayamai*, however, the upper canine is slightly higher-crowned with the mesial shoulder more elevated from the cervix. The upper canines of *Ouranopithecus* are heavily worn and/or damaged, but in some specimens, such as RPl128 (presumed male) and RPl775 [sex disputed (30, 31)], there seems to be a swelling on the basal part of the lingual aspect. It does not appear, however, to be so clearly differentiated as in *N. nakayamai*. In presumedly female specimens (NKT 89, RPl208), the relatively well preserved upper canines do not have such a swelling, and the lingual cingulum is more weakly expressed than in *N. nakayamai*. Some upper canines (but not all) of *Sivapithecus* have the long axis of the root cross section strongly rotated externally so that the maximum crown dimension is oriented more or less buccolingually. Consequently, the upper canine crown is sometimes buccolingually broadened, but it does not show the characteristic lingual morphology of *N. nakayamai* (SI Fig. 13).

Because *C. abyssinicus* from Ethiopia was published after our article was submitted, we do not yet know how *N. nakayamai* relates to *C. abyssinicus*. As far as we can recognize from the descriptions and figures in ref. 18, *N. nakayamai* differs from *C. abyssinicus* in the following features: The distal portion of M_3 is well developed, having large hypoconid, entoconid, and hypoconulid and a large distal fovea with a faint tubercle on the distal cingulum, so that the buccal and lingual margins of the crown run approximately parallel to each other except for the distal end. The buccal cingulum on M_3 is much more strongly expressed. The size ranges of the Nakali and Chorora specimens suggest that *C. abyssinicus* could be larger than *N. nakayamai*.

Paleoenvironments

The known faunal assemblage of Nakali (SI Table 4) is similar to that of Samburu Hills (Namurungule Formation) (32, 33). These early Late Miocene faunas of East Africa contain components similar to the Pikermian Biome, which was established on seasonal sclerophyllous evergreen woodlands covering Greece, Turkey, Iran, and the Sahara (34). This suggests that *N. nakayamai*, *Samburupithecus*, and *Ouranopithecus* may have lived under more or less similar ecological circumstances.

Nevertheless, there were probably some differences in paleoenvironments among Nakali, Samburu Hills, and Greece. Stable isotopic studies have indicated that the paleoenvironment of Nakali was C_3-plant-dominant whereas that of Samburu Hills was in an intermediate stage between C_3-plant-dominant and C_4-plant-dominant conditions (refs. 35 and 36 and T. Cerling, personal communication). The presence of small non-cercopithecoid catarrhines and a colobine monkey (SI Table 4) supports the interpretation that the paleoenvironment of Nakali was more forested than at the *Samburupithecus* site. The stable isotopic study by Quade *et al.* (37) suggests that C_3/C_4 transition did not occur in Greece. This is likely because of the higher latitudes of the region, as is the case of North America, where C_3/C_4 transition is not observed in the area above 37° N (38). It is therefore difficult to compare the paleoenvironments between Greece and Nakali based on stable isotopic studies. However, *Ouranopithecus* has more inflated cusps and thicker enamel, with the occlusal surface becoming more flatly worn compared with *N. nakayamai*. In other words, *Ouranopithecus* is probably more specialized in its molar morphology to adapt to hard/abrasive-object feeding than *N. nakayamai*. These differences suggest that *Ouranopithecus* may have lived in a drier and more open, and perhaps more seasonal, paleoenvironment than Nakali.

Discussion

The discovery of *N. nakayamai* has great importance for research on African great ape and human origins because of the poor nature of the hominoid fossil record in Africa after the mid-Miocene. An exception is *S. kiptalami*, the type maxilla of which was discovered from Samburu Hills by the Kenya–Japan Joint Project team in 1982 (39). Despite subsequent fieldwork through more than two decades, no additional hominoid specimen has been recovered from the Samburu Hills. The Nakali Expedition, however, has revealed that *Samburupithecus* is not the only hominoid that survived in Africa during 10–9 Ma. Nakali is close to Samburu Hills, both geographically and chronologically, but *N. nakayamai* is clearly different from *Samburupithecus* in a number of morphological features. In addition, the Nakali material includes an isolated P^3 (KNM-NA46434) that is quite dissimilar to that of either *N. nakayamai* or *Samburupithecus*, suggesting the presence of another, more primitive large hominoid taxon at Nakali (SI Table 4). It has, therefore, turned out that the diversity of large-bodied hominoids in the early Late Miocene of East Africa (10–9 Ma) was higher than previously recognized.

Because of the paucity of African hominoid fossils in the later Miocene and the presence of some Eurasian apes that show affinities to extant great apes, it has been suggested that some Eurasian Miocene hominoid may have come back to Africa in the early Late Miocene to become the last common ancestor of extant African great apes and humans (11, 13). However, the Nakali and Samburu Hills primate faunas show that three large hominoids and two small non-cercopithecoid catarrhines coexisted with a small colobine monkey at ≈10 Ma, even within a relatively small area in Kenya. The primate fauna from the slightly older Ngorora localities (≈12.5 Ma) probably includes three large hominoids, a small non-cercopithecoid catarrhine, and a primitive cercopithecoid (5, 38, 40). These findings support

the idea that non-cercopithecoid catarrhines survived and kept their diversity through the Middle to Late Miocene in Africa. Consequently, it has become less likely that hominoid primates were extinguished completely in Africa and were reintroduced from Eurasia.

It is interesting that, among the known fossil hominoids, *N. nakayamai* resembles *Ouranopithecus* from the early Late Miocene of Greece, in size and some dentognathic features. *Ouranopithecus* has often been suggested to be close to the ancestry of the African great ape and human clade (11, 12, 41, 42), but it was known only from Greece in southeastern Europe. However, the possibility that *Ouranopithecus* or a very similar genus would be discovered in Africa in the future has not been discounted (43). On the other hand, *Nakalipithecus* occurs in Africa and shows more primitive features, such as better expressed molar cingula, less inflated molar cusps, and more spacious occlusal basins and foveae. Moreover, the age of Nakali (9.9–9.8 Ma) predates the currently known First Appearance Date of *Ouranopithecus* (9.6 Ma). More fossil discoveries are needed to elucidate the phylogenetic relationship between the Nakali and the Greek hominoid and the actual circumstances of the hominoid dispersals between Africa and Eurasia. Nevertheless, given the retention of more primitive features and the slightly older age of *N. nakayamai*, even if the morphological similarities between *Nakalipithecus* and *Ouranopithecus* indicate their close phylogenetic relationship rather than the result of convergence, it appears more likely that dispersal may have occurred from Africa to southeastern Europe. There is also another possibility that the morphological similarities of *N. nakayamai* to *Ouranopithecus* may have been acquired for similar functional requirements, very likely for dietary adaptations in drier and more open environments. In either case, the discovery of *N. nakayamai* in the early Late Miocene of East Africa suggests that it is highly probable that large-bodied hominoids survived through the Middle to Late Miocene in Africa, giving rise to the last common ancestor of African great apes and humans. The Chorora findings by Suwa *et al.* (18) also support this idea. Three large-bodied hominoids are now known from the African early Late Miocene (Nakali and Samburu in Kenya and Chorora in Ethiopia). Although more fossil discoveries and analyses are needed to reveal the phyletic relationships among them and to other hominoids, it is likely that these early Late Miocene African hominoids are more or less close to the last common ancestor of the African great apes and humans, although any of them may not be the last common ancestor itself.

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