A second hominoid species in the early Late Miocene fauna of Nakali (Kenya)

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Abstract Nakali is an early Late Miocene fossil locality in north-central Kenya, where the Kenya–Japan Joint Expedition team has carried out fieldwork since 2002. Previously, a large hominoid Nakalipithecus nakayamai was reported from site NA39 of this locality. In addition to Nakalipithecus, the hominoid material collected from Nakali includes an isolated P3, which shows a considerably different morphology from the P3 assigned to Nakalipithecus, suggesting the presence of a different hominoid species. The general morphology of this P3 is reminiscent of that of primitive hominoids such as Proconsul, which are mainly known from the Early Miocene of East Africa. Although the present material is limited, the presence of a primitive-looking second hominoid species in Nakali indicates a higher hominoid (and hominoid-like catarrhine) diversity in the early Late Miocene of Africa than previously envisaged.

Key words: Late Miocene, catarrhines, hominoid diversity, East Africa

Introduction Recent molecular studies suggest that the divergence among the extant African great apes and humans occurred during the late Middle and early Late Miocene (Steiper and Young, 2006). At present, however, there is a large chronological gap (12.5–7 Ma) in the African hominoid fossil record (Figure 1). In 1982, a maxillary fragment of a large hominoid was discovered from early Late Miocene deposits (9.6 Ma) in the Samburu Hills, Kenya (Figure 2; Ishida et al., 1984); this hominoid was later assigned to Nakalipithecus, suggesting the presence of a different hominoid species. The general morphology of this P3 is reminiscent of that of primitive hominoids such as Proconsul, which are mainly known from the Early Miocene of East Africa. Although the present material is limited, the presence of a primitive-looking second hominoid species in Nakali indicates a higher hominoid (and hominoid-like catarrhine) diversity in the early Late Miocene of Africa than previously envisaged.
similarities suggest that *Nakalipithecus* might be ancestral to the Eurasian *Ouranopithecus*, but parallelism due to similar functional demands for hard-object/abrasive food feeding cannot be excluded (Kunimatsu et al., 2007). As the presently available material for *Nakalipithecus* is comprised of a single mandibular fragment with heavily worn molars and a handful of isolated teeth, more specimens are needed to determine the phylogenetic position of *Nakalipithecus* with more certainty. Nonetheless, considering its place of discovery (Africa), chronological age, and less specialized dental morphology compared to *Samburupithecus* or *Ouranopithecus*, *Nakalipithecus* is important for elucidating the last common ancestor of extant African great apes and humans. *Chororapithecus abyssinicus* was discovered from a Late Miocene locality in Ethiopia (Chorora, ~8.5 Ma) (Suwa et al., 2007, 2015). The material consists of a few isolated teeth, many of which are damaged (Suwa et al., 2007). Based on the morphology of the dentine–enamel junction of the molars, Suwa et al. (2007) suggested a phylogenetic link between *Chororapithecus* and gorillas. In addition to these two hominoids, Pickford et al. (2008, 2009a) reported the discovery of a possible Late Miocene hominoid in a museum collection, which was sent from Niger to France in the past and stored for decades in the National Museum of Natural History in Paris. Unfortunately, the specimen is very fragmentary, and it is difficult to determine its taxonomic status with certainty.

Among these Late Miocene localities, Nakali is the richest in primate fossils, including hominoids, cercopithecoids, non-cercopithecoid small catarrhines, and prosimians (Kunimatsu et al., 2007; Nakatsukasa et al., 2010). The majority of the hominoid fossils recovered from Nakali were attributed to *Nakalipithecus nakayamai* (Kunimatsu et al., 2007). However, another large hominoid species coexisted with *Nakalipithecus* at Nakali.

At present, the second hominoid species is represented only by an isolated upper third premolar (P3: KNM-NA...
46434). It was discovered in situ through excavation from the Hominoid Point at site NA39, where the type mandible (KNM-NA 46400) of *Nakalipithecus* and the majority of its hypodigm have been recovered. Hominoid Point is a small gulley, and fossils were obtained from a relatively thin layer of pale green sandy mud. P3 (KNM-NA 46434) was found three days after the P3 specimen assigned to *Nakalipithecus* (KNM-NA 46431) had been excavated. However, its crown morphology is considerably different from that of *Nakalipithecus*, strongly suggesting that it belongs to a different species. Because of the pauciity of the available material, we prefer to identify it as Hominoidae indet. at present. In general morphology, however, the second species is more reminiscent of the primitive hominoids from the Early to early Middle Miocene of East Africa. We here provide a description of KNM-NA 46434 and discuss its implications for hominoid evolution.

**Geological Background**

Nakali is an early Late Miocene fossil locality at the eastern edge of the Eastern (Gregory) Rift Valley in Kenya. It is located ~300 km north of Nairobi, and ~80 km south of the *Samburupithecus* locality. Previous researchers briefly visited the Nakali area in 1960s and 1970s, and the mammalian fauna indicated an early Late Miocene age (Aguirre and Leakey, 1974). In 2002, we began paleontological/geological fieldwork, and succeeded in recovering more than 4000 vertebrate and plant fossils, including primates. Since the field season of January/February 2005, we have discovered large hominoid fossils, mainly from site NA39.

The Nakali Formation is stratigraphically divided into the Lower, Middle, and Upper Members, with a combined thickness of 340 m. The Lower Member consists mainly of lacustrine turbidite and debrite sedimentary rocks and associated tuffs and lapilli tuffs. Pyroclastic flow deposits occur in its lowest part. The Middle Member is characterized by tuffaceous beds including ~40 m thick pyroclastic flow deposits. The Upper Member is composed of sedimentary rocks, tuffs, and lapilli tuffs including volcanic mud flow (lahar) and pyroclastic flow deposits. It consists of deltaic deposits characterized by repetition of laminated mudstones and sandstones with wave-generated structures (lake deposits) and cross-stratified gravel beds (fluvial channel deposits). Some of the pebbly mudstones in this member are associated with matrix consisting mainly of pyroclastic materials and crystals derived from volcanic rocks and hence may represent volcanic mud flows.

The fossiliferous deposits are located in the uppermost part of the Lower Member and in the lower part of the Upper Member of the Nakali Formation. The hominoid fossils are known only from the Upper Member with the estimated age of 9.9–9.8 Ma, based on 40Ar–39Ar dating and paleomagnetostratigraphy (Kunimatsu et al., 2007; Sakai et al., 2013).

**Description**

KNM-NA 46434 is a right upper P3. The crown is mesiodistally short and buccolingually broad (Table 1). It shows strong cusp heteromorphy with a sharp paracconule being much larger and higher than the protocone (Figure 3). The protocone and paracne are widely separated from each other, and are slightly compressed buccolingually. Consequently, the occlusal basin is spacious. The paracne has three ridges: preparacrista, postparacrista, and a third ridge that runs from the apex mesiolingually to meet the mesial marginal ridge at a point slightly buccal to the midline. Between the preparacrista and the mesiolingual ridge lies a prominent vertical groove, which runs from near the apex up to the mesial marginal ridge. There is a very fine ridge running from the protocone apex towards the mesiolingual ridge of the paracne. Distal to it, there is no distal transverse ridge between the paracne and protocone, although fine wrinkles are observed on the occlusal slopes of the paracne and protocone. In buccal view, the buccal face of the crown makes an asymmetric pentagon, as the preparacrista is vertically steep and much longer than the postparacrista, and the buccal enamel margin runs up onto the mesiobuccal root. The occlusal outline is asymmetric. The buccal moiety of the crown is mesiodistally much longer than the lingual moiety. The mesial margin runs obliquely, and it is strongly concave mesially. There is no lingual cingulum. The buccal cingulum is nearly absent except for a very short and weak remnant at the base of the preparacrista. There are two buccal roots and one lingual root, but the distobuccal root is broken away. Moderate wear facets are developed along the preparacrista and postparacrista, and on the apex of the protocone. A narrow area of dentine is exposed along the postparacrista, and a small patch of dentine is exposed at the base of the wear facet on the preparacrista.

**Comparison**

KNM-NA 46434 is only slightly smaller in size than KNM-NA 46431, an upper P3, which was previously recovered from the same site (NA39) and assigned to *Nakalipithecus nakayamai* (Table 1). However, these two premolars are considerably different in morphology. The upper P3 of *Nakalipithecus* (KNM-NA 46431) has a relatively more mesiodistally elongated crown (Table 1), and shows weaker cusp heteromorphy. The paracne is relatively low compared to that of KNM-NA 46434, and the preparacrista and

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**Table 1. Measurements (mm) of P3 of the early Late Miocene hominoids in Africa**

<table>
<thead>
<tr>
<th>Acc. No.</th>
<th>Field No.</th>
<th>Tooth</th>
<th>MD</th>
<th>BL</th>
<th>MD/BL %</th>
<th>Taxon</th>
</tr>
</thead>
<tbody>
<tr>
<td>KNM-NA 46434</td>
<td>NA39-7841'05</td>
<td>Rt P3</td>
<td>8.0</td>
<td>12.1</td>
<td>66.1</td>
<td>Hominoidae indet.</td>
</tr>
<tr>
<td>KNM-NA 46431*</td>
<td>NA39-7828'05</td>
<td>Rt P3</td>
<td>9.3</td>
<td>12.1</td>
<td>76.9</td>
<td><em>Nakalipithecus nakayamai</em></td>
</tr>
<tr>
<td>KNM-SH 8531</td>
<td>SH22-385'82</td>
<td>Lt P3</td>
<td>10.4</td>
<td>11.9</td>
<td>87.4</td>
<td><em>Samburupithecus kiptalami</em></td>
</tr>
</tbody>
</table>

* NB: The buccolingual breadth of this specimen was typed as 11.1 mm in Table 1 in Kunimatsu et al. (2007), but it should read as 12.1 mm.
postparacrista are short and of similar length. In addition, the cusps are more voluminous, and are linked to each other by a low and thick mesial transverse ridge and a more faint distal transverse ridge. The apex of the paracone is more peripherally positioned with the steep buccal surface being slightly concave midway, while KNM-NA 46434 has a more medially positioned paracone apex with an apicocervically convex buccal surface and better developed buccal basal flare. In mesial view, the paracrista is rather straight in *Nakalipithecus*, but it curves slightly and is convex buccally in KNM-NA 46434 (Figure 3). The mesial and distal cingula are wide and elevated high in *Nakalipithecus*, while the corresponding cingula are narrow and positioned closer to the cervix in KNM-NA 46434 (Figure 3). In the P3 of *Nakalipithecus*, the buccal cingulum is better expressed as short but distinct clefts at the bases of the preparacrista and postparacrista, and the mesial and distal styles are also better developed (Figure 3). Although these parts are worn in KNM-NA 46434, it does not seem that the styles were as prominent as in *Nakalipithecus*.

KNM-NA 46434 is presumed to be a premolar of a male individual, based on such features as the paracone being very sharp and much higher than the protocone, the preparacrista being vertically steep and much longer than the postparacrista, and the mesial margin of the crown being strongly concave mesially, which may correspond to a large upper canine. On the other hand, KNM-NA 46431 presumably belonged to a female, based on its crown morphology and the size distribution of all the dental specimens assigned to *Nakalipithecus* (Kunimatsu et al., 2007). If these sex attributions are correct, and if we take into account the strong sexual dimorphism generally seen in Miocene hominoids, the second species may have been smaller than *Nakalipithecus*. This is, however, a tentative interpretation, as the available material is quite limited.

Compared to the penecontemporaneous *Samburupithecus* (KNM-SH 8531), KNM-NA 46434 differs in being slightly smaller, with a mesiodistally short and relatively much broader crown, better developed buccal basal flare, strong cusp heteromorphy, thinner and more widely separated cusps, and more spacious occlusal basin (Ishida and Pickford, 1997; Pickford and Ishida, 1998; Sawada et al., 1998). The P3 of *Samburupithecus* is also different from that of *Nakalipithecus* in having a more mesiodistally elongated crown (Table 1), more inflated cusps, thicker occlusal ridges, more medially placed paracone apex, and more restricted occlusal foveae.

The second hominoid taxon from Nakali retains primitive features such as a relatively broad crown and strong cusp heteromorphy. The P3's of African Early to early Middle

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**Figure 3.** Occlusal (stereo) (a), lingual (b), buccal (c), distal (d), and mesial (e) views of the P3's of *Nakalipithecus nakayamai* (KNM-NA 46431) (upper in (a), and right in (b)–(e)) and the second Nakali hominoid (KNM-NA 46434) (lower in (a) and left in (b)–(e)).
Miocene hominoids tend to have relatively broader crowns than extant great apes (Figure 4). KNM-NA 46434 is plotted among the former, while Nakalipithecus (KNM-NA 46431) and Samburupithecus (KNM-SH 8531) share relatively narrower P3 crowns with extant great apes (Figure 4). Compared to early Middle Miocene hominoids from East Africa, the second Nakali hominoid differs from Equatorius africanus (~15 Ma) in stronger cusp heteromorphy with steeper pre- and postparacrista, the cusp tips being more widely separated from each other, more spacious occlusal basin, and weaker mesial and distal marginal ridges (Pickford, 1985, 1986; Ward et al., 1999; Kelley et al., 2002). No P3 is known for Kenyapithecus wickeri (~14 Ma) (Andrews, 1978; Pickford, 1985, 1986; Harrison, 1992). Inferring from the P4 morphology of K. wickeri, however, it seems unlikely that the second Nakali hominoid belongs to the same taxon. The second Nakali hominoid is rather more similar to Nacholapithecus kerioi (~16–15 Ma), yet it is distinguished from the latter by much larger size, more peripherally positioned and buccolingually compressed cusps, more spacious occlusal basin, more vertical side walls of the cusps, and lack of the distal transverse ridge (Kunimatsu et al., 2004).
Compared to Early Miocene hominoids, the second Nakali hominoid is different from *Afropithecus* (Leakey and Leakey, 1986; Leakey et al., 1988) and *Morotopithecus* (Gebo et al., 1997) in being much smaller, with weak basal flares, buccolingually more compressed and with more peripherally positioned cusps, the paracone being much higher than the protocone, and a more spacious occlusal basin. Although KNM-NA46434 is similar in size to smaller P3’s of *Ugandapithecus major* (Figure 4), the above-mentioned morphological features also distinguish between them (Senut et al., 2000; Pickford et al., 2009b). On the other hand, in those features that distinguish the Nakali P3 from *Afropithecus*, *Morotopithecus*, and *Ugandapithecus*, it resembles those of *Proconsul* (Andrews, 1978), though it is larger than *P. nyanzae* (Figure 4, Figure 5).

**Discussion**

The discovery of KNM-NA 46434 (a right P3) indicates that, in addition to *Nakalipithecus*, there is a second large hominoid species in the early Late Miocene primate fauna of Nakali. Compared to *Nakalipithecus*, this hominoid seems to be more primitive, showing a relatively broad crown and strong cusp heteromorphy of P3. While it differs from either the early Middle Miocene hominoids, such as *Equatorius*, *Nacholapithecus*, and probably *Kenyapithecus*, and Early Miocene hominoids, such as *Afropithecus*, *Morotopithecus*, and *Ugandapithecus*, it rather resembles that of *Proconsul* from the Early Miocene of East Africa. The presence of KNM-NA 46434 suggests that a primitive hominoid was present in the Nakali fauna, similar in premolar morphology to the Early Miocene *Proconsul* species, had survived to the early Late Miocene (~10 Ma), being contemporaneous with a more derived large hominoid (= *N. nayakayami*).

Previous findings in the Tugen Hills also support this interpretation. Although the African fossil hominoid record is extremely poor after the early Middle Miocene, there are a few hominoid specimens reported from the Ngorora Formation (late Middle Miocene, ~12.5 Ma) in the Tugen Hills (Hill and Ward, 1988; Pickford and Senut, 2005). The Ngorora material includes a large P3 (KNM-BN 10489). It is different from the P3 of *Nakalipithecus* (KNM-NA 46424) in having more centrally positioned protoconid and metacodon, more limited mesial and distal foveae, and more distinct buccal cingula. Hill and Ward (1988) reported that it bears closest anatomical similarity to *Proconsul* (sensu lato) but has a few differences such as the crown shape and the differential levels of the trigonid and talonid. Although it is difficult to assess the taxonomic position precisely based on only a single P3, KNM-BN 10489 provides a good possibility that there was a hominoid with primitive aspects in East Africa at the mid-Middle Miocene (~12.5 Ma). In addition, the Ngorora Formation has also yielded an upper molar of a large hominoid, which Hill (1994) considered to be morphologically most similar to extant chimpanzees, although it is larger and not identical in morphology. Pickford and Senut (2005) reported the discovery of a chimpanzee-like or *Dryopithecus*-like lower molar from the Ngorora Formation.

In addition to East Africa, *Otavipithecus namibiensis* is known from the late Middle Miocene (~13 Ma) of Berg Aukas in Namibia (Conroy et al., 1992). *O. namibiensis* is represented by the type mandible and several other cranial and postcranial specimens, including a frontal fragment, an atlas vertebra, an ulna fragment, and a manual phalanx (Conroy et al., 1992, 1993; Pickford et al., 1997; Senut and Gommery, 1997). The available evidence suggests that *O. namibiensis* was a relatively primitive hominoid, being a generalized quadruped (Senut and Gommery, 1997), though some features may be more derived. For example, the atlas vertebra retains the posterior bridge but lacks the lateral bridge, a pattern that is frequently seen in extant chimpanzees (Le Minor and Tröstl, 2010). The atlas vertebrae of *Nacholapithecus kerioi*, 2–3 million years older than *Otavipithecus*, retain a more primitive pattern with both of the posterior and lateral atlas bridges completely formed, which is widely observed in extant non-hominoid primates (Kunimatsu et al., 2004; Yamamoto and Kunimatsu, 2006; Kikuchi et al., 2012).

In sum, hominoids, which more or less retained primitive features, survived to ~12.5 Ma and were distributed from eastern to southern Africa. After these rare records of hominoid fossils around 12.5 Ma, however, no such hominoid had been known in the African fossil record except for the above-mentioned *Samburupithecus*. Previously, the paucity of hominoid fossils during the late Middle to early Late Miocene of Africa led to the hypothesis that the hominoid diversity declined after the early Middle Miocene and that they were replaced by cercopithecoids (Andrews, 1981; Fleagle, 2013). However, this view overlooks the potential sampling bias of African Miocene fossil sites (Cote, 2004). Although the available evidence, such as the Ngorora and Otavi material, is still sparse, it may suggest that the African hominoid fauna had more likely retained its diversity even after the early Middle Miocene. In fact, the recent discoveries of *Nakalipithecus* in Kenya and *Chororapithecus* in Ethiopia have shown a greater diversity of African hominoids in the early Late Miocene than previously presumed.

The present finding from Nakali may extend the time range of the survival of primitive hominoids in East Africa from 12.5 Ma to ~10 Ma. It is interesting that such a primitive hominoid was discovered with a more derived hominoid (= *Nakalipithecus*), which may have been close to the stem of extant African great apes and humans (Kunimatsu et al., 2007; Harrison, 2010). Some authors have suggested that *Samburupithecus* is a late survivor of *Proconsul*-like primitive hominoids (Begun, 2007; Olejniczak et al., 2009; Begun et al., 2012). It is true that *Samburupithecus* retains primitive features, but its dentition also shows fairly specialized conditions (Ishida and Pickford, 1997; Pickford and Ishida, 1998). Among the specialized features, elongated premolar and molar crowns might be shared derived characters with extant great apes, especially gorillas, although such features could have resulted from parallel evolution related to dietary functions. In fact, the dentition of *Samburupithecus* is partially reminiscent of the specialized conditions in *nyanzapithecines* from the Late Oligocene to Middle Miocene of Africa (Harrison, 1986, 2010; Kunimatsu, 1992, 1997; Stevens et al., 2013) in having elongated crowns, strongly inflated cusps, and strongly restricted occlusal foveae and basins on cheek teeth, though *Samburupithecus* is apparently much
larger than any known nyanzapithecines and lacks the characteristic upper premolar morphology in this group (Harrison, 1986, 2010). At present, the phyletic relationships of Samburupithecus with other extant and extinct hominoids are unclear.

Apart from whether Samburupithecus is a late surviving member of primitive hominoids such as Proconsul (Begun, 2007; Olejniczak et al., 2009; Begun et al., 2012) or a member of hominoids which are more closely related to extant great apes (Andrews, 1992; Ishida and Pickford, 1997; Pickford and Ishida, 1998), the recent evidence from Nakali suggests that both primitive and more derived hominoids inhabited East Africa contemporaneously in the early Late Miocene (Kunimatsu et al., 2007 and this study). Because the majority of the remains of Nakalipithecus and the primitive-looking upper premolar described in this article were recovered from the same thin mud flow layer in the same small gully of the site NA39 in Nakali (Figure 1), it is likely that these two hominoid species would have lived sympatrically, at least, in a broad sense. Although the presently available samples from Nakali are quite limited, the difference of the occlusal morphology, suggesting a dietary differentiation and a possible difference in body size, implies that Nakalipithecus and the second hominoid species may have divided ecological niches in the same area, as modern gorillas and chimpanzees do in tropical rainforests in Central Africa today (Yamagiwa and Basabose, 2006, 2009; Head et al., 2011). In addition, previous studies in the Samburu Hills and Nakali have shown that even though these two fossil localities are nearly contemporaneous and are located close to each other along the Eastern Rift Valley in Kenya, their paleoenvironments would have been different from each other, with Nakali having been more forested than Samburu Hills (Cerling et al., 1999; Kunimatsu et al., 2007; Nakaya et al., 2011; Uno et al., 2011). This paleoenvironmental difference might be reflected in the more specialized occlusal morphology of Samburupithecus and the fact that in spite of long-term, intensive fieldwork in the Samburu Hills, the type maxilla of Samburupithecus is the only primate fossil discovered from this locality, while Nakali has yielded various primate species including the two large hominoids discussed in this article, cercopithecoids, and prosimians (Kunimatsu et al., 2007; Nakatsukasa et al., 2010).

In conclusion, the early Late Miocene is very likely a transitional period for the African catarrhine fauna, in which primitive forms still survived while more modern forms were emerging. By the late Late Miocene (~7.5 Ma), the small non cercopithecoid catarrhines seem to have become extinct, and non-human hominoids had declined greatly. Instead, modern Old World monkeys ( cercopithecines and colobines) became dominant in the African primate fauna and have diversified into the present various taxa since then. In addition, hominins also began to appear in the fossil record after the mid-Late Miocene. The earliest members include Orrorin tugenensis from Kenya (Sensu et al., 2001), Ardipithecus kadabba from Ethiopia (Haile-Selassie, 2001), and Sahelanthropus tchadensis from Chad (Brunet et al., 2002), all of which were recovered from the African late Late Miocene (~7–5 Ma). Through the Plio-Pleistocene, hominins evolved into various taxa (Ar. ramidus, Australo-

\[ \text{spp., Paranthropus spp., and Homo spp.) (Wood, 2010), while other hominins are nearly absent in the African fossil record of this period, except for a few isolated teeth discovered from the Tugen Hills in Kenya (~0.5 Ma) and assinged to Pan sp. (McBreart and Jablonski, 2005). The diversity of the fossil hominins is in strong contrast to the extreme paucity of fossil non-hominin hominoids after the mid-Late Miocene. Most likely, the emergence of hominin lineage is also set within the same framework of the paleoenvironmental and primate faunal changes in Africa during the early Late Miocene, though the fossil evidence has yet to be discovered.

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References


Pickford M., Senut B., Morales J., and Braga J. (2008) First homi-


