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NEW LATE MIOCENE ELEPHANTOID (MAMMALIA: PROBOSCIDEA) FOSSILS FROM LEMUDONG'O, KENYA

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ABSTRACT

The late Miocene marked a time of significant geographic dispersal and radiation for many mammalian taxa within Africa, including the proboscidean lineages. The ~6.1 Ma site of Lemudong'o, Kenya, yielded two elephantoid specimens. The first is a mandibular fragment with the third molar. This specimen represents a primitive member of the *Anancus kenyensis* lineage, with similarities to a specimen from Lukeino, another late Miocene site in Kenya. The second specimen is a shattered isolated mandibular molar with associated fragments of a second tooth. Although this second specimen is fragmentary, it may represent a new elephantid taxon as it has a combination of unique crown and root characters that do not align it with any currently known taxa.

Introduction

During the late Miocene, the proboscidean lineages experienced great morphological and adaptive changes that preceded their vast radiation during the glacial and inter-glacial climatic cycles of the Pleistocene. Africa is considered the continent where elephants originated and where the basic features of the three major genera of elephants, *Loxodonta*, *Elephas*, and *Mammuthus*, evolved. Two lines of evidence support this. First, the most primitive form of elephants, *Stegotetrabelodon* (Maglio, 1973; Tassy, 1986; Kalb and Mebrate, 1993) is found in Africa (Maglio, 1973; Beden, 1985; Tassy, 1986; Kalb et al., 1996), the adjacent Arabian Peninsula (Tassy, 1999), and southern Italy (Ferretti, 2003). Second, the most primitive species of the three major genera of elephants, *Loxodonta*, *Elephas*, and *Mammuthus*, are only known in Africa (Aguirre, 1969; Maglio, 1973; Beden, 1983, 1985, and 1987). Fossils of late Miocene proboscideans, especially those from Africa, are therefore critical to the understanding of all subsequent proboscidean evolutionary events, including the origins of the extant elephants.

Our current understanding of late Miocene Proboscidean evolution is limited due to a paucity of fossil sites and scarce and fragmentary remains. The sites of Lemudong'o Localities 1 and 2 have yielded important elephantoid specimens that date by $^{40}\text{Ar}/^{39}\text{Ar}$ single crystal laser fusion to ~6.1 Ma (Ambrose et al., 2003; Ambrose, Hlusko, and Kyule, 2007; Ambrose, Nyamai, et al., 2007; Deino and Ambrose, 2007). Like most other penecontemporaneous sites, proboscidean fossils are also poorly represented in the

Lemudong'o fauna, comprising only the two specimens described below. However, these two specimens, especially that of the elephantid, provide us with precious information about the relatively unknown late Miocene proboscideans of eastern Africa.

The previously known late Miocene proboscidean African fossils have been described from: Sahabi, Libya (Petrocchi, 1954; Gaziry, 1987); Ukondo, Uganda (Tassy, 1995); Mpesida, Kenya (Maglio, 1973; Tassy, 1986; Sanders, 1999); Lukeino, Kenya (Maglio, 1973; Tassy, 1986); Lothagam, Kenya (Maglio, 1973; Tassy, 2003); the Middle Awash, Ethiopia (Kalb and Mebrate, 1993); Manonga Valley, Tanzania (Sanders, 1997); and Toros-Menalla, Chad (Vignaud, et al., 2002). Except for recently collected samples from the Middle Awash, Ethiopia and Toros-Menalla, Chad, most of the assemblages from these localities are composed of only a handful of specimens. Because of this paucity of specimens, basic dental features such as the presence of lower tusk (*Primelephas*: Maglio, 1973; Tassy, 2003) or fourth premolar (*Anancus kenyensis*: Tassy, 1986) are still a matter of debate. The new species of primitive elephants from Ukonodo, Uganda (Tassy, 1995) and Lothagam, Kenya (Tassy, 2003) suggest that the early radiation of elephants was a rather complicated process that is currently known only from very small samples.

Terminology

In the description of the gomphothere from Lemudong'o we employ the dental terminology used by Tassy (1986, 1996) and Metz-Muller (1995). However, these authors' definitions differ for

one feature. In the lower molars of *Anancus*, the anterior pretrite central conule is much reduced and fused with the mesoconelet of the same half-lophid (Tassy, 1986, p. 87 and 94, fig. 3 of pl. XIII). This fusion results in the formation of a cusp being located mesio-axially to the main cusp and more or less rudimentary. This cusp contacts both the posterior pretrite central conule of the preceding lophid and the posttrite mesoconelet of the same lophid. Tassy (1986) calls this feature neither a mesoconelet nor an anterior pretrite central conule, but rather just the "anterior tubercle," because of the amalgamate nature of the cusp. On the other hand, Metz-Muller (1995) called the same tubercle of *Anancus arvernensis* a mesoconelet, although it can also be an amalgam of the mesoconelet and the central conule. We find that this amalgam is always single and not subdivided. Therefore, we follow the terminology of Metz-Muller (1995) and call this amalgam a "mesoconelet," irrespective of its relative position to the main cusp.

We find that the current anatomical terminology does not suffice to describe molar morphological variation adequately, and we introduce several new terms here. A full account of this new nomenclatural system will appear elsewhere, but the terms relevant for the mandibular molars are briefly introduced here. The root system of the proboscidean molars has been only briefly described and discussed previously (e.g., Anthony and Friant, 1941), except for Sher and Garutt (1987). Their description of the general feature of the root of the elephants molar is obviously based on what can be seen in highly derived elephants, *Mammuthus*, and thus what is described in their paper cannot be directly applicable to the molars of early elephants, stegodons and gomphotheres. The following is a generalization of the molar root of Elephantoida.

For the mandibular molars of Elephantoida, the root has three components: the mesial, intermediate, and distal roots. The mesial root (= main anterior root of Sher and Garutt, 1987) supports the anterior cingulum and first lophid, but as shown below, the second lophid is also supported by it in elephants and stegodons. The rest of the crown is supported by the distal root (= middle and posterior segment of Sher and Garutt, 1987), although frequently its mesio-lingual margin is separated from the rest of the root and forms a smaller intermediate root. The apical half of the distal root is frequently subdivided into numerous apices. These apices may be erroneously perceived as separate roots rather than as parts of a single distal root.

Abbreviations and Metrics

KNM	National Museum of Kenya, Nairobi.
NK	Fossils from the Narok District, Kenya.
L	Greatest distance between the mesial and distal ends of the crown.
h	Height of the lophids.
H	Greatest height of the molar.
w	Distance between the buccal and lingual ends of the lophid.
W	Greatest width of the molar.
e	Thickness of the enamel measured at the wear surface or broken surface of the crown.
LF (lamellar frequency)	The lamellar frequency is calculated following the method described in Maglio (1973).
m	Mandibular molar.
ccprp	Posterior pretrite central conule.

All measurements were made by L. H. from the original specimens and casts.

Systematic Paleontology

PROBOSCIDEA Illiger, 1811

ELEPHANTOIDEA Gray, 1821

GOMPHOTHERIIDAE Hay, 1922

ANANCUS Aymard in Dorlhac, 1855

ANANCUS KENYENSIS (MacInnes, 1942)

Figures 1–2

Referred material

KNM-NK 41502, fragment of left hemi-mandible with lower m3 and distal root of m2.

Description

All dental measurements of KNM-NK 41502 are given in Table 1.

KNM-NK 41502 is a left hemi-mandible with m3 crown and distal root of m2. The hemi-mandible lacks the mandibular condyle, much of the coronoid process, distal margin of the mandibular angle, anterior one-third of the horizontal ramus, and the mandibular symphysis. The mandibular corpus is robust and its ventral border curves distinctly ventrally, as is usual in *Anancus*. The mandibular angle is damaged but the remaining morphology suggests that it was flat medio-laterally and located slightly high at the distal end of the corpus mandibulae. Although KNM-NK 41502 lacks its symphysis, features of the ventral border of the corpus and mandibular angle perhaps suggest a brevirostrine condition for the mandible. The mandibular foramen is relatively small and located about the halfway between the condyle and the distal end of the third lower molar. The mylohyoid groove is clearly visible and runs from the mandibular foramen (foramen mandibulae) anteroinferiorly.

The third molar is preserved intact and erupting from the jaw such that the distal third of the crown is partially hidden in the crypt. It has a mesial cingulum, five lophids, and a postcingulum. Thus the lophid formula of the molar can be expressed as X5X. The molars are at an early wear stage with dentine exposed only at the mesial cingulum and pretrite half of the first lophid. The lophids are not closely packed together and the crown tapers distally.

The main cusps and mesoconelets of the first and second lophids are set in a line running slightly oblique to the mesiodistal axis of the molar, except for the mesoconelet of the second pretrite half-lophid, which is slightly displaced mesially. On the third and fourth lophids, however, the posterior central conule of the pretrites are slightly displaced distally, and they shallowly mesh with the mesoconules of the posttrite half-lophids making a weak zigzag pattern along the median axis of the molar. Thus, only the distal half of the molar shows faint anancoidy.

The first to fourth posttrite half-lophids are each composed of a main cusp and a lower and smaller mesoconelet. The mesoconelet of the first posttrite half-lophid is only slightly smaller than the corresponding main cusp in occlusal view. However, the mesoconelets are smaller on the more posterior lophid, and at the fourth lophid, the mesoconelet is about one fifth of the accompanying main cusp in occlusal view. Nevertheless, the mesoconelets of the posttrite half-lophids are always larger than those of the pretrite of the same lophid. On the first and the second pretrite half-lophids, the mesoconelets are about

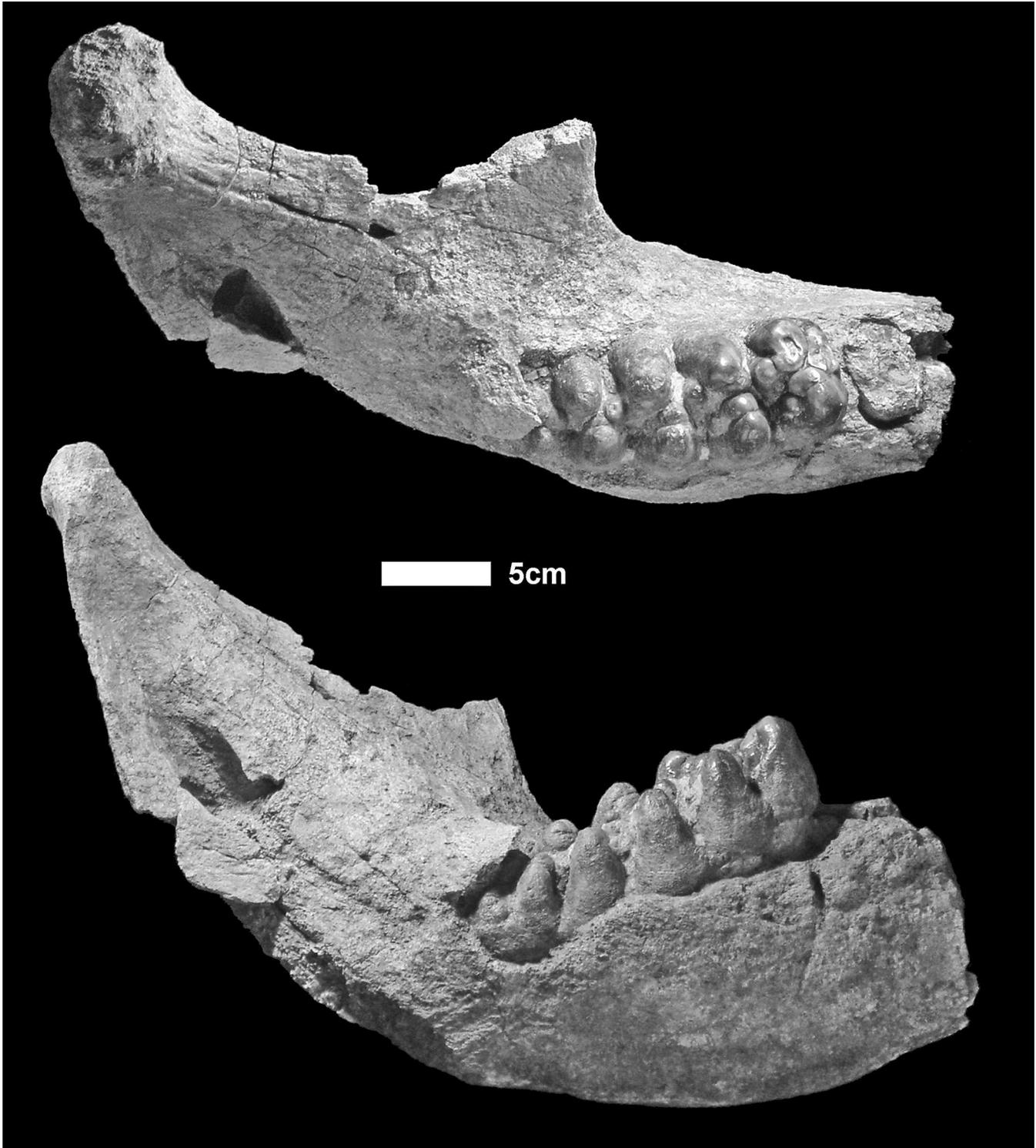


Figure 1. *Anancus kenyensis*, KNM-NK 41502, left hemi-mandible with m3. Top: occlusal view, anterior is to the right, and lingual is to the bottom of page. Bottom: lingual view, anterior is to the right of the page.

the one third of the main cusps in occlusal view and are separated from the latter by a distinct groove, while those of the third and fourth pretrite half-lophids are very small, flat transversally, and separated from the much larger main cusp by a faint groove. The fifth lophid is composed of a pair of pre- and posttrite main cusps

only. It is followed by the postcingulum consisting only of a single large tubercle.

On the distal face of the first to fourth pretrite half-lophids, there are large and distinct central conules (ccprp1–4). They are reduced slightly on the more distal lophids. The ccprp are clearly

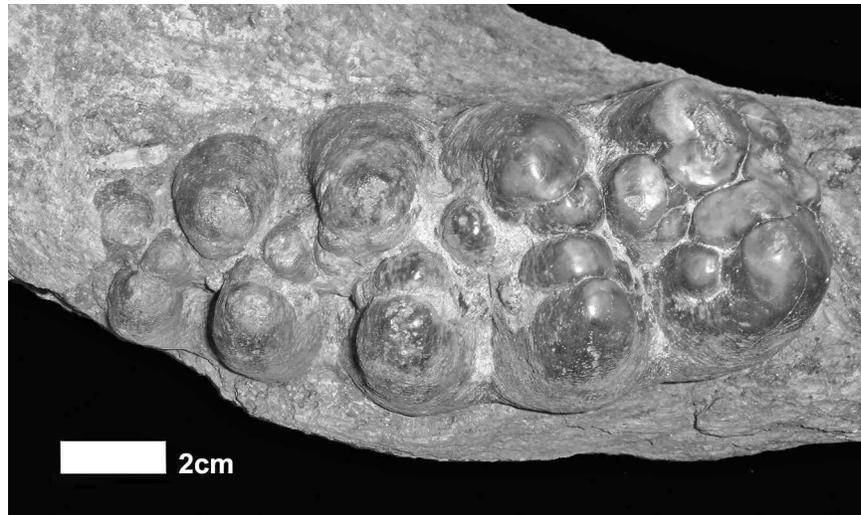


Figure 2. *Anancus kenyensis*, KNM-NK 41502, left m3. Closeup occlusal view, anterior is to the right, and lingual is to the bottom of the page.

detached from the main cusps and mesoconelets, but they are connected with the mesoconelet on first lophid and the main cusp on the second to fourth lophids by strong protuberances or blunt ridges on the distal side.

Posterior posttrite central conules are present on the distal flank of the first to third posttrite half-lophids. The conule on the first lophid is fairly distinct with its apex superficially subdivided. Those conules on the second and third lophids are subtle swellings on the middle height of the distal face of the half-lophids. There is no anterior central conule on either side of the lophids.

Thin cement remains in the bottom of the inter-lophid valleys. Judging from the rugged condition, the present surface of the cement does not represent the original wear surface. However, the enamel surface of the valley is polished for about two thirds of its depth, suggesting that the cement cover was removed by wear at least to that degree during the life of the animal.

Only the distal root of the second molar is preserved in the alveolus.

Discussion

KNM-NK 41502 represents a member of the genus *Anancus* because the anterior pretrite central conule is degenerated and

merged with the mesoconelet, and the distal displacement of the pretrite main cusp is more or less accentuated, as diagnosed by Tassy (1986, p. 87).

According to Tassy (1986), there are two morphotypes within *Anancus*: primitive *kenyensis* and derived *petrocchii* morphs. The former and the latter are represented respectively by the type specimen of *A. kenyensis* from Kanam, Uganda originally described by MacInnes (1942) and the *Anancus* sample from Sahabi, Libya described by Petrocchi (1954). The *petrocchii* morph is distinguished from *kenyensis* morph by the derived traits of molars and is thought to represent an evolutionary level of *Anancus kenyensis*. Although both morphs were treated as two evolutionary levels of *A. kenyensis* by Tassy (1986), he did not define them as distinct taxonomic units or evolutionary levels of a species because of the presence of an intermediate morphotype. KNM-NK 41502 is also somewhat intermediate between these two morphs because it has incipient posterior posttrite central conules on the second and third lophids, which is a derived feature shared by the *petrocchii* morph.

Despite this one derived feature, we attribute KNM-NK 41502 to the *kenyensis* morphotype within *Anancus* because it has a smaller dimension of the cheek teeth relative to that of *Anancus arvernesis*, has weak or no anancoidy, and has development of cement in the interlophids (following Tassy, 1986).

Table 1. Dental Measurements (in mm) of elephantoid specimens from Lemudong'o.

KNM-NK 41502 (m2)						
L	W	H	LF	e		
168	69.4	45.7	3.2	7.25		
lophids	1st	2nd	3rd	4th	5th	6th
w	60	66.7	69.4	–	–	–
h	45.7	45.4	44.7	–	–	–
KNM-NK 42396 (m3)						
L	W	H	LF	e		
163	95.7	57.1	3.5	–		
lophids	1st	2nd	3rd	4th		
w	89.7+	90.3	92.5	95.7		
h	–	–	57.1	–		

Kalb and Mebrate (1993) divided sub-Saharan *Anancus* into four successive taxonomic units, *Anancus kenyensis*, *Anancus* sp. (Lagebaanweg type), *Anancus petrocchii*, and *Anancus* sp. (Sagantole type), mostly based on the specimens from the Middle Awash, Ethiopia. They then used them in a cladistic analysis of elephantoids, but did not give these units formal scientific names or definite morphological diagnoses (Kalb and Mebrate, 1993).

Kalb and Froehlich (1995) and Kalb et al. (1996) compared their *Anancus* “*kenyensis*” from the Middle Awash with Tassy’s “*kenyensis* morph,” but they did not address the relationship between “*petrocchii* morph” of Tassy (1986) and their *Anancus* sp. (Lagebaanweg type), *Anancus petrocchii*, and *Anancus* sp. (Sagantole type). Recently, Tassy (2003) added the new samples from Lothagam to his morph *kenyensis* and *petrocchii*, but he did not review the four taxonomic units of *Anancus* proposed by Kalb and Mebrate (1993), Kalb and Froehlich (1995), and Kalb et al. (1996).

Although these analyses are incomplete because they do not consider the entirety of the available fossil evidence, they do suggest that there is an evolutionary trend within the African *Anancus* towards greater complexity of the crown pattern over time. At this time though, there is not enough evidence with which to define new species or subspecies within this evolving lineage. Unfortunately, this new specimen from Lemudong’o does not resolve the current situation, but rather bolsters the need for a new analysis investigating the relative frequency of morphological variation within this growing late Miocene fossil assemblage.

As noted by Tassy (2003), some derived traits, for instance pentalophodonty, are not always associated with other derived features, such as supplementary accessory cusps. Anancoidy, number of loph(id)s, supplementary cusps, and cementodonty, are the morphological traits that have been used in the characterization of morphological types or informal taxonomic units in previous studies. However, new fossil finds are showing that they do not appear to evolve in a coordinated manner. Derived and primitive features can be combined almost at random in any given collection, as is seen in the new sample from the Late Miocene of the Middle Awash (personal observations of H. S. and Y. Haile-Selassie). No morphological feature can be found universally in all populations.

KNM-NK 41502 is characterized by the lowest level of the development of anancoidy among the East African *Anancus*, which differentiates it from the late Miocene specimens from the Middle Awash. Of the previously described anancine m3’s from eastern Africa, the Lemudong’o specimen is most similar to that from Lukeino (KNM-LU 57). The pretrite main cusp of the second lophid of the Lemudong’o specimen appears to be located more mesially than that of KNM-LU 57. However, this difference in appearance could be explained by the difference in the degree of the wear rather than an actual difference of the position of the cusps; because the distal wall of the main cusp slopes more gently than the mesial one does, the worn figure of the cusp extends more distally than mesially, and this gives the impression that the center of the worn cusp is located more distally than that of the un-worn cusp. The extent of the dislocation of the 3rd and 4th pretrite half-lophids of KNM-NK 41502 is comparable to that of KNM-LU 57 figured in Tassy, Plate XIII, fig. 4, and is not as marked as those of the “*petrocchii* morph.” The size and arrangement of the cusps and conules of these lophids are fairly similar to that of KNM-LU 57, except for the rudimentary size of the pretrite mesoconelets. Strong degeneration of the pretrite mesoconelet may be a derived feature of *Anancus*, as it is

frequently observed on lower molar of species in this genus. On the other hand, in *Tetralophodon longirostris* from *Dinotherium* sands, the pretrite mesoconelet and ccprp are basically the same size; the pretrite mesoconelet is never degenerated and only in few cases it is smaller than the ccprp (Saegusa, unpublished observation). KNM-NK 41502 is slightly more derived in having incipient posterior posttrite central conules on the second and third lophids, but such a subtle difference could result from mere individual variation seen in the same taxon.

Because of these similarities, we place the *Anancus* from Lemudong’o in the most primitive evolutionary level of *A. kenyensis*, together with that from Lukeino. The current evidence suggests that KNM-NK 41502 is older and more primitive than the *Anancus* from the Middle Awash (personal observations of H. S. and Haile-Selassie), which is dated ca. 5.6 Ma, although this relationship is clearly tentative since it is based on only a single specimen from Narok.

ELEPHANTIDAE Gray, 1821

Genus and species indeterminate

Figure 3

Referred Material

KNM-NK 42396, right lower second molar and fragments of an associated tooth.

Description and remarks

At the first glance, KNM-NK 42396 looks like an upper intermediate molar because of its mesiodistally shortened crown proportions. However, the following four features of KNM-NK 42396 indicate that the molar is a lower one:

- 1) *The structure of the root.* On the convex side of KNM-NK 42396, the mesial two lophids are supported by a mesial root (= anterior root of Sher and Garutt, 1985), while the rest of the lophids are supported by a distal root (= the middle and posterior segment of Sher and Garutt, 1985). The relationship between the roots and the lophids observed at the convex side of KNM-NK 42396 is precisely like that of early elephants and stegodons, in which the mesial root supports the mesial two lophids at the lingual side (= convex side) (Saegusa et al., 2005; the holotype of *E. nawatensis* described by Tassy, 2003). In contrast, the mesial root supports the first lophid only at the buccal side (= convex side) of the upper molars of stegodons and early elephants.
- 2) *The angle of the eruption of the molar.* In KNM-NK 42396, the wear surface develops on the first lophid only, and the molar is still at its early stage of wear. At the same time, the angle of the eruption is fairly low, judging from the angle between the wearing surface of the first lophid and the cervical line. The low angle of eruption at such an early stage of molar wear is consistent with identification as a lower molar rather than that of an upper molar.
- 3) *No divergence of lophids in lateral view.* Lophids of upper intermediate molars of early elephants and stegodons diverge markedly in lingual and buccal view (e.g., KNM-LT 358, figured in Maglio and Ricca, 1978, pl. 2). In KNM-NK 42396, the lophids run parallel to each other in lingual and buccal view rather than diverge.
- 4) *Strong buccal curvature and twist of the molar crown.* The extent of the curvature and S-twist of the crown of KNM-NK 42396 is comparable to that of lower intermediate

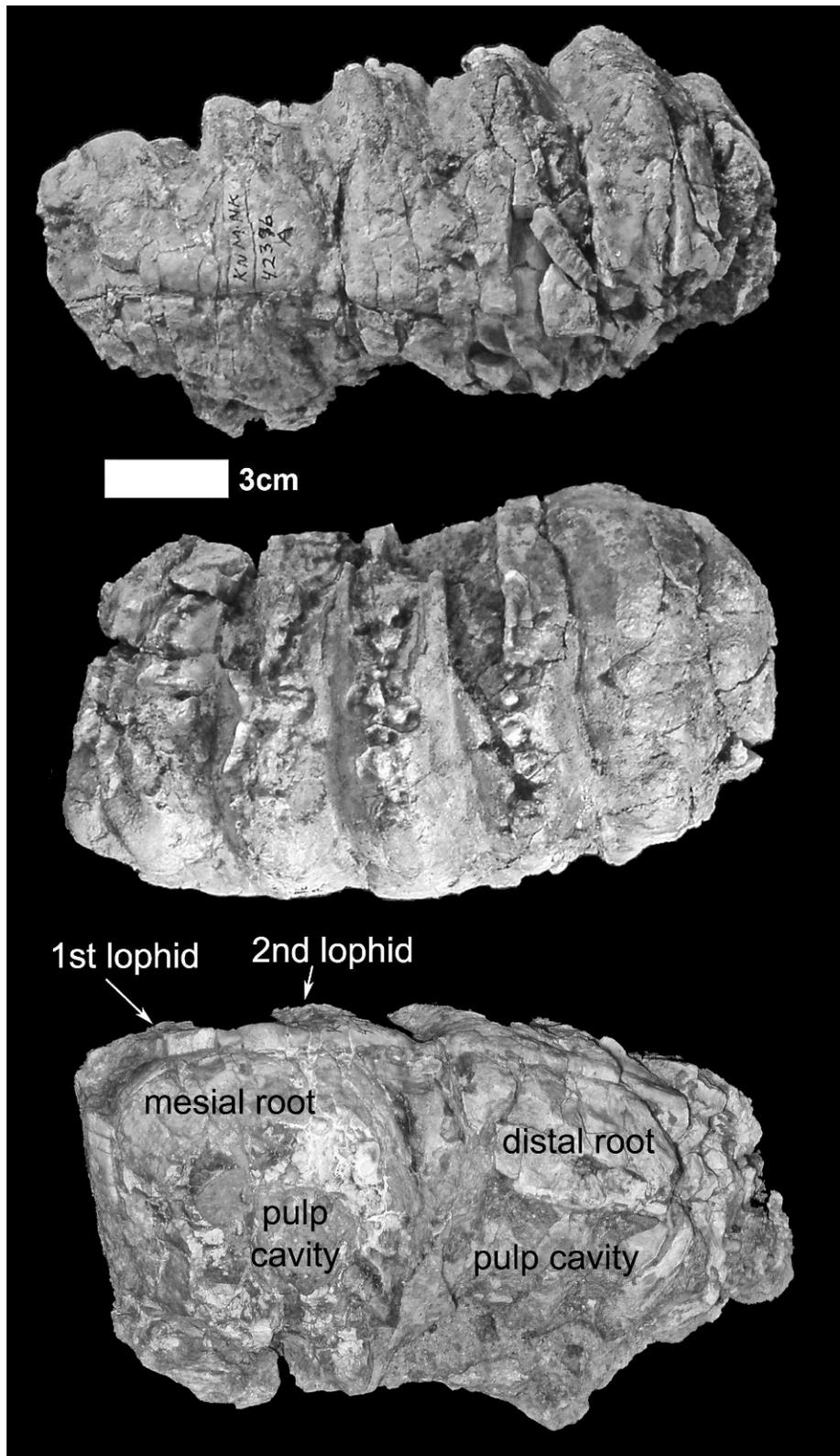


Figure 3. Elephantidae gen. and sp. indet., KNM-NK 42396, right m2. Top: lingual view, mesial is to the left of the page. Middle: occlusal view, mesial is to the left, and the buccal is to the top of the page. Bottom: apical view, mesial is to the left, and the lingual is to the top of the page.

molars of early elephants and stegodons rather than that of the upper intermediate molars of these taxa.

Besides the ratio of length to width of the molar, the only marked feature that contradicts the above identification of KNM-NK 42396 as a lower molar is the development of the mesial cingulum at the mesio-lingual corner of the molar. As has been suggested by Tassy (1994, p. 86), antero-lingual cingulum is reduced in Elephantoida and this feature can be considered as a synapomorphy of this group. Although most primitive elephants and stegodons follow this rule, in some lower molars of these taxa the antero-lingual cingulum is only slightly thinner than the buccal one (e.g., Coll. Dub. No. 2231 figured in Hooijer, 1955, pl. 3). In such cases, the thickness of the mesial cingulum cannot be used for the distinction of the upper and lower molars unless the both sides of the cingulum are fully preserved. In KNM-NK 42396, the thickness of the buccal half of the anterior cingulum cannot be reliably estimated because of the postmortem distortion.

This molar has five fully developed lophids and a postcingulum. Although it is quite damaged, there is a lingual part to the mesial cingulum as well. Thus, the lophid formula of the molar can be expressed as X5X. The lophids and cingula are packed tightly. The crown is twisted to the extent that the last lophid is rotated lingually about 15 degrees relative to the first lophid. The mesial three lophids are straight transversally, while the distal two lophids are slightly convex-convex shaped. The last lophid and postcingulum are nearly covered up with the cement. On the mesial four lophids, the enamel surface can be seen on the lateral faces and their apices.

The basal part of the mesial root is also preserved. This mesial root supports the first and second lophids, while the distal root is totally damaged such that the pulp cavity of the third to postcingulum is widely exposed. The root of the molar shows the derived condition shared by elephants and stegodons.

Most of the apex and the buccal wall of the first to third lophids are damaged. The lingual wall along the cervix of the last two lophids is also damaged. Because of the damage, it is not clear how many mammillae were present on each lophid but it appears that there were no less than five mammillae on each lophid. Where the lophids are exposed above the worn cement surface, it is evident that the apical ends of at least the second and third lophids are mesio-distally compressed. The groove separating the mammillae appears to be very shallow and restricted to the upper part of the lophids, judging from the smoothness of the exposed surface of the upper part of the second lophid. The enamel folding also appears to be very weak or absent. At the distolingual face of the first and the second lophids there are small median columns which are compressed to the main body of the lophids. Presence or absence of the central conule on the more distal lophids cannot be determined because of the thick cement cover. Overall, the tooth is low crowned and pentalophodont with mesial and distal cingula.

The mesial root supports the first and second lophids, while the distal root supports the rest of the molar. The first and second lophids are worn. The fifth lophid is almost completely covered with cement, while only the lower one-third of the depth of the first valley is filled. Behind the first and second lophids, there are centrally located columns (posterior central conule), half embedded in the wall of the distal faces of the lophids.

The width of the crown does not increase markedly toward the rear part of the crown (Table 1).

Discussion

KNM-NK 42396 is a m2 of a primitive elephant, but it does not resemble any of the known m2's of *Stegotetralodon*, *Primelephas* or the Elephantidae gen. et sp. indeterminate from Lothagam. The molar is comparable to that of *Stegotetralodon orbus* in having only five lophids, but it differs in showing no posterior enlargement of the crown. KNM-NK 42396 is also different from the m2 of *Primelephas gomphotheroides* (KNM-LT 358) because it has only five lophids and a much transversally wider crown. It differs from the m2 of Elephantidae gen. et sp. indeterminate from Lothagam (KNM-LT 350) described by Tassy (2003) in that it has only five lophids, and lacks the marked distal widening of the crown. In KNM-NK 42396, the median pillar (distal central conule) is more compressed to the main body of the lophid than is seen in the m2 of *P. gomphotheroides*, *S. orbus* and Elephantidae gen. et sp. indet. from Lothagam. In this respect, KNM-NK 42396 is definitely derived relative to these other taxa.

The KNM-NK 42396 mesial root supports the first and second lophids. This is the same condition as is seen in the lower second molar of *Stegodon zdanskyi* from North China (unpublished data of H. S.) and *Primelephas gomphotheroides* (Maglio and Ricca, 1978), and is derived compared to that of the gomphotheres.

This unique combination of the derived root and primitive crown characters in KNM-NK 42396 suggests that it represents a previously unrecognized diversification of the early elephants, and precludes the allocation of this specimen to any known taxon of Elephantidae. However, it would be premature to establish a new taxon based on such a fragmentary lower molar. Pending further findings of primitive elephants from East Africa, the specimen is identified as Elephantidae gen. and sp. indeterminate.

Conclusions

KNM-NK 41502 can be allocated to the most primitive evolutionary level of the *A. kenyensis* lineage, together with specimens from Lukeino, Kenya. Although KNM-NK 42396 is identified as Elephantidae gen. and sp. indeterminate, it may represent a new primitive elephantid.

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References

- Aguirre, E. 1969. Evolutionary history of the elephant. *Science*, 164:1366–1376.
- Ambrose, S. H., L. J. Hlusko, and M. D. Kyule. 2007. History of paleontological research in the Narok District of Kenya. *Kirtlandia*, 56:1–37.

- Ambrose, S. H., L. J. Hlusko, D. Kyule, A. Deino, and M. Williams. 2003. Lemudong'o: a new 6ma paleontological site near Narok, Kenya Rift Valley. *Journal of Human Evolution*, 44:737–742.
- Ambrose, S. H., C. M. Nyamai, E. M. Mathu, and M. A. J. Williams. 2007. Geology, geochemistry, and stratigraphy of the Lemudong'o Formation, Kenya Rift Valley. *Kirtlandia*, 56:53–64.
- Anthony, R., and M. Friant. 1941. Introduction à la connaissance de la dentition des Proboscidiens. *Mémoire de la Société Géologique et Minéralogique de Bretagne*, 6:1–104.
- Beden, M. 1983. Family Elephantidae, p. 40–129. *In* J. M. Harris (ed.), *Koobi Fora Research Project, Volume 2*. Clarendon Press, Oxford.
- Beden, M. 1985. Les proboscidiens des grands gisements à hominidés Plio-Pléistocène d'Afrique Orientale. *In* L'Environnement des Hominidés au Plio-Pléistocène, Colloque international, Foundation Singer-Polignac, 21–44. Masson, Paris.
- Beden, M. 1987. Les Eléphantidés (Mammalia, Proboscidea), p. 1–162. *In* Y. Coppens and F. C. Howell (eds.), *Les faunes Plio-Pléistocène de la basse vallée de l'Omo (Ethiopie)*, Volume 2. Cahiers de Paléontologie, Travaux de Paléontologie Est-Africaine. Centre National de la Recherche Scientifique, Paris.
- Deino, A. L., and S. H. Ambrose. 2007. $^{40}\text{Ar}/^{39}\text{Ar}$ dating of the Lemudong'o late Miocene fossil assemblages, southern Kenya Rift. *Kirtlandia*, 56:65–71.
- Dorlhac, J. 1855. Notice géologique sur le cratère de Coupet et sur son gisement de gemmes et d'ossements fossiles. *Annales de la Société d'Agriculture, Sciences et Arts et commerce du Puy*; 19 (for 1854):497–517.
- Ferretti, M. P., L. Rook, and D. Torre. 2003. *Stegotrabelodon* (Proboscidea, Elephantidae) from the Late Miocene of Southern Italy. *Journal of Vertebrate Paleontology*, 23(3): 659–666.
- Gray, J. E. 1821. On the natural arrangements of vertebrate animals. *London Medical Repository*, 15(88): 296–310.
- Gaziry, A. W. 1987. Remains of Proboscidea from the early Pliocene of Sahabi, Libya. p. 183–203. *In* N. T. Boaz, A. El-Arnauti, A. W. Gaziry, J. de Heinzelin, and D. D. Boaz (eds.), *Neogene Paleontology and Geology of Sahabi*, A. R. Liss, New York.
- Hay, O. P. 1922. Further observations on some extinct elephants. *Proceedings of the Biological Society of Washington*, 35:97–101.
- Hooijer, D. A. 1955. Fossil Proboscidea from the Malay Archipelago and the Punjab. *Zoologische Verhandlungen*, 28:1–146.
- Illiger, C. D. 1811. *Prodromus systematis mammalium et avium additis terminis zoographicis utriusque classis*. Salfeld, Berlin, xviii + 301 p.
- Kalb, J. E., and A. Mebrate. 1993. Fossil elephantoids from the Hominid-bearing Awash Group, Middle Awash Valley, Afar depression, Ethiopia. *Transactions of the American Philosophical Society, New Series*, 83(1): 1–114.
- Kalb, J. E., and D. J. Froehlich. 1995. Interrelationships of Late Neogene elephantoids: new evidence from the Middle Awash Valley, Afar, Ethiopia. *Geobios*, 28(6): 727–736.
- Kalb, J. E., D. J. Froehlich, and G. L. Bell. 1996. Phylogeny of African and Eurasian Elephantidae of the late Neogene, p. 101–116. *In* J. Shoshani and P. Tassy (eds.), *The Proboscidea: Evolution and Palaeoecology of Elephants and Their Relatives*. Oxford University Press, Oxford.
- MacInnes, D. G. 1942. Miocene and Post-Miocene Proboscidea from East Africa. *Transactions of Zoological Society of London*, 25:33–106.
- Maglio, V. J. 1973. Origin and evolution of the Elephantidae. *Transactions of the American Philosophical Society, New Series*, 63(3):1–149.
- Maglio, V. J., and A. B. Ricca. 1978. Dental and skeletal morphology of the earliest elephants. *Verhandelingen der Koninklijke Nederlandse Akademie van Wetenschappen, Afdeling Natuurkunde, Eerste Reeks*, 29:1–51.
- Metz-Muller, F. 1995. Mise en évidence d'une variation intraspécifique des caractères dentaires chez *Anancus arvernensis* (Proboscidea, Mammalia) du gisement de Dorkovo (Pliocène ancien de Bulgarie, biozone MN14). *Geobios*, 28(6): 737–743.
- Petrocchi, C. 1954. I proboscidiati di Sahabi. *Rendiconti Accademia Nazionale dei XL*, ser. 4, 4/5:1–66.
- Saegusa, H., Y. Thasod, and B. Ratanasthien. 2005. Notes on Asian stegodontids. *Quaternary International*, 126–128:31–48.
- Sanders, W. J. 1997. Fossil Proboscidea from the Wembere-Manonga Formation, Manonga Valley, Tanzania, p. 265–310. *In* T. Harrison (ed.), *Neogene Paleontology of the Manonga Valley, Tanzania*. Topics in Geobiology, Number 14. Plenum Press, New York.
- Sanders, W. J. 1999. Oldest record of *Stegodon* (Mammalia: Proboscidea). *Journal of Vertebrate Paleontology*, 19(4): 793–797.
- Sher, A. V., and V. Ye Garutt. 1987. New data on the morphology of elephant molars. *Transactions Doklady of the USSR Academy of Sciences: Earth Science Sections*, 285(1–6): 195–199. (Translation from the Russian original, dated December 1985.)
- Tassy, P. 1986. Nouveaux Elephantoidea (Mammalia) dans le Miocène du Kenya. *Cahiers de paléontologie, Travaux de Paléontologie Est-Africaine*. Centre National de la Recherche Scientifique, Paris. 135 p.
- Tassy, P. 1994. Origin and differentiation of the Elephantiformes (Mammalia, Proboscidea). *Verhandlungen des Naturwissenschaftlichen Vereins in Hamburg. N. F.*, 34:73–94.
- Tassy, P. 1995. Les proboscidiens (Mammalia) fossiles du Rift Occidental, Ouganda, p. 217–257. *In* B. Senut and M. Pickford (eds.), *Geology and Palaeobiology of the Albertine Rift Valley, Uganda-Zaire*, Volume 2: Palaeobiology. CIFEG Publication Occasionelle, Numbre 29. Centre International pour la Formation et les Echanges Géologiques, Orléans.
- Tassy, P. 1996. Dental homologies and nomenclature in the Proboscidea, p. 21–25. *In* J. Shoshani and P. Tassy (eds.), *The Proboscidea: Evolution and Palaeoecology of Elephants and Their Relatives*. Oxford University Press, Oxford.
- Tassy, P. 1999. Miocene elephantids (Mammalia) from the Emirate of Abu Dhabi, United Arab Emirates: palaeobiogeographic implications, p. 209–233. *In* J. Whybrow and A. Hill (eds.), *Fossil Vertebrates of Arabia: Late Miocene Faunas, Geology, and Palaeoenvironments of the Emirate of Abu Dhabi, United Arab Emirates*. Yale University Press, New Haven and London.
- Tassy, P. 2003. Elephantoides from Lothagam, p. 331–358. *In* M. G. Leakey and J. M. Harris (eds.), *Lothagam: The Dawn of Humanity in Eastern Africa*. Columbia University Press, New York.
- Vignaud, P., P. Düringer, H. T. Mackaye, A. Likius, C. Blondel, J.-J. Boisserie, L. De Bonis, V. Eisenmann, M.-E. Etienne, D. Geraads, F. Guy, T. Lehmann, F. Lihoreau, N. Lopes-Martinez, C. Mourer-Chauvire, O. Otero, J.-C. Rage, M. Schuster, L. Viriot, A. Zazzo, and M. Brunet. 2002. Geology and palaeontology of the Upper Miocene Toros-Menalla hominid locality, Chad. *Nature*, 418:152–155.