New specimens of a primitive hippopotamus, *Kenyapotamus coryndonae*, from the Upper Miocene Nakali Formation, Kenya

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Received November 6, 2014
Accepted January 23, 2015

**Abstract:** New dental and astragalar specimens of a primitive hippopotamus, *Kenyapotamus coryndonae* (Mammalia, Cetartiodactyla, Hippopotamidae, Kenyapotaminae) from the lower Upper Miocene Nakali Formation at the Nakali locality, central Kenya, are described and illustrated. The new specimens increase the known morphological and size variations of the dentition and astragalus in this primitive hippopotamid species, which is important to understand the origin and early evolution of the Hippopotamidae.

Keywords: Hippopotamidae, Kenya, Kenyapotaminae, *Kenyapotamus*, Miocene, Nakali

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**Introduction**

*Kenyapotamus coryndonae* Pickford, 1983 (Mammalia, Cetartiodactyla, Hippopotamidae, Kenyapotaminae) is a species of primitive fossil hippopotamuses in the Miocene of Africa (Boisserie et al., 2010). It is an important species in the African mammalian chronology and in the origin of the Hippopotamidae (e.g., Pickford, 1983, 1989, 1990, 2007, 2008; Boisserie et al., 2010). In particular, the origin of hippos is hotly debated recently (e.g., Pickford, 2007, 2008, 2011; Boisserie et al., 2010; Orliac et al., 2010; Tsubamoto et al., 2011). However, the fossil collection size of the species is not enough to understand the morphology and variation of the species precisely, so that the early evolution of hippos is not well resolved.

Since 2002, a joint research team from Kyoto University and the National Museums of Kenya has been conducting field geological and paleontological research in the lower Upper Miocene Nakali Formation at the Nakali locality, central Kenya (Nakatsukasa et al., 2006). The team has discovered many vertebrate fossils including a new great ape, *Nakalipithecus nakayamai*, which attracted a great deal of attention from anthropologists and primatologists because the species is a candidate for the latest common ancestor of the extant African great apes and humans (Kunimatsu et al., 2007). Handa et al. (in press) has recently described one dental specimen from a fossil rhinoceros from the Nakali Formation discovered by the joint team.

This material report describes and illustrates new dental and astragalar specimens of *K. coryndonae* from the Nakali Formation discovered by the joint research team from Kyoto University and the National Museums of Kenya. Only a few specimens of *K. coryndonae* from the Nakali Formation have been described by previous researchers (Pickford, 1983; Boisserie et al., 2010). The specimens from the Nakali Formation will contribute to a more precise understanding of the morphology and variation of the species and to the analyses of the origin of the hippos from the paleontological perspectives.

**Dental terminology.**—Mostly follows Boisserie et al. (2010) and Orliac et al. (2010).

**Dental abbreviations.**—M/m, upper/lower molars. P/p, upper/lower premolars.


**Systematic paleontology**

Family Hippopotamidae Gray, 1821
Subfamily Kenyapotaminae Pickford, 1983
Genus *Kenyapotamus* Pickford, 1983
Kenyapotamus coryndonae Pickford, 1983  
Figs. 1–3

Kenyapotamus corydoni Pickford, 1983 [sic].

Comments on the specific name.—The specific name  
was originally spelled as 'corydoni' (Pickford, 1983),  
but it was later corrected to a feminine form 'corydon-  
nae' as it is named after a woman (Boisserie et al.,  
2010; also see Articles 31.1, 32.4, and 32.5 of the  
International Code of Zoological Nomenclature, Ride et al.,  
1999).

New material.—KNM-NA 45748, a left M3; KNM-NA  
52678, a distal part of the right upper molar; KNM-NA  
47535, a right M3; NA12-12276’06, a right P2;  
KNM-NA 45747, a left maxillary fragment with P4;  
KNM-NA 45751, a broken left p3; KNM-NA 45754A,  
a broken left p3; KNM-NA 45746, a right mandibular  
fragment with p4; KNM-NA 45752, a right p4; KNM-NA  
45749, a left m3; KNM-NA 45756, a trigonid of a  
right lower molar; KNM-NA 45735A, a broken talonid  
of left m3; KNM-47284, a broken talonid of right  
m3; NA11-12238’06, a left astragalus; KNM-NA 52680A,  
a right astragalus; KNM-NA 47290, a fragmentary  
tusk. The specimen numbers starting with NA  
are formal field numbers in KNM. They will eventually  
be numbered with the prefix of KNM-NA.

Repository.—Palaeontology Section, National Museums of Kenya, Nairobi, Kenya.

Locality.—Nakali locality (approx. 1°11’N and 36°22’E),  
which is located on the eastern shoulder of the central  
Kenya Rift, about 40 km west of Maralal, central Kenya  
(Kunimatsu et al., 2007).

Formation and horizon.—Nakali Formation. It  
is characterized by tuffaceous sandstones and mudstones  
with conglomerate interbeds, a thick pyroclastic flow  
deposit, and tuff beds (Kunimatsu et al., 2007; Sakai et  
al., 2013). It is stratigraphically subdivided into the  
"Lower,” “Middle,” and "Upper” Members. The vertebrate  
fossils come from the upper part of the "Lower"  
Member and from the "Upper" Member. KNM-NA 52678,  
47535, 45735A, 47284, and 52680A are from the "Upper"  
Member. All other present specimens described here  
are from the upper part of the "Lower” Member.

Age.—The age of the vertebrate fossils from the  
Nakali Formation is around 10.0–9.8 Ma (early Tortonian,  
early Late Miocene). This age is correlated to the  
Vallesian European Land Mammal Age (Steininger et al.,  
1996). According to the 40Ar–39Ar dating by Kunimatsu  
et al. (2007), the tuff bed in the upper most part of the  
"Lower” Member was dated at 9.90±0.09 and 9.82±0.  
09 Ma and the tuff bed in the lower most part of the  
"Upper” Member was dated at 10.10±0.12 Ma. Based  
on these 40Ar–39Ar ages and magnetostratigraphic analy-  
sis by Kunimatsu et al. (2007), the age of the Nakali  
Formation ranges from the Paleomagnetic Polarity  
Chron C5n.2n to C5n.1n, with the Chron C5n.1r (9.92–  
9.88 Ma) corresponding to the upper part of the "Lower"  
Member to the lower most part of the "Upper” Member.

Dental measurements.—Shown in Table 1.

Astragalar measurements (in mm).—NA11-12238’06:  
lateral proximo-distal length (a) = 61.5; medial proximo-  
distal length (b) = 51.8; medio-lateral width of tibial  
trochlea (c) = 33.2; medio-lateral width of distal troch- 
lea (d) = 39.9; medial dorso-plantar height (e) = 30.2;  
lateral length of tibial trochea (f) = 37.3; medial length  
of tibial trochea (g) = 34.7. KNM-NA 52680A: (b) =  
48.1; (d) = 36.7. The measurement positions (a–g) are  
the same as in Tsubamoto and Tsogtbaatar (2008).

Comparative description.—P2 (NA12-12276’06; Fig.  
1A) is two-rooted and is as large as the previously re-  
ported P2 specimen of K. coryndonae (Table 1). It dif-  
fers from P3 of K. coryndonae in lacking a protocone  
and from P2 of the other kenapotamine species Pal-  
eopotamus ternani in being more developed and more  
P3-like (Pickford, 1983, 2007; Boisserie et al., 2010).

P4 (KNM-NA 45747; Fig. 1B) is as large as the previ-  
ously reported P4 specimen of K. coryndonae (Table 1).  
It has three roots. The first is below the mesial part  
of the paracone. The second is below the distal part of  
the paracone. The third is below the protocone. However,  
the second and third roots are conjoined and are contin-  
uous with each other, resulting in P4 superficially hav-  
ing two roots (a smaller mesiobuccal one and a larger  
distal one), as seen in the previously reported P4 speci-  
men of K. coryndonae (Pickford, 1983).

The two M3 specimens (KNM-NA 45748 and 47535;  
Fig. 1C, 1E) are moderately worn and have no intersti-  
tial wear facets on the distal face, indicating that they  
are definitely M3s. KNM-NA 45748 is as large as the previ-  
ously reported M3 specimens of K. coryndonae, and  
KNM-NA 47535 is somewhat smaller than the previ-  
ously reported specimens (Table 1). In both specimens,  
the parastyle appears to be more mediomesially located  
than that of P. ternani (Pickford, 1983, 2007; Boisserie  
et al., 2010), also implying that these specimens should  
be assigned to K. coryndonae.

KNM-NA 52678 (Fig. 1D) is a distal part of an upper  
molar and is only slightly worn. No interstitial wear fac-  
et can be observed on the distal facet.
Fig. 1. Upper molars and premolars of *Kenyapotamus coryndonae* Pickford from Nakali, Kenya (Miocene). A, NA12-12276’06, a right P2: A1, occlusal view (stereo pair); A2, buccal view; A3, lingual view. B, KNM-NA 45747, a left maxillary fragment with P4: B1, occlusal view (stereo pair); B2, buccal view; B3, lingual view; B4, mesial view; B5, distal view. C, KNM-NA 45748, a left M3: C1, occlusal view (stereo pair); C2, buccal view. D, KNM-NA 52678, a distal part of right upper molar, occlusal view (stereo pair). E, KNM-NA 47535, a right M3: E1, occlusal view (stereo pair); E2, buccal view.
Fig. 2. Lower molars and premolars of *Kenyapotamus coryndonae* Pickford from Nakali, Kenya (Miocene). A, KNM-NA 45751, a broken left p3, occlusal view (stereo pair). B, KNM-NA 45754A, a broken left p3: B1, occlusal view (stereo pair); B2, buccal view; B3, lingual view. C, KNM-NA 45746, a right mandibular fragment with p4: C1, occlusal view (stereo pair); C2, lingual view; C3, buccal view. D, KNM-NA 45732, a right p4: D1, occlusal view (stereo pair); D2, lingual view; D3, buccal view. E, KNM-NA 45749, a left m3: E1, occlusal view (stereo pair); E2, lingual view; E3, buccal view. F, KNM-NA 45756, a trigonid of right lower molar: F1, occlusal view (stereo pair); F2, distal view. G, KNM-NA 45755A, a broken talonid of left m3, occlusal view. H, KNM-NA 47284, a broken talonid of right m3, occlusal view.
The lower premolar specimens, broken p3 (KNM-NA 45751 and 45754A; Fig. 2A–2B) and p4 (KNM-NA 45746 and 45752; Fig. 2C–2D), are comparable in size and morphology to the previously reported p3 and p4, respectively, of *K. coryndonae* (Table 1; Pickford, 1983; Tsujikawa, 2005). On the p4 specimen, there is a metaconid on the distolingual face of the protoconid, and a hypoconid, an entoconid, and a smaller distostylid are present on the talonid. The metaconid on the p3 specimen is smaller and lower than that on p4. The talonid on p3 is buccolingually narrower than that on p4. The talonid cusps on p3 are less developed than those on p4.

The three m3 specimens (KNM-NA 45749, 45735A, and 47284; Fig. 2E, 2G, 2H) are comparable in size and morphology to the previously reported m3 specimens of *K. coryndonae* (Pickford, 1983; Nakaya et al., 1987). There is an ectohypocristulid. These specimens differ from m3 of *P. ternani* in that the postectohypocristid is very weak or cannot be observed (Boisserie et al., 2010).

In the molar trigonid specimen (KNM-NA 45756; Fig. 2F), the basal part of the trigonid crown is somewhat broken. In distal view (Fig. 2F), a well-developed M-structure on the distal trigonid wall is visible, consisting of the postectoprotocristid, postprotocristid, postmetacristid, and postectometacristid.
The astragalar specimens (NA11-12276’06 and KNM-NA 52680A; Fig. 3A–3B) are comparable in size and morphology to the previously reported astragali of *K. coryndonae* (Pickford, 1983; Nakaya et al., 1984; Boisserie et al., 2010). The cuboid facet on the distal trochlea is as wide as the navicular facet. The keel between the two facets on the distal trochlea is centered medio-laterally.

The tusk (canine) (KNM-NA 47290; Fig. 3C) is broken. Its cross-section is ovate triangular (or D-shaped), like the previously reported root of the lower canine of *K. coryndonae* (Tsujikawa, 2005). This tusk differs from that of the suids in having thicker enamel.

**Remarks.**—The present specimens have following features compared to the previously described specimens of *K. coryndonae*, increasing the known morphological variation of the species (Pickford, 1983, 1990; Nakaya et al., 1987; Tsujikawa, 2005; Boisserie et al., 2010).

On the present M3 specimens, KNM-NA 45748 and 47535 (Fig. 1C, 1E), the lingual cingulum of the protocone is slightly discontinuous on the lingual aspect of the cusp, whereas it is continuous in the previously reported M3s of *K. coryndonae*. Also, on KNM-NA 45748, the ectostyle, entostyle, and paraconule are developed better than those of any other M3s of *K. coryndonae*. In buccal view, the crown height of KNM-NA 45748 is relatively higher than other M3s of *K. coryndonae* and is slightly lower than M3 of *K. aff. coryndonae* (KNM-NA 251; Boisserie et al., 2010).

On p3, the expression of the postprotocristid is variable (Fig. 2A–2B). The postprotocristid is shorter and disappears midway before it reaches the hypoconid in KNM-NA 45754A (Fig. 2B), whereas it is longer and extends down to the small hypoconid in KNM-NA 45751 (Fig. 2A) and KNM-SH 40142 (Tsujikawa, 2005), as in p4.

On a present m3 specimen (KNM-NA 45749; Fig. 2E), there are short but prominent cingular shelves on the distolingual and distobuccal aspects of the hypoconulid and several prominent small tubercles between the hypoconulid and both of the entoconid and hypoconid. These characteristics are also seen in KNM-NA 250C (m3 of *K. cf. coryndonae*; Boisserie et al., 2010). In contrast, these characteristics are not developed on the other m3 specimens of *K. coryndonae* (Fig. 2G–2H). In addition, KNM-NA 45749 (Fig. 2E) and the present molar trigonid (KNM-NA 45756; Fig. 2F) differ from other lower molar specimens of *K. coryndonae* in having a weaker mesial cingulum.

**Acknowledgments**

We are grateful to the Government of Kenya for research permission and to Martin Pickford (Muséum National d’Histoire Naturelle, Paris) for review. We also thank Fredrick Kyalo Manthi, Mary Muungu, and Francis Ndiritu (National Museums of Kenya, Nairobi) for graciously providing access to the specimens examined. This research was supported by JSPS KAKENHI Grant Number 25257408 (to M. Nakatsukasa).

**References**


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Table 1. Dental measurements (in mm) of *Kenyapotamus coryndonae* Pickford from Nakali, Kenya (Miocene). The ranges of the previously reported specimens are from Pickford (1983, 1990), Nakaya et al. (1987), Tsujikawa (2005), and Boisserie et al. (2010).

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Abbreviations: L, mesiodistal length; W, buccolingual width; W-m, width of mesial part; W-d, width of distal part; W-etr, trigonid width; W-tad, talonid width.


