NYANZACHOERUS SYRTICUS (ARTIODACTYLA, SUIDAE) FROM THE LATE MIOCENE OF LEMUDONG'O, KENYA

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ABSTRACT

Lemudong'o Locality 1 is a late Miocene mammalian-dominated fossil site in the Narok District of southern Kenya. Suidae specimens from this site are scarce and fragmentary, however the recovered specimens can be confidently assigned to *Nyanzachoerus syrticus* based on the size and morphology of the third molars and the relative size of the third and fourth premolars. This species designation indicates a late Miocene/early Pliocene biochronological age, which accords with $^{40}Ar/^{39}Ar$ determinations of ~6.11 Ma (Deino and Ambrose, 2007). These Lemudong'o specimens indicate that *N. syrticus* inhabited the southern part of what is now Kenya by 6 Ma, the earliest known appearance of the species south of Lothagam, Kenya.

Introduction

Lemudong'o is a 6-million-year-old fossil site in the Narok District of southern Kenya (Ambrose et al., 2003, 2007; Deino and Ambrose, 2007). Primarily, mammalian fossils have been recovered from the Lemudong'o Locality 1 (LEM 1) and nearby contemporaneous localities, consisting of a large number of colobine primates and hyracoids. Along with other taxa, there is a relatively sparse and fragmentary assemblage of suids. Collecting between 1997 and 2004 yielded 44 suid specimens, representing less than 1% of the total collection (Ambrose et al., 2007). Eight of these are postcranial specimens, twenty-eight specimens are isolated teeth, and six are associated teeth or partial jaws. The more complete specimens for which exact stratigraphic proveniences are known come from the sands at or near the base of the fossiliferous sequence at LEM 1.

The fossil record documents relatively rapid morphological evolution in several well-represented Plio-Pleistocene suid lineages (e.g., Harris and White, 1979; Brunet and White, 2001). Given that suids are commonly found at terrestrial fossil sites, and much of their evolution is relatively well-understood, various taxa in the family are often used as biochronological markers (e.g., White and Harris, 1977; Cooke, 1985). As such, the African Suidae have played a significant role in our understanding of the evolution of many other African mammals, including that of humans. Suid taxa can also provide insight into paleoecology (Bishop, 1999).

The last decade has witnessed a dramatic increase in the recovery of late Miocene and early Pliocene mammalian fossils from sites in eastern and central Africa such as Lothagam (Harris and Leakey, 2003) and Lukeino (Pickford and Senut, 2001) in Kenya, Aramis and the West Margin of the Middle Awash (WoldeGabriel et al., 1994; Haile-Selassie et al., 2004) in Ethiopia, the Warwire and Nkondo Formations in the Albertine Rift of Uganda and Zaire (Pickford et al., 1994), and Toros-Menalla in Chad (Brunet and M.P.F.T., 2000; Vignaud et al., 2002). Many new suid specimens have been recovered from these sites, including at least two new species: *Kolpochoerus deheinzelini* and *Kolpochoerus cookei* (Brunet and White, 2001). Because of this significant increase in the fossil data, our current understanding of African suid evolution has been subjected to major revisions (van der Made, 1999; for previous reviews of African suids and Old World suids see Pickford [1986, 1993, respectively]).

The LEM 1 suid assemblage, although fragmentary and sparse, contributes new specimens of tetraconodontines to the growing late Miocene database. Given the fragmentary nature of the Lemudong'o suid assemblage and lack of taxonomic diversity, we do not undertake a full revision here. Rather, we describe the relevant Narok specimens in order to facilitate the revisions undertaken by researchers with larger collections. We follow the taxonomy used in Haile-Selassie (2001), based on Cooke (1987).

The LEM 1 suid material represents a single species in the Tetraconodontini. This tribe is thought to have migrated into

Africa from Asia during the late Miocene (van der Made, 1999). Almost all of the LEM 1 suid teeth fall into the size and morphological range of *N. syrticus* from the Lower Nawata of Lothagam, and therefore represent some of the earliest members of this taxon in eastern Africa. Two dental features that are of particular importance to deciphering the various genera and species within the Tetraconodontinae are the relative size of the premolars and the size and complexity of the third molars (van der Made, 1999). Here, we focus our discussion on these characters.

Abbreviations

KNM	Kenya National Museum.
KNM-NK	Narok District, Kenya, indicates fossils are from localities within this district, including Lemudong'o Localities 1 and 2, Enamankeon Localities 1, 2, and 3, and Kasiolei Locality 1. Locality, when different from Lemudong'o Locality 1, is noted in the text. See also Appendix 1 in Ambrose et al. (2007).
KNM-LT	Lothagam, Kenya, indicates fossils from this site.
KL	Kalb Locality; here this refers to fossils now known to be from the Adu-Asa Formation in the Afar Region of Ethiopia.
Ma	million years ago.

Dental abbreviations follow these conventions:

R. M1	right maxillary first molar.
L. p4	left mandibular fourth premolar.
md	maximum mesiodistal measurement of the crown not accounting for wear.
bl	maximum buccolingual width of the crown through the mesial pair of cusps.

Systematic Paleontology

Class MAMMALIA Linnaeus, 1758
Order ARTIODACTYLA Owen, 1848
Family SUIDAE Gray, 1821
Tribe TETRACONODONTINAE Simpson, 1945
Genus *NYANZACHOERUS* Leakey, 1958
NYANZACHOERUS SYRTICUS (Leonardi, 1952)
Figure 1

Remarks

Nyanzachoerus was first described by Leakey (1958, p. 4) as a suid with enlarged 3rd and 4th lower premolars that are laterally more compressed than seen in *Tetraconodon*. The genus was rediagnosed by Cooke and Ewer (1972, p. 154) and Harris and White (1979) as having, in part, cheek teeth similar to modern *Potamochoerus* but with much more columnar and hypsodont molar cusps, and with relatively larger third and fourth premolars compared to the second premolar and molars. This genus was an Asian migrant that entered Africa during the late Miocene (van der Made, 1999, p. 220). Therefore, the fossils recovered from the Narok District in southern Kenya represent some of the earliest specimens of this genus in eastern Africa.

Specimens from Sahabi, Libya, were first referred to *N.* (= *Sivachoerus* Pilgrim, 1926) *syrticus* by Leonardi (1952). Morphologically similar specimens from eastern Africa were named *N. tulotos* (Cooke and Ewer, 1972), given that the original *N. syrticus* material was temporarily lost and unavailable for comparison (Cooke, 1987, p. 256). Subsequent to the recovery and revised description of the Sahabi specimens (Kotsakis and Ingino, 1980), *N. tulotos* has since been recognized as a junior synonym of *N. syrticus* (White and Harris, 1977; Cooke, 1987). This species has been documented from numerous late Miocene African sites such as Beglia in Tunisia (Pickford, 1990), Toros-Menalla in Chad (Vignaud et al., 2002), Middle Awash, Ethiopia (Haile-Selassie et al., 2004), and Lothagam, Kenya (Harris and Leakey, 2003). It has also been documented from late Miocene deposits of the Baynunah Formation in Abu Dhabi, United Arab Emirates (Bishop and Hill, 1999).

Nyanzachoerus syrticus is characterized as being the least advanced *Nyanzachoerus* species due to its retention of both the maxillary and mandibular first premolars (Arambourg, 1968; White and Harris, 1977; Cooke, 1978). This species also has large third and fourth maxillary and mandibular premolars (such that the length of the P3 and P4 is more than half that of the molar row), and relatively low-crowned third molars composed of only two pairs of lateral cusps and a small talon or talonid (Harris and White, 1979, p. 11, for *N. tulotos*).
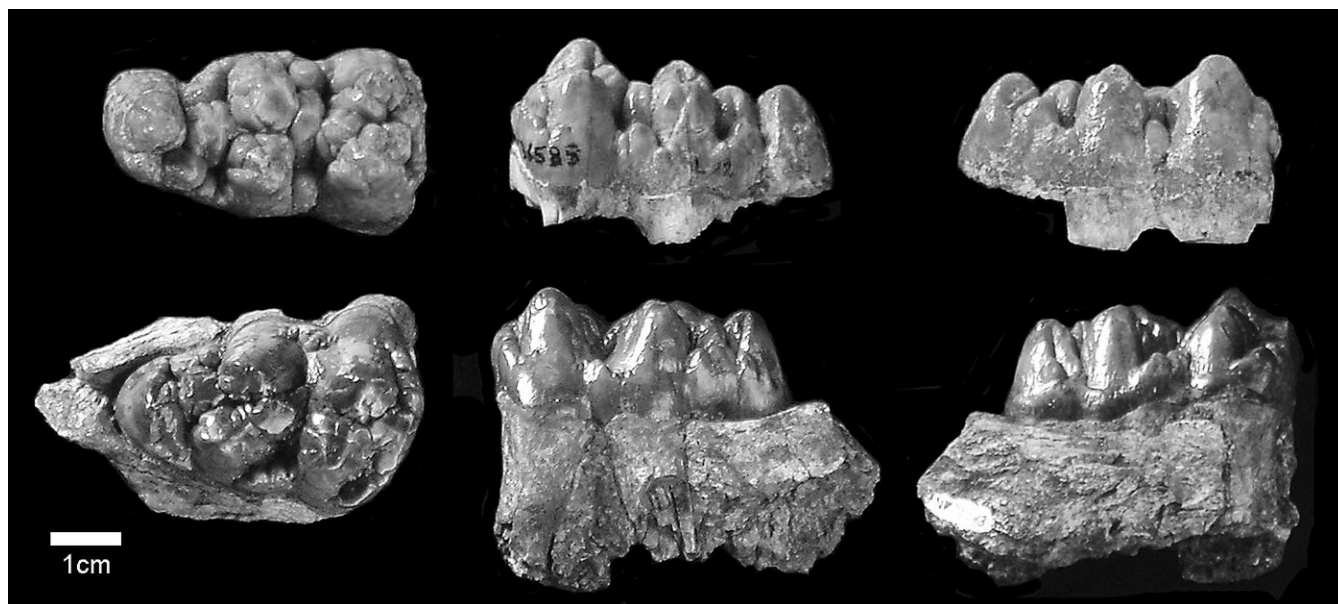

Figure 1. *Nyanzachoerus syrticus.* Top row: KNM-NK 36585, a left m3; bottom row: KNM-NK 45783, a right M3. From left to right: occlusal, buccal, and lingual views.

Table 1. Narok suid mandibular third-molar metrics compared to other *Nyanzachoerus* samples.

Specimen number	md*	mbl	dbl
KNM-NK 36585	45.3	25.9	24.4
KNM-NK 44803	–	23.8	–
KNM-NK 36568a (left)	–	–	20.83
KNM-NK 36568b (right)	–	–	20.7
mean	45.3	24.9	22.0
N. syrticus (Lothagam)[1]			
n	20	21	20
mean (stdv.)	43.5 (3.0)	24.2 (1.2)	21.7 (1.4)
N. devauxi (Lothagam)[1]			
n	8	7	8
mean (stdv.)	37.0 (1.6)	21.3 (1.8)	19.1 (1.3)
N. pattersoni (= *kanamensis*) (Kanapoi)[2]			
n	20	21	n/a
mean (stdv.)	53.0 (3.1)	25.1 (1.8)	n/a
N. kanamensis (Manonga Valley)[3]			
n	2	2	n/a
mean (stdv.)	59.4 (2.0)	28.2 (0.1)	n/a
N. kanamensis australis (Langebaanweg)[4]			
n	18	18	n/a
mean (stdv.)	61.1 (3.4)	29.6 (2.3)	n/a

[1] Data from Harris and Leakey (2003, tables 10.14 and 10.20).

[2] Data from Harris et al. (2003, p. 80–83, table 26).

[3] Data from Bishop (1997, p. 209, table X).

[4] Data from Cooke and Hendy (1992, p. 8, table 3).

* Mesiodistal length = md; mbl = buccolingual width across the mesial cusp pair; dbl = buccolingual width across the second, or distal, cusp pair.

Material

KNM-NK 36568, R. & L. m3 distal fragments (one originally labeled as KNM-NK 41417); KNM-NK 36585, L. m3; KNM-NK 44803, L. mandible with p4-m3 (fragment); KNM-NK 45783, R. M3.

Description

KNM-NK 44803 is a left mandibular specimen with complete p4–m2, and the mesial portion of the m3 (measurements presented in Table 1). The molars are quite worn, and the m1 is preserved merely as a ring of enamel around dentine. The mandibular body is broken, only preserving about half of the corpus inferior to the tooth row. This specimen is morphologically quite similar to KNM-LT 23752 from the Lower Nawata Formation at Lothagam (Harris and Leakey, 2003, p. 488–491), although the KNM-NK 44803 molar row would have been a bit longer if the m3 were complete. The p4s of KNM-LT 23572 and KNM-NK 44803 are similarly sized and the mesial aspect of KNM-NK 44803 is more worn so that the cingulum on the anterior/mesial surface is not as pronounced as on KNM-LT 23752. The large premolars, relative to the molars, align this specimen with *N. syrticus* rather than other members of this genus who are characterized by relatively reduced premolars.

KNM-NK 36585 is a virtually unworn left m3 preserved to just below the cervix (Figure 1 top row, Table 1). There is very slight wear on the protoconid, but no dentine is exposed. This molar has features characteristic of *N. syrticus* (Harris and White, 1979, p. 10–19), such as: two cusp pairs and a terminal cusp; buccal cingulum; small endostyle between metaconid and entoconid; single median pillar behind distal pillar pair; talonid has only one primary cusp and two small distolingual cusplets. KNM-NK 36585 is very similar to KNM-LT 388 from Lothagam, which is

assigned to *N. syrticus tulotos*. The Lemudong'o specimen KNM-NK 36585 is larger than the Lothagam *N. devauxi*, broader than the Upper Nawata *N. syrticus*, and greater in both dimensions from the Lower Nawata *N. syrticus* (Harris and Leakey, 2003, fig. 10.44, p. 491).

KNM-NK 36585 is also similar to specimens from the Adu-Asa Formation of Ethiopia assigned to *N. syrticus*. When KNM-NK 36585 is compared to KL 164-1, a specimen from the Adu-Asa Formation, they have the same crown height although the cusp tips are slightly more worn on KNM-NK 36585. KNM-NK 36585 also has a small endostyle between the metaconid and entoconid whereas KL 164-1 does not. The development of the buccal cingulum is equivalent in both specimens and the talonid morphology and complexity are almost identical (KL 164-1 md = 43.5 mm and bl = 22.8 mm). Another specimen from the Adu-Asa Formation, KL 174-1, has approximately the same crown height as KNM-NK 36585, although the cusps on the former are a little more worn. The morphological differences between KNM-NK 36585 and KL 174-1 are the same as between KNM-NK 36585 and KL 164-1 noted above (KL 174-1 md = 43 mm and bl = 21.9 mm).

KNM-NK 36568 consists of right and left m3 distal fragments (not figured). These specimens preserve only the worn talonid region of the mandibular third molars. Although found separately in 1997 and 1999, these two m3's appear to be perfect mirror images with the same morphology and amount of wear. Therefore, they are interpreted to be antimeres from the same individual. The crowns are low and with a simple talonid region, identical to that of KNM-NK 36585 although more worn.

All of the Lemudong'o m3 specimens described above show characteristic *N. syrticus* morphology and size. They are generally smaller than all ~4.1-Ma specimens identified as *N. pattersoni* (= *N. kanamensis*) from Kanapoi (see Table 1; Feibel, 2003; Harris et al., 2003), *N. kanamensis* from Manonga Valley (Bishop, 1997), *N. kanamensis australis* from Langebaanweg in South Africa (Cooke and Hendy, 1992), and even more so when compared to the younger *N. jaegeri* from the Apak Member of Lothagam (data not shown, Harris and Leakey, 2003). In contrast, the Lemudong'o m3's are much larger than *N. devauxi* from Lothagam (see Table 1; Harris and Leakey, 2003). Morphologically, the Lemudong'o m3's have only two cusp pairs and a small talonid, differentiating them from the expanded talonids and added cusp pairs of all other known *Nyanzachoerus* species with the exception of *N. devauxi*.

KNM-NK 45783 (Figure 1, bottom row; Table 1) is a right M3 with some of the alveolar bone preserved. As for the m3's, this crown is less hypsodont and with less complex distal occlusal morphology than is seen in *N. kanamensis*, and shows strong similarities to the M3's from Lothagam, especially KNM-LT 26110, a right M3 from the Upper Nawata. Both crowns have a reduced talon region; KNM-LT 26110 is overall slightly larger. Measurements for KNM-NK 45783 are as follows: mesiodistal length = 44.0 mm; buccolingual width across the mesial pair of pillars = 31.4 mm; buccolingual width across the second pair of pillars = 26.9 mm.

NYANZACHOERUS CF. *SYRTICUS* (Leonardi, 1952)

Material

KNM-NK 36573, L. m1; KNM-NK 36574, P3 germ; KNM-NK 36584, L. dp4; KNM-NK 40990, R. p1; KNM-NK 41362, R. p3; KNM-NK 41435, L. m2; KNM-NK 41462, L. i1, L.; p1, R.

dp4, R. m1, L. m1; KNM-NK 42370, R. I1; KNM-NK 42385, broken i1 and R. p2; KNM-NK 44760, R. di2; KNM-NK 44887, L. m2; KNM-NK 44888, R. m1; KNM-NK 44889, R. di1; KNM-NK 44890, L. p4.

Description

Almost all of these teeth fall into the size range of *N. syrticus* from Lothagam, except for KNM-NK 41462 that is slightly more narrow relative to its length (Table 1; Harris et al., 2003). Morphologically, there are no characteristics that would preclude the inclusion of any of these teeth within that species. However, they also lack any derived characteristics that would confirm a *N. syrticus* designation. Therefore, these teeth are tentatively assigned to *N.* cf. *syrticus* since no other suid taxon has been found from the site.

Discussion

The age of LEM 1 was initially determined biochronologically using the limited number of suid specimens. Later ^{40}Ar/^{39}Ar dating has refined this initial late Miocene biochronological date to ~6.11 Ma (Deino and Ambrose, 2007). Since then, the suid collection has not increased substantially, particularly in the number of relatively complete specimens. Despite the fragmentary and sparse nature of the LEM 1 collection, these fossils of *N. syrticus* indicate that members of this genus had a wider distribution in eastern Africa extending from the Middle Awash in the north to as far south as southern Kenya before 6 Ma.

Although widely known from late Miocene fossil localities across northern and eastern Africa and the Arabian Penninsula, *N. syrticus* appears not to be present in the late Miocene sediments of the Manonga Valley (Ibole Member, 5.5–5 Ma), Tanzania (Harrison and Mbago, 1997, p. 16). The difference in the faunal composition of these two sites (Lemudong'o and Manonga Valley) is interesting given their temporal and geographic proximity. The Manonga Valley is located in the northern part of Tanzania, relatively close to the southern Kenyan site of Lemudong'o.

The Manonga Valley specimens have been attributed to *N. kanamensis* (Bishop, 1997), a more derived species of *Nyanzachoerus* known from Pliocene deposits (Harris and White, 1979), such as the 5–4 Ma deposits in the Albertine Rift Valley of Uganda and Zaire (Pickford, 1994, p. 352). The Manonga Valley third-molar specimens are larger than the third molars of *N. kanamensis* described from other eastern African localities (Table 1; Bishop, 1997). The Manonga Valley third-molar metrics are comparable to those reported for the subspecies of *N. kanamensis australis* (= *N. australis*) from the ca. 5.5–4.8 Ma deposits of Langebaanweg in South Africa (Table 1; Cooke and Hendey, 1992). Bishop (1997, p. 215) argues that the Manonga Valley suid dental metrics are not statistically significantly different from the Langebaanweg specimens attributed to *N. k. australis*, but, she argues, given the lack of comparable cranial specimens, Mangonga Valley suids cannot be attributed to this new subspecies/species.

However, the Manonga Valley specimen counts are quite small (e.g., $n = 2$ for m3's), and therefore statistical tests would be expectedly non-robust. Therefore, the Langebaanweg and Manonga Valley specimens may ultimately prove to sample the same taxon. But whether or not the Manonga Valley specimens remain categorized as *N. kanamensis* or are moved to a new species or subspecies of *Nyanzachoerus*, it is unlikely that they are *N. syrticus*. Therefore, it appears as though *N. syrticus* either evolved quite rapidly in the region of northern Tanzania into *N. kanamensis* or another larger species, or there were two congeneric species existing in close temporal and geographic space.

A number of *N. syrticus* specimens have been recovered from the Adu-Asa Formation of the Middle Awash, Ethiopia (Haile-Selassie, 2001). The sediments that yielded these specimens are radiometrically dated to between 5.77 and 5.54 Ma (WoldeGabriel et al., 2001), an age slightly younger than Lemudong'o (Deino and Ambrose, 2007). However, despite the minor age difference, the upper and lower third molars assigned from both sites to *N. syrticus* are metrically and morphologically similar. The Middle Awash *N. syrticus* upper molars range in their length from 40.2 mm to 43.5 mm ($n = 6$). The length of the Lemudong'o *N. syrticus* M3 (44 mm) lies slightly above the highest range of the Middle Awash sample, even though it lies within the range of the larger sample of *N. syrticus* from the Nawata Formation of Lothagam (Harris and Leakey, 2003). Morphologically, they are united by the small and simple talon, which is characteristic of *N. syrticus*. The lower third molars are also metrically and morphologically similar, other than the minor differences described above. However, it should be noted that there are a number of variations in the number and size of cusplets on third-molar talonids in a larger sample of the species such as the Lothagam sample.

The scarcity of suids in the Lemudong'o collection stands in contrast to many other mammalian-dominated fossil sites from this time period (e.g., Lothagam, Harris and Leakey, 2003; Middle Awash, Haile-Selassie et al., 2004). Given that the main fossil horizon at LEM 1 samples a fairly restricted ecology, it is reasonable to surmise that *N. syrticus* was either not abundant in this habitat, or was not preyed upon by the carnivorous birds which have been thought to have accumulated much of this assemblage (Ambrose et al., 2007). *Nyanzachoerus* has been associated with more forested, or closed habitats (Harris, 1983; Pickford, 1994; see Harris and Cerling, 2002 for a contrary view), and therefore its recovery may suggest that such habitats were not far from the sands in which these specimens were fossilized.

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