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

**LESLEA J. HLUSKO**
Department of Integrative Biology
University of California, 3060 Valley Life Sciences Building
Berkeley, California 94720-3140
hlusko@berkeley.edu

AND **YOHANNES HAILE-SELASSIE**
The Cleveland Museum of Natural History
1 Wade Oval Drive
Cleveland, Ohio 44106-1767

**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 40Ar/39Ar 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**

<table>
<thead>
<tr>
<th>Abbreviation</th>
<th>Description</th>
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<tbody>
<tr>
<td>KNM</td>
<td>Kenya National Museum.</td>
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<tr>
<td>KNM-NK</td>
<td>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 Kasiole Locality 1. Locality, when different from Lemudong’o Locality 1, is noted in the text. See also Appendix 1 in Ambrose et al. (2007).</td>
</tr>
<tr>
<td>KNM-LT</td>
<td>Lothagam, Kenya, indicates fossils from this site.</td>
</tr>
<tr>
<td>KL</td>
<td>Kalb Locality; here this refers to fossils now known to be from the Adu-Asa Formation in the Afar Region of Ethiopia.</td>
</tr>
<tr>
<td>Ma</td>
<td>million years ago.</td>
</tr>
<tr>
<td>Dental abbreviations</td>
<td>follow these conventions:</td>
</tr>
<tr>
<td>R. M1</td>
<td>right maxillary first molar.</td>
</tr>
<tr>
<td>L. p4</td>
<td>left mandibular fourth premolar.</td>
</tr>
<tr>
<td>md</td>
<td>maximum mesiodistal measurement of the crown not accounting for wear.</td>
</tr>
<tr>
<td>bl</td>
<td>maximum buccolingual width of the crown through the mesial pair of cusps.</td>
</tr>
</tbody>
</table>

**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**

*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.

**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 re-diagnosed 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*).
YANZACHOERUS CF. SYRTICUS (Leonardi, 1952)

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 also similar to specimens from the Adu-Asa Formation, KL 174-1, 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 Hendey, 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.

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

<table>
<thead>
<tr>
<th>Specimen number</th>
<th>md*</th>
<th>mbl</th>
<th>dbl</th>
</tr>
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<tbody>
<tr>
<td>KNM-NK 36585</td>
<td>45.3</td>
<td>25.9</td>
<td>24.4</td>
</tr>
<tr>
<td>KNM-NK 44803</td>
<td>23.8</td>
<td>23.8</td>
<td>20.7</td>
</tr>
<tr>
<td>KNM-NK 36584 (left)</td>
<td>20.3</td>
<td>20.3</td>
<td>20.3</td>
</tr>
<tr>
<td>KNM-NK 36586b (right)</td>
<td>20.7</td>
<td>20.7</td>
<td>20.7</td>
</tr>
<tr>
<td>mean</td>
<td>45.3</td>
<td>24.9</td>
<td>22.0</td>
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</table>

N. syrticus (Lothagam)

<table>
<thead>
<tr>
<th>n</th>
<th>20</th>
<th>21</th>
<th>20</th>
</tr>
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<tbody>
<tr>
<td>mean (stdv.)</td>
<td>43.5 (3.0)</td>
<td>24.2 (1.2)</td>
<td>21.7 (1.4)</td>
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</table>

N. devauxi (Lothagam)

<table>
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<th>n</th>
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<th>8</th>
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</thead>
<tbody>
<tr>
<td>mean (stdv.)</td>
<td>37.0 (1.6)</td>
<td>21.3 (1.8)</td>
<td>19.1 (1.3)</td>
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N. pattersoni (= kanamensis) (Kanapoi)

<table>
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<tr>
<td>mean (stdv.)</td>
<td>53.0 (3.1)</td>
<td>25.1 (1.8)</td>
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N. kanamensis (Manonga Valley)

<table>
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</thead>
<tbody>
<tr>
<td>mean (stdv.)</td>
<td>59.4 (2.0)</td>
<td>28.2 (0.1)</td>
<td>n/a</td>
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</table>

N. kanamensis australis (Langebaanweg)

<table>
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<th>18</th>
<th>18</th>
<th>n/a</th>
</tr>
</thead>
<tbody>
<tr>
<td>mean (stdv.)</td>
<td>61.1 (3.4)</td>
<td>29.6 (2.5)</td>
<td>n/a</td>
</tr>
</tbody>
</table>

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 Hendey (1992, p. 8, table 3).
5 Mesiodistal length = md; mbl = buccolingual width across the mesial cusp pair; dbl = buccolingual width across the second, or distal, cusp pair.

YANZACHOERUS 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. 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 ⁴⁰Ar/³⁹Ar 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 cuspsets on third-molar talonids in a larger sample of the species such as the Lohagam 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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**References**


Owen, R. 1848. Description of teeth and portions of jaws of two extinct anthracotheroid quadrupeds (Hyopotamys vectianus and Hyopotamys bovinus) discovered by the Marchioness of Hasting in the Eocene deposits on the N.W. coast of the Island of Wright: With an attempt to develop Cuvier’s idea of the classification of pachyderms by the number of their toes. Quarterly Journal of the Geological Society of London, 4:103–141.


