LATE MIOCENE HIPPOPOTAMIDAE FROM LEMUDONG'O, KENYA

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ABSTRACT

The late Miocene deposits from Lemudong'o have yielded few and fragmentary remains of hippopotamids. These remains document the presence of a large hippopotamid and extend southward the late Miocene distribution of the family. Although the general morphology of the dentition is similar to that of other late Miocene Hippopotaminae, some peculiarities were noted in molar endocrista development and the relative size of the premolars. This could indicate a distinct form at Lemudong'o, but further evidence is required for confirmation.

Introduction

Up to 8 million-years-ago (Ma), the family Hippopotamidae is mostly represented by material attributed to the genus _Kenyapotamus. Kenyapotamus coryndoni_ Pickford, 1983, is recorded between 11 Ma and 9 Ma, from Ngorora, Nakali, and Ngeringerowa in Kenya (Pickford, 1983), from the Beglia Formation in Tunisia (Pickford, 1990), and from Chorora in Ethiopia (Geraads et al., 2002). Only known in Kenya, _K. ternani_ Pickford, 1983, has more uncertain affinities with the family Hippopotamidae and is dated from 15.7 Ma at Kipsaramon (Behrensmeyer et al., 2002) to ca. 14 Ma at Fort Ternan (Pickford, 1983). The fragmentary and rare material assigned to these forms indicates that hippopotamids were rather infrequent in middle and early late Miocene African ecosystems.

After 8 Ma, however, their frequency seems to have dramatically increased. At Lothagam in Kenya, hippopotamids were mostly found in the late Miocene Nawata Formation and are the most frequently collected mammals, accounting for 27% of the mammal specimens collected (Weston, 2003). They are also among the most common mammals in the upper Miocene of Toros-Ménalla in Chad (Vignaud et al., 2002; Boisserie et al., 2005), representing more than 20% of the total assemblage.

Several species coexisted at Lothagam (Weston, 2000, 2003) and may also be the case at Toros-Ménalla (Boisserie et al., 2005). The dominant species (_Archaeopotamus harvardi_ (Coryndon, 1977) at Lothagam and _Hexaprotodon garyam_ at Toros-Ménalla) were large-sized, almost as large as the modern _Hippopotamus amphibius_ Linné, 1758, and were interpreted as dwellers of riparian environments (Boisserie, 2002; Weston, 2003).

Other late Miocene hippopotamids have been recorded from the late Miocene Baynunah Formation at Abu Dhabi, United Arab Emirates (Gentry, 1999), and from Sahabi, Libya (Gaziry, 1987). By 7 Ma, Hippopotaminae, excluding the dentally more archaic Kenyapotaminae (Pickford, 1983), were geographically disperse, very abundant in some localities, and taxonomically diverse with at least five different forms. After this date, which is also the last appearance date of the Anthracotheriidae in Africa (Vignaud et al., 2002), the Hippopotamidae solely occupied the niche of large semi-aquatic herbivores in African ecosystems.

In this regard, hippopotamids constitute an important element of African wetland dynamics and ecology. This is well illustrated by the significant impact of extant _Hip. amphibius_ on those environments, in terms of hydrographic-network geomorphology (McCarthy et al., 1998; Deocampo, 2002), trophic input and quality of waters (Wolanski and Gereta, 1999; Grey and Harper, 2002), and surrounding vegetation growth and diversity (Field, 1970; Lock, 1972; Olivier and Laurie, 1974; Eltringham, 1999).

The end of the late Miocene is also a critical period for the evolutionary history of the Hippopotamidae in terms of their biogeography. The late Miocene records the oldest known hippopotamids outside of Africa, in southern Europe (Made, 1999) and in the Indian sub-continent, with a first-appearance date at 5.9 Ma in the Pakistani Siwalik hills (Barry et al., 2002).

As a consequence, the discovery of any new hippopotamid remains from this time period is important, including those recovered from the late Miocene of Lemudong'o, near Narok in southern Kenya (Ambrose, Kyule, and Hlusko, 2007). These fossils represent the most southern known late Miocene Hippopotamidae, and date to 6.087 ± 0.013 to 6.12 ± 0.07 Ma (Deino and Ambrose, 2007). Although they are few and fragmentary, I here provide a brief description of the more significant specimens and compare them to other known late Miocene hippopotamids.

Abbreviations

KNM = Kenya National Museum; KNM-NK = indicates fossils from localities within the Narok district (Ambrose, Kyule, and Hlusko, 2007); KNM-LT = indicates fossils from Lothagam.
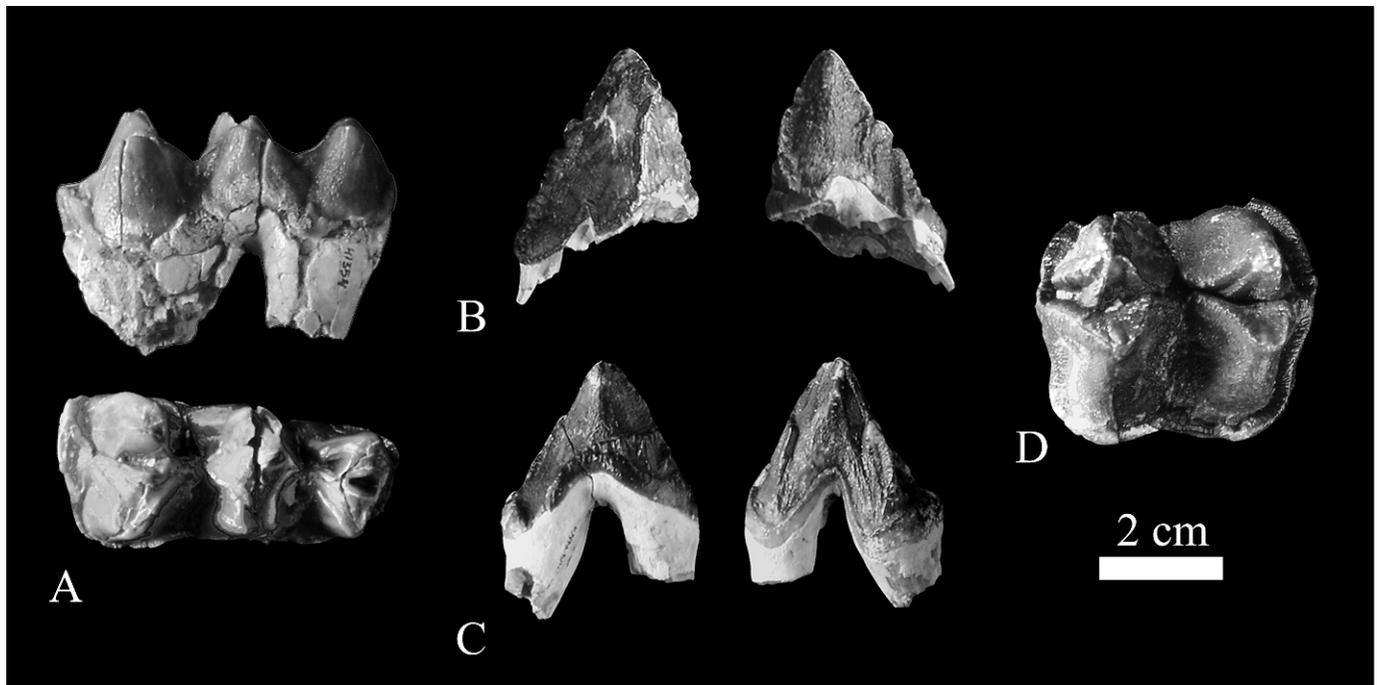
Figure 1. Dentition of Hippopotamidae indet. from Lemudong'o, Kenya. A, right d4 KNM-NK 41354 in buccal view (top) and occlusal view (bottom); B, right P1 KNM-NK 41353 in buccal view (left) and lingual view (right) (these two pictures were inversed in order to facilitate comparison with the tooth below); C, left D2 KNM-NK 41353 in buccal view (left) and lingual view (right); D, right M1 KNM-NK 41353 in occlusal view.

Dental abbreviations follow this convention: M1 = maxillary first molar; p4 = mandibular fourth premolar.

Systematic Paleontology

Class Mammalia Linnaeus, 1758
Order Artiodactyla Owen, 1848
Family Hippopotamidae Gray, 1821
Subfamily Hippopotaminae Gray, 1821
Hippopotaminae indeterminate
Figure 1

Studied material

KNM-NK 36501, upper incisor; KNM-NK 36503, fragmentary p4; KNM-NK 36504, fragmentary M; KNM-NK 36506, fragmentary m; KNM-NK 36537, apical fragment of lower incisor; KNM-NK 36875, premolar fragments; KNM-NK 36876, fragmentary molar; KNM-NK 36964, apical fragment of lower canine; KNM-NK 36965, p1 fragment?; KNM-NK 38315, fragmentary molar; KNM-NK 38317, molar fragments; KNM-NK 40857, molar and premolar fragments; KNM-NK 40915, fragmentary lower molar; KNM-NK 41147, fragmentary m1 or m2; KNM-NK 41352, lower molar fragments; KNM-NK 41353, right P1, D2, and M1; KNM-NK 41354, right d4.

A dozen fragmentary postcranial remains were also collected at Lemudong'o, but given their weak significance to taxonomic considerations, they are not included in this publication.

Description

KNM-NK 41354 is a right d4 (Figure 1A). The crown of this tooth is almost complete and well preserved. It exhibits a moderate stage of wear that could roughly correspond to an individual of *Hip. amphibius* from Laws' age group III to IV, i.e., between 1 and 3 years old (Laws, 1968). The tooth retains three pairs of cuspids and its width increases from the mesial pair to the distal pair. A finely crenulated cingulum is present mesially. It remains low and thin. Buccally, the cingulum is attenuated, being essentially expressed between cuspids and on the hypoconid. No cingulum appears lingually. In contrast, the distal side exhibits a higher and thicker cingulum that protrudes distally. The enamel is finely wrinkled.

The first pair of cuspids exhibits a strong and simple primoconid (nomenclature following Made, 1996), triangular to crescentiform in shape. The paraconid is the most selenodont cuspid of the tooth, and bears a strong endocristid. Although the protoconid and the metaconid are in an early stage of wear, their dentine islands are already totally fused medially. In occlusal view, they display the trilobate shape characteristic of hippopotamid molars, although it is not strongly expressed here. The wear pattern of the largest cuspid, the hypoconid, is clearly trilobate. On the contrary, the smaller entoconid appears bucco-lingually compressed and simple in shape, lacking mesial and distal lobes.

KNM-NK 41353 is a set of three teeth that most probably belonged to the same individual given their proximity on the outcrop and similar degrees of wear. The first tooth (Figure 1B) is an unworn right P1 lacking its roots. Its general shape is triangular in lateral views. In occlusal view (not shown), it is mesio-distally elongated with a transverse constriction. A low and thin cingulum appears on each side of the tooth, being slightly thicker mesially. The main cusp is asymmetrical in lateral view, the apex being mesially positioned. On the mesial side of the main cusp, a finely crenulated mesial crest links the apex to the

cingulum and flares lingually. Its distal counterpart runs straight between the apex and a small accessory cuspule positioned at mid-height of the crown, then divides into two roughly crenulated crests that delimit a distal triangular area of heavily pustulate enamel. Other parts of the crown enamel are only wrinkled.

The second tooth is a slightly worn left D2 (Figure 1C) that retains most of its distal and mesial roots. Its general shape is similar to that of the P1. However, while it is still proportionally elongated, the crown is proportionally wider and shorter. In occlusal view (not shown), this tooth is also divided in two lobes (the distal one being wider) separated by a transverse constriction. A cingulum is present on each side, but it is reduced to a simple thin strip of enamel lingually. The distal cingulum is the most developed, while the others (mesial and buccal) are intermediate in thickness. The main cusp is less asymmetrical and more robust than on the P1. Its mesial crest is marked apically, but divides just above mid-height of the crown into a smooth and robust lingual crest almost similar to an accessory cuspule, and in a buccal crenulated crest that runs disto-lingually along the buccal side of the crown and joins the top of the buccal cingulum at the level of maximal tooth constriction. The lower part of the mesial crown exhibits ridged to pustulate enamel, in opposition to the wrinkled to smooth enamel of the rest of the crown. The distal crest gives rise to short crests just above the cingulum. On its buccal flange, the crown is slightly concave and limited at its base by an inflated portion of the distal cingulum. A conical accessory cuspule is positioned distolingually at mid-height of the crown.

KNM-NK 36503 is the distal portion of a p4 in an advanced stage of wear. The distal cingulum is stronger than in the aforementioned premolars. However, the lateral cingula are very attenuated. Two conical accessory cuspids of unequal sizes are inserted between the distal cingulum and the main cuspid. The enamel of the tooth is smoother than is that of KNM-NK 41353.

KNM-NK 41147 is a fragmentary m1. Both mesial and distal sides are missing. The tooth is heavily worn and cuspid morphology cannot be recognized. However, it shows the presence of lateral cingula, more developed on one side. On the opposite side, the transverse valley bears a strong transverse crest. The enamel appears rather smooth and the cingula are not crenulated.

The third tooth of specimen KNM-NK 41353 is the unworn crown of a right M1 that lacks most of its buccal cervix area. The tooth appears low-crowned and subquadrangular in occlusal view (Figure 1D). Cingula are present and form a continuous low circle around the crown. However, the mesial cingulum and the buccal part of the distal cingulum are much more developed, especially in height. The protocone and metaconule are similar in shape, exhibiting an occlusal trilobate pattern with a bulging lingual lobe. The paracone is more triangular with poorly individualized mesial and distal lobes. It exhibits a small apico-basal crest on its lingual aspect similar to an endocrista. The metacone is more complex in shape, with a general trilobate pattern altered by a well-developed endocrista. No accessory cusps are visible, and the enamel is finely wrinkled, including that of the cingula.

Discussion and Conclusion

All of these specimens were collected in the early years of work at this site (1995 and 1999; Ambrose, Kyule, and Hlusko, 2007), and therefore exact stratigraphic data are unknown. However, the nature of the preservation on many of these specimens suggests that they derive from the lowest fossiliferous horizon at Lemudong'o (L. Hlusko, personal communication), which is

a coarse gritty sand (Ambrose, Kyule, and Hlusko, 2007; Ambrose, Nyamai, et al., 2007). The minimum number of hippopotamid individuals collected in this sand is at least two. In the material described above, given its wear stage, the d4 KNM-NK 41354 could belong to the same individual as the dental series KNM-NK 41353. The m1 KNM-NK 41147 shows a more advanced juvenile stage. On the contrary, the distal part of p4 KNM-NK 36503 is already well worn, some dentine appearing even on the distal cingulum. This tooth corresponds to a fully adult specimen clearly distinct from the one represented by the d4. The anatomical attributions of the other remains do not bring more information in this regard.

Cranio-mandibular features traditionally played a major role in the study and identification of fossil Hippopotamidae, and in the reconstruction of their phylogenetic relationships (Coryndon, 1977; Gèze, 1980). More recent accounts on taxonomy and phylogeny of the family (Weston, 2003; Boisserie, 2005) also emphasized the importance of those characters, notably of key regions like the mandibular symphysis. In contrast, dentition, and particularly cheek teeth, are considered less informative: "It is unfortunate that, as far as hippopotamids are concerned, molar teeth are very conservative in development and are possibly the least useful element for diagnosis, slight variation in enamel pattern often reflecting slight differences in feeding habits rather than morphogenetic characters" (Coryndon, 1977, p. 63). Whether or not hippopotamid cheek teeth vary accordingly to diet is still to be determined, but variation is found in most mammalian species known by a sufficiently large tooth sample.

In this regard, it is not surprising that the above description of material from Lemudong'o generally matches that of teeth from other African Mio-Pliocene hippopotamids. Most of the morphology can be found in the variation ranges of the two best known late Miocene hippopotamids: 1) *Archaeopotamus harvardi* from Lothagam, Kenya, described in detail by Weston (2003) and previously named *Hexaprotodon harvardi* (new classification following Boisserie, 2005); and, 2) *Hexaprotodon garyam* from Toros-Ménalla, Chad (Vignaud et al., 2002; Boisserie et al., 2005). The d4 KNM-NK 41354 differs from that of KNM-LT 1 (*A. harvardi*, Lothagam) only by the somewhat more developed cuspid distal lobes, whereas the same general cuspid pattern is observed in the worst preserved remains from Toros-Ménalla.

As for Lemudong'o lower premolars, multiple distal crests, cingula surrounding the crown but stronger distally in p3, locally pustulate enamel, and the possible presence of a lingual accessory cusp are features seen in *A. harvardi* and *Hex. garyam*. For the p4, the distal morphology observed in KNM-NK 36503 is similar to what is seen for *A. harvardi* KNM-LT23908 (Weston, 2003, fig. 10.18, p. 392) and *Hex. garyam* TM069-98-001. For m1, invagination of the cingulum between mesial and distal cusps forming a strong transverse crest and cingula on the lateral faces of the lower molars may occur in both species, although lateral cingula tend to be attenuated in *Hex. garyam*. Finally, the M1 morphology also agrees with that of both species, including the often simpler shape of metaconules and paracones (Weston, 2003), the latter case being found in KNM-NK 41353. This specimen exhibits a marked difference from the equivalent teeth of *A. harvardi* and *Hex. garyam* in that its metacone bears a well-developed endocrista. According to personal observations, the most similar structure in *A. harvardi* and *Hex. garyam* is a poorly developed lingual ridge that may occur on the M1 metacone. Measurements show that the Lemudong'o P1 and M1 fall in the

Table 1. Cheek-tooth measurement ranges of late Miocene hippopotamid remains from Lemudong'o, Kenya, compared to various hippopotamids. Abbreviations used: NK = Hippopotamidae indeterminate (Lemudong'o); KEN = *Kenyapotamus coryndoni* (Ngeringerowa and Nakali, Kenya) (data from Pickford, 1983); LT = *Archaeopotamus harvardi* (Lothagam, Kenya) (data partially from Weston, 2003); LUK = Hippopotamidae indet. (Lukeino, Kenya) (data from Coryndon, 1978); WRi = *Hexaprotodon ? imagunculus* (Western Rift, Uganda) (data from Faure, 1994); WRk = *Hippopotamus kaisensis* (Western Rift, Uganda) (data from Pavlakis, 1987); A-A = Hippopotamidae indeterminate (Adu-Asa Formation, Ethiopia); ABU = *Archaeopotamus* aff. *lothagamensis* (Abu Dhabi, United Arab Emirates) (data from Gentry, 1999); TM, *Hexaprodoton garyam* "TM" (Toros-Ménalla, Chad). Bracketed numbers are estimated. Measurements are rounded to the nearest mm.

		NK	KEN	LT	LUK	WRi	WRk	A-A	ABU	TM
d4	n	1		4					1	1
	L	56		44–53					44	49
	w	26		21–26						27
P1	n	1	1	4				1		5
	L	27	16	26–28				26		23–28
	w	21	11	17–23				19		19–23
D2	n	1								
	L	32								
	wd	19								
M1	n	1	1	13	1	3	2	1		21
	L	46	25	31–46	45	27–32	36–40	40		36–49
	wm	(40)	24	32–46	42	27–30	27	30		31–43

same general range of size as *A. harvardi* and *Hex. garyam* (Table 1).

The morphology of the teeth from Lemudong'o does not exclude with certainty an attribution to any of the following late Miocene to early Pliocene hippopotamids: *A. lothagamensis* (Weston, 2000) from Lothagam, Kenya; *A.* aff. *lothagamensis* from Abu Dhabi, United Arab Emirates (Gentry, 1999); the specimens from Lukeino and Mpesida (Kenya) described by Coryndon (1978); the specimens collected in the Adu-Asa Formation, Middle Awash, Ethiopia (Boisserie and Haile-Selassie, in prep.); aff. *Hip. dulu* (Boisserie, 2004) from the Sagantole Formation, Middle Awash, Ethiopia; *Hex. ? imagunculus* (Hopwood, 1926); or, *Saotherium* cf. *mingoz* (Boisserie, 2003) from Kossom Bougoudi, Chad. However, it must be noted that the author has not found a developed endocrista similar to that of M1 KNM-NK 41353 in any of these taxa.

However, linear measurements of the Lemudong'o M1 KNM-NK 41353 clearly exceed the range of variation for the small-sized *Hex. ? imagunculus* (Table 1). Additionally, two other possible attributions can be ruled out with some certainty: those to the genera *Kenyapotamus* and *Hippopotamus*. The teeth of the middle to late Miocene *Kenyapotamus* exhibit a simpler, less trilobate wear molar pattern (Pickford, 1983) and are significantly smaller than those of Lemudong'o (Table 1). The latter differ also from the teeth of *Hippopotamus* by their low cuspids and cingula as well as by their wear pattern being more triangular-trilobate rather than trefoliate. The earliest member of this genus is *Hip. kaisensis*, mostly known from Western Rift sites in Uganda (Cooke and Coryndon, 1970; Pavlakis, 1990; Faure, 1994) where it may occur as early as 5.0 Ma (Faure, 1994). Its tooth dimensions are slightly larger than those of Lemudong'o teeth (Table 1).

To conclude, without further material from Lemudong'o, the present evidence does not support a more precise attribution of those hippopotamid remains than to an indeterminate early member of the subfamily Hippopotaminae. However, the dental peculiarities observed in this material (developed endocrista on M1 metacone) may indicate a distinct hippopotamid. It would be particularly interesting to recover more material from this area

and time period, given the lack of knowledge of the early history of African Hippopotaminae south of the Equator.

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