Suidae from Kanapoi

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ABSTRACT

The whole collection of Suidae from Kanapoi is revised in the context of the systematics and evolution of *Nyanzachoerus* in the Pliocene of Eastern Africa. It contains only two species, *Nyanzachoerus kanamensis* and *Notochoerus jaegeri*. The size and morphology of their premolars overlap, but not those of their m3s. No transitional form between them is known in Kenya, but some populations from Uganda and Ethiopia display intermediate characters, suggesting that *No. jaegeri* could be descended from a *kanamensis*-like ancestor. However, the cranial remains of *No. jaegeri* from Kanapoi are insufficient to formally establish the affinities of the species. On the basis of the dentition, *Notochoerus euilus* could be descended from *No. jaegeri*. The noticeable absence of *Kolpochoerus* at Kanapoi (and in the whole Turkana Basin at that time) remains unexplained. The presence of a species with affinity to *Nyanzachoerus tulotos* at Ekora raises the possibility that uppermost Miocene sediments occur there.

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1. Introduction

Cooke and Ewer (1972) described in detail the suid material collected by the Harvard University expeditions. They assigned the bulk of the material to two new species of *Nyanzachoerus* (hereafter *Ny.*), *Ny. pattersoni* and *Ny. plicatus*, but also attributed a few, mostly incomplete or weathered specimens to *Notochoerus* (hereafter *No.*), tentatively calling them *No.* cf. *capensis* Broom, 1925 and *No.* cf. *euilus* Hopwood, 1926. Harris et al. (2003) revised this material and additionally described the material collected in the 1990s by the National Museums of Kenya expeditions. They accepted *Ny. pattersoni* as a valid species but, following Harris and White (1979), they regarded *Ny. plicatus* as a synonym of *Ny. jaegeri* Coppens, 1971, first described from Tunisia. However, they assigned this species to *Notochoerus* and included in it the material identified as *Notochoerus* by Cooke and Ewer (1972). In addition, they considered that a mandible (KNM-KP 30184) represents *No.* cf. *euilus*. Last, Geraads et al. (2013) concluded that there are only two species, *No. jaegeri* and *Ny. kanamensis*. We have revised the whole collection from Kanapoi, stored in the National Museums of Kenya (KNM), including all the material collected up to 2016. It numbers more than 300 specimens, including a large number of premolars and

third molars. Comparisons have mostly been conducted with the Suidae from other Kenyan sites in the KNM and with those from some Ethiopian sites in the National Museum of Ethiopia, Addis Ababa (NME); some additional specimens have been examined in the Muséum National d'Histoire Naturelle, Paris (MNHN), and in the Natural History Museum, London (NHMUK). Measurements follow the methodology of Harris and White (1979), i.e., length (L) is taken at the cervix along the crown midline and width (W) is maximum. Almost all of those used in the graphs were taken by ourselves; we checked that those published by Harris et al. (2003) differ little from ours. It should be noted, however, that we could not find some of the specimens reported by these authors. Specimens with accession numbers higher than KNM-KP 38980 were found recently and not mentioned by Harris et al. (2003).

2. Systematic paleontology

Family Suidae Gray, 1821
Subfamily Tetraconodontinae Lydekker, 1876

We follow here the tradition of placing the genera *Nyanzachoerus* and *Notochoerus* (see Supplementary Online Material [SOM] for the use of this name) in this subfamily, which remains poorly defined by features such as the reduction of P2/p2 (but this is also true of the Suinae *Potamochoerus*) and the large size of the

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distal premolars (Orliac et al., 2010), but this is obviously not true of *Notochoerus*. Van der Made (1999) added that the metacone of P4 is indistinct, but this is not true in unworn teeth. Pickford (2014) concluded that the subfamily is probably paraphyletic; clearly, the validity of this subfamily remains to be better substantiated.

Genus *Nyanzachoerus* Leakey, 1958.

Nyanzachoerus is a large suid that has characteristic zygomatic inflations. They differ from those of *Notochoerus* in being quite rounded, not protruding very far, and being directed laterally or slightly ventro-laterally, and from those of *Kolpochoerus* in being restricted to the anterior part of the zygomatic arch, so that the skull abruptly narrows immediately behind them. The forehead is broad, depressed, and bordered by longitudinal swellings above the orbit, which is not shifted backwards. It has a shallow ante-orbital depression, and the supra-canine flange is moderate, showing that its snout muscles were weaker than in fossorial suids such as *Potamochoerus*. The sexually dimorphic canines are not very large, the upper and lower last two premolars are quite large, and the third molars undergo some lengthening in evolution, but remain short.

2.1. Nyanzachoerus kanamensis *Leakey, 1958*

= *Nyanzachoerus pattersoni* Cooke and Ewer, 1972.

Cooke and Ewer (1972), followed by Harris et al. (2003), described the most common suid species at Kanapoi as *Ny. pattersoni*, whose molars were said to be broader than those of *Ny. kanamensis* defined at Kanam West but, as noted by Geraads et al. (2013), the narrowness of the latter are only due to their heavy weathering, and we shall use the name given by L.S.B. Leakey, which has priority.

Harris and White (1979) had noted that *Ny. kanamensis* differs from the earlier *Ny. tulotos* from Lothagam in its larger size, longer third molars, relatively smaller premolars, larger zygomatic inflation, and weaker supra-orbital ridges and supra-canine flange. In males, there is a distinct longitudinal supra-canine flange and the lateral borders of the nasals also form slight longitudinal ridges that contribute to protect the muscles of the rostrum and their tendons, but both of these structures are much less pronounced than in *Potamochoerus*. The P2 and p2 are small, but the posterior premolars, especially p3 and p4, are quite large, as is characteristic of tetraconodonts.

The specimens found by the early Patterson expeditions were described by Cooke and Ewer (1972), and some of those discovered more recently were illustrated by Harris et al. (2003); these authors provided the general characteristics of the species, but some specimens merit further description. The features of the third molars and tooth proportions are discussed below.

KNM-KP 18566 is a left maxillary fragment with unerupted M3. The unworn P4 is large and distinctly broader than M1, but otherwise its morphology differs little from that of other African suids. The metacone is smaller than the paracone and closely appressed against it, but these cusps are distinct and well defined. There is no raised mesial or distal cingula, so that with wear the lingual and buccal parts of the tooth would have been separated by a longitudinal groove extending from the mesial to the distal borders.

KNM-KP 30160 (Fig. 1H) is the right half of a female mandible that shows an i3 much smaller than the central incisors, a verrucose canine inserted rather vertically, and a minute p2 inserted against p3.

KNM-KP 30161 (Fig. 1D) is another partial, male mandible in which the broken bone exposes the base of the large left canine, which extended far behind p3.

KNM-KP 30177 consist of several fragments that confirm some of the characters visible in the above mentioned specimens: on the little worn right P4, the paracone and metacone are distinct but these cusps are separated from the protocone, and i3 is much smaller than i1 and i2.

KNM-KP 30186 (Harris et al., 2003: their Fig. 17) is an almost complete male skull, but lacking most of the teeth. It is quite similar to KNM-KP 264, the paratype of *Ny. 'pattersoni'* (Cooke and Ewer, 1972: their Pls. 2C and 3), in having expanded, rounded zygomatic protuberances limited to the anterior part of the zygoma, a depressed cranial roof bordered by strong lateral ridges in front of the orbits and sharply delimited from the temporal fossae by elevated crests, weak but distinct supra-canine flanges, and a naso-maxillary suture forming a longitudinal ridge. In addition, it shows that the area immediately anterior to the orbit forms a depression that is less deep (especially dorsally) than in *Potamochoerus*, but much more distinct than in *Hylochoerus*. This depression is less clear in KNM-KP 264, but this area is less well preserved. It obviously served as an area of insertion of the rostral muscles (Ewer, 1958, 1970), confirming that these muscles were intermediate between these two modern genera in their development.

KNM-KP 30205 and KNM-KP 30410 are the anterior portions of female mandibles, with short diastemas and small i3s.

KNM-KP 30267 is also the anterior portion of a mandible but the size of its right canine shows that it belongs to a male; the diastema is also short.

KNM-KP 30433 is a palate with moderately worn teeth, showing the incipient fusion of the buccal cusps of both P4s with wear and their clear separation from the protocone.

KNM-KP 38978 (Fig. 1G) is a partial mandible, probably male, with the right cheek-teeth. The diastema is short. Although the m3 leaves no doubt as to species identification, the premolars are rather small for *Ny. kanamensis*.

KNM-KP 49362 is a maxilla with well-worn right cheek-teeth. On P4 the paracone and metacone are fused and separated from the protocone by a groove extending over the whole length of the tooth.

KNM-KP 50736 (Fig. 1E) is a mandibular symphysis with the base of the left canine and the roots of the premolars, which show that p3 and p4 must have been very large, thus definitely identifying the specimen as *Ny. kanamensis*. As in other specimens, the diastema is short, but the symphysis is also broad and dorsoventrally flattened (perhaps accentuated by crushing).

KNM-KP 51146 (Fig. 1F) is an almost complete mandible that shows the same small i3 and short diastema as the previously mentioned female mandibles, KNM-KP 30160, KNM-KP 30205, and KNM-KP 30410, but differs in the larger size of the right canine and is thus male.

KNM-KP 56175 is an incomplete, juvenile, perhaps female cranium showing almost no zygomatic expansion, as in the female holotype of *Ny. 'pattersoni'* KNM-KP 239 (Cooke and Ewer, 1972: their Pl. 1). In contrast to males, it shows no longitudinal supraorbital ridges and no broadening of the skull roof at post-orbital level. We assume that these features result both from the sex and ontogenic age of the specimen.

KNM-KP 59955 is an associated set of upper teeth, including the left M3. The protocone of the right P3 is relatively large. The two P4s display a sub-equal paracone and metacone and, although the teeth are well-worn, these cusps are still separated by deep lingual and buccal clefts.

Figure 1. A–H) Some of the most complete suid mandibles from Kanapoi: (A and B) *Notochoerus jaegeri* and (C–H) *Nyanzachoerus kanamensis*. A) KNM-KP 30178, male; B) KNM-KP 30452, male; C) KNM-KP 239, female; D) KNM-KP 30161, male; E) KNM-KP 50736, male; F) KNM-KP 51146, male; G) KNM-KP 38978, male?; H) KNM-KP 30160, female; I) *Nyanzachoerus* cf. *tulotos*, left M3 KNM-EK 270 in mesial and occlusal views. Scale = 20 cm for Figures A–H, 5 cm for Figure I.

2.2. Notochoerus jaegeri *(Coppens, 1971)*

= *Nyanzachoerus plicatus* Cooke and Ewer, 1972.

As for the previous species, we add here descriptions of the newly discovered specimens. Cooke and Ewer (1972) described the upper canines of the holotype KNM-KP 251, of KNM-KP 252, and of KNM-KP 262, but these are all female specimens. They correctly noted that they are directed less inferiorly than *Ny. kanamensis*. By contrast, they assigned the large, male upper canines KNM-KP 242 and KNM-KP 267 (Cooke and Ewer, 1972: their Pl. 27A) to *No.* cf. *capensis*. KNM-KP 57038 is an additional, similar, almost complete large male upper canine; it is quite long, gently twisted, almost completely devoid of enamel, and has a rounded, slightly triangular cross-section. Because there is no definite evidence of *No. capensis* at Kanapoi, and because there is no other canine that could be attributed to *No. jaegeri*, we assign these teeth to the latter species; they greatly resemble those of *No. euilus*.

The upper premolars of skull KNM-KP 30617 are poorly preserved, and those of KNM-KP 211, which are definitely smaller than those of *Ny. kanamensis*, are very worn, so that the only well preserved P3 and P4 that definitely belong to *No. jaegeri* are those of the snout KNM-KP 257 (Cooke and Ewer, 1972: their Pl. 13D). They are not significantly smaller than those of *Ny. kanamensis*, and the only possible morphological difference is the seemingly smaller size of the lingual cusps; this could also be true of KNM-KP 30162, which is possibly also of *No. jaegeri*, but on the whole, no morphological feature consistently distinguishes the upper premolars of the two species. The ventral part of skull KNM-KP 30617

(Harris et al., 2003: their Fig. 19) is relatively well preserved. Compared to *Ny. kanamensis* (KNM-KP 264, KNM-KP 30186), the tooth-row is distinctly more anterior and the snout looks both longer and broader, especially across the canines and premaxillae. The palate is also much longer behind the M3s. The shape of the zygomatic expansions is unknown because the arches are very incomplete, but in ventral view they emerge much less transversally than in *Ny. kanamensis*, with a backward slope more similar to *No. euilus*. The occipital is not broad, but it appears so because the deep notch that separates the occipital from the posterior part of the zygoma and auditory canal in *Ny. kanamensis*, and still more so in *Ny. tulotos* (e.g., KNM-LT 23771), is filled by a bony plate increasing the areas of insertion of both the temporalis and nuchal muscles. In this regard, KNM-KP 30617 resembles *No. euilus*.

No significant mandibular remains have been discovered recently. We had previously explained (Geraads et al., 2013) why the mandible KNM-KP 30184 can satisfactorily be included in *No. jaegeri* rather than in *No.* cf. *euilus*, as was done by Harris et al. (2003). Cooke and Ewer (1972) also assigned a number of specimens to *No.* cf. *capensis*, but these were transferred to *No. jaegeri* by Harris and White (1979) and Harris et al. (2003). An incomplete lower m3 (KNM-KP 245) assigned to *No.* cf. *euilus* by Cooke and Ewer (1972) was also re-identified as *No. jaegeri* by Harris et al. (2003).

2.3. Nyanzachoerus cf. tulotos *Cooke and Ewer, 1972*

The only specimen from the Kanapoi beds that cannot be placed in either *Ny. kanamensis* or *No. jaegeri* is KNM-EK 270, which

consists of associated right P4 and incomplete M1, and left M3 (Fig. 1I). It comes from Ekora but below the Kalokwanya basalt, so that its age is greater than 3.4 Ma, but presumably younger than the main Kanapoi fauna. It was briefly described by Cooke and Ewer (1972), who assigned it to *Ny.* cf. *pattersoni* (recte: *Ny. kanamensis*), but compared to this species, the P4 (17.8 × 25.3 mm) is broader relative its length and broad relative to M3. In addition, M3 (41.8 × 28.7 mm) is very brachyodont and much shorter, thus relatively much broader relative to its length. This M3 is also relatively much broader than those of *Kolpochoerus* (see e.g., Cooke, 1976: his Fig. 3) and much larger than *Kolpochoerus* of this age. These tooth dimensions and proportions compare favorably with those of *Ny. tulotos* from Lothagam and Nkondo (NK 50′88 is virtually identical in dimensions and morphology: Pickford, 1994: his Pl. 3, Fig. 9), but the pattern of P4 looks distinct. In *Ny. tulotos*, the buccal cusps make up most of the crown (Fig. 5 of Harris and White, 1979, is incorrect in this regard; compare Cooke and Ewer, 1972: their Pl. 24A) and they are clearly separated from the lingual cusp complex by a deep longitudinal groove, whereas in KNM-EK 270 they are less dominant on the crown surface, more similar to other species of *Nyanzachoerus*. Harris and White (1979) believed KNM-EK 270 was intermediate between *Ny. tulotos* and *Ny. kanamensis*. A few specimens from the Apak Mb of Lothagam have also been described as *Ny. tulotos* (Harris and Leakey, 2003), but from their dimensions they are less clearly distinct from *Ny. kanamensis* and match that species better. KNM-EK 270 is too incomplete for formal identification, but it is certainly close to *Ny. tulotos*, suggesting either a late survival of this species at Ekora, the occurrence of beds of earlier age in this region, or the reworking of some fossils.

3. Discussion

3.1. Distinction of Ny. kanamensis and No. jaegeri and evolution of Pliocene Nyanzachoerus

An excellent introduction to the taxonomic history of African Pliocene suids of the *Nyanzachoerus-Notochoerus* group has been provided by Haile-Selassie (2009), and there is no need to repeat it here (see also Bishop, 2010, for an overview of the systematics of African suids). The pioneering publication of Leakey (1958) was not followed by a modern revision until White and Harris (1977, Harris and White, 1979), in parallel with Cooke and colleagues (Cooke and Ewer, 1972; Cooke, 1978; Cooke and Wilkinson, 1978) who elaborated the first attempt to understand the evolution of this group. Pliocene *Nyanzachoerus* is supposed to be derived from '*Propotamochoerus*' *devauxi* Arambourg, 1968 from the early late Miocene of

Algeria. Several species of the genus have been named, although no agreement has been reached as to their definition. As in several other African suid lineages, it is assumed that their third molars increased in length and complexity through time. From Hamada Damous in Tunisia, a site with a poorly constrained age, Coppens (1971) described, a derived form with lengthened third molars that he called *Ny. jaegeri*. Because of this derived character and the shape of its mandibular symphysis, Harris et al. (2003) regarded it as representing an early form of the genus *Notochoerus*, contributing to filling the gap between those genera. This generic assignment has generally been accepted since then, but Gebreyesus (2011) questioned it on the basis of cranial characters (see below). Obviously, the distinction or transition between those genera remains one of the key issues regarding Pliocene African suids.

According to Harris et al. (2003), one of the main distinguishing features of *No. jaegeri*, by comparison with *Ny. kanamensis*, is the spatulate shape of the mandibular symphysis, which is broad, with relatively flat dorsal and ventral surfaces, and with the incisors arranged in a transverse line rather than along an arch (Fig. 1). These differences are probably true as a whole, but they are hard to recognize because of the frequent transverse crushing of the mandibles and imperfect preservation of the incisive alveolar border. In addition, KNM-KP 50736, which is definitely *Ny. kanamensis*, also has a broad, spatulate symphysis (Fig. 1E). In fact, by far the best distinguishing feature in the mandible is the length of the postcanine diastema (Table 1), which shows no overlap between both species. A correlated measurement, symphysis length, also shows no overlap when sexes are distinguished. The role of this longer diastema in *No. jaegeri* is not just to accommodate a longer canine root, as shown by KNM-KP 30161 (Fig. 1D), a mandible of *Ny. kanamensis*, because in this specimen the canine root is very long (it reaches at least the posterior part of p4). This lengthening of the anterior portion of the mandible correlates with a lengthened snout, as suggested by the type of '*Ny. plicatus*,' but too few specimens are preserved to demonstrate this conclusively.

In almost all mandibles of *Ny. kanamensis* where this area is preserved, a small p2 is present, closely appressed against p3. In rare instances, it may be absent or single-rooted. By contrast, this tooth is normally either absent or separated from p3 by a diastema in the Kanapoi *No. jaegeri* (although this is not true of the type specimen from Hamada Damous). Upper and lower posterior premolars of *No. jaegeri* are smaller than those of *Ny. kanamensis*, but their size ranges widely overlap (Figs. 2 and 3). Plots of the length vs. width of these teeth show no bimodality, and only the largest teeth can be definitely identified as *Ny. kanamensis*.

Table 1
Measurements of the most complete mandibles of *Nyanzachoerus* and *Notochoerus* from Kanapoi.[a]

	Species	Sex	Minimum width at diastema	Width over i3s	L from canine to p3	L symphysis	L m3	Max. MD diameter of the canine
KP-30184	*No. jaegeri*	Female ?	78	−	80	131	72.5	30
KP-30452	*No. jaegeri*	Male	92.5	65	113	185	70	43.5
KP-30178	*No. jaegeri*	Male	106.5	89	140	185	80.2	46.5
KP-226	*No. jaegeri*	Male ?	120	100	110	190	−	43
KP-239	*Ny. kanamensis*	Female	61	60	55	115	53	23
KP-30160	*Ny. kanamensis*	Female	66	62	60	120	51.3	22.5
KP-30177	*Ny. kanamensis*	Female	70	65	50	100	55	−
KP-30205	*Ny. kanamensis*	Female	67	60	67	−	−	(small)
KP-30410	*Ny. kanamensis*	Female	70.5	−	62	116+	53.5	(small)
KP-50736	*Ny. kanamensis*	Male	100	69.5	60	c. 130	−	c. 37
KP-264	*Ny. kanamensis*	Male	−	−	c. 50	−	56.3	35
KP-59727	*Ny. kanamensis*	Male	72	−	58	105−110	47.5	−
KP-51146	*Ny. kanamensis*	Male	92	77.5	65	147	57.8	34
KP-38978	*Ny. kanamensis*	Male ?	91.5	71.5	73	138	53.4	−

[a] Some measurements are approximate, but this does not affect the clear distinction between the two species. MD = mesiodistal.
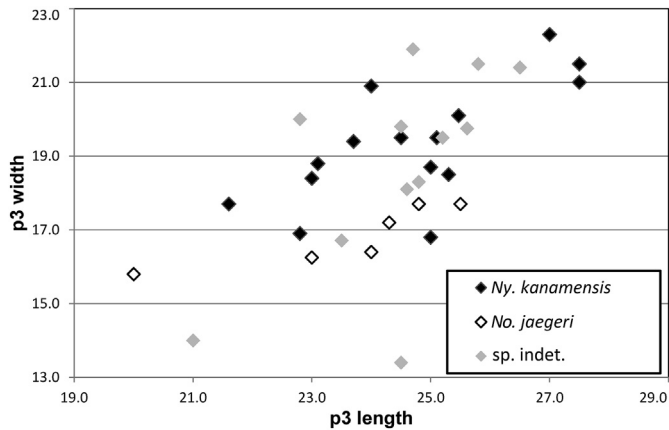
Figure 2. Plot of length vs. width of p3 of *Ny. kanamensis* and *No. jaegeri* from Kanapoi. Teeth identified to species are those that are associated with m3s.
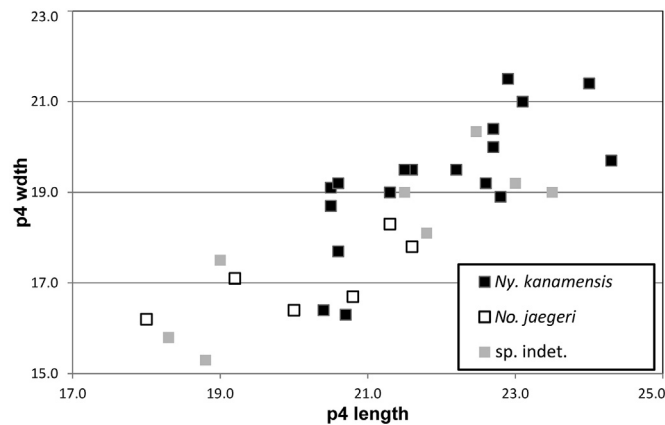

Figure 3. Plot of length vs. width of p4 of *Ny. kanamensis* and *No. jaegeri* from Kanapoi. Teeth identified to species are those that are associated with m3s.

Cooke and Ewer (1972) stated that *Ny.* '*pattersoni*' is brachyodont, whereas '*Ny. plicatus*' would be 'slightly hypsodont'. In fact, the difference in hypsodonty is at most slight. Unworn m3s of *Ny. kanamensis* (KNM-KP 30409, KNM-KP 30620) are slightly taller than broad; there is no unworn m3 of *No. jaegeri*, but slightly worn ones suggest that the difference between height and width was not much larger.

The talonid of the third lower molars of *Ny. kanamensis* consists of one well-formed pair of pillars, plus a distal part that may consist of more than a single tubercle, but remains asymmetrical and never forms a fourth pair of pillars. The m3s of *No. jaegeri* always have at least an incipient fourth pair; it may be followed by one or more accessory posterior cuspid(s), but these may also be fully absent (KNM-KP 30180). Thus, the difference in talonid development behind the third pair of pillars may be slight, but the criterion of an incipient fourth pair works perfectly to distinguish the two species. It is clear, however, that this difference in talonid development fails to fully explain the difference in length of the m3s, which is achieved by a lengthening of each individual pair of pillars. Indeed, in teeth assigned to *Ny. kanamensis*, the pillars are mushroom-shaped, whereas in those of *No. jaegeri*, they assume the shape of a horizontal H (i.e., with deeper anterior and posterior groves), as in other *Notochoerus*. In addition, in upper M3s of *Ny. kanamensis*, the pillars of the second pair come in full contact in the midline of the tooth, whereas in those of *No. jaegeri* (KNM-KP 234, KNM-KP 253 [Cooke and Ewer, 1972: their Pl.17G-H], KNM-KP 257 [Fig. 11 of Harris and

White, 1979, is incorrect in this regard—see instead Cooke and Ewer, 1972: their Pl.16], KNM-KP 30617, KNM-KP 49367), central accessory pillars intervene between them. This difference is sometimes hard to appreciate because of the irregular shape of the pillars and changes with wear, but is observable in the majority of specimens. This lack of contact is common in *Metridiochoerus*, as noted by Pickford (2013). By contrast, in almost all other specimens of *Nyanzachoerus* that we have seen, including several specimens of *No. jaegeri* from the Omo, the pillars of the second pair come into contact in the midline, and this is also true of the type specimen (Coppens, 1971: his Pl.2). In *No. euilus*, the contact may be present or not, even at a similar wear stage (compare Harris and White, 1979: their Figs. 29 and 31). Thus, we believe that not too much weight should be placed upon this character (contra Pickford, 2013), not only because it is sometimes hard to appreciate, but also because it varies between closely related species, if not within species (see also SOM).

A graph of the measurements of a large number of Pliocene and early Pleistocene East African *Nyanzachoerus* and *Notochoerus* is presented in Figure 4 and the SOM. Harris et al. (2003) stated that male 'teeth' (third molars being probably meant) of *Ny. kanamensis* are larger than those of females, but the available sample of specimens that can definitely be sexed does not confirm this assertion, and there is no evidence that *Nyanzachoerus* differs in this regard from modern *Sus*, where sexual dimorphism in molar dimensions is virtually absent (Van der Made, 1991). Lower teeth have been chosen in preference to upper ones because both isolated teeth and associated sets of molars and premolars are more numerous. They illustrate the main features commonly assumed to characterize species of this group: the lengthening of the third molars (Lm3 x Wm3, Fig. 4) and the relative width of the premolars (Lm3 x Wp3 and Lm3 x Wp4, SOM Figs. 1−2).

The first obvious result is that, although we sampled a large time interval (from the late Miocene to the early Pleistocene), two main clouds can be distinguished, with few intermediate forms, although some marginal specimens plot outside the main clouds (Fig. 4). The left cloud (with short m3s) includes teeth assigned to typical *Nyanzachoerus*. The sample from the Lower Nawata Mb of Lothagam, assigned to *Ny. tulotos*, has short but relatively broad m3s. Most of the remaining specimens have homogeneous L/W proportions and belong to *Ny. kanamensis*: the type and paratype of Leakey (1958), from Kanam West, the large sample from the Hadar Formation, the Kanapoi sample, and some specimens from the Turkana Basin and Galili (the teeth from Manonga [Bishop, 1997] would also plot here). This cloud also includes the early Pliocene material of the Middle Awash that Haile-Selassie (2009) called *Ny. australis*. He based his identification on the absence of a central cuspid between the third pair and the terminal pillar in m3s but, in the Kanapoi *Ny. kanamensis*, this central cuspid is at most minute, and completely absent in about half of the teeth, so that the difference is inconstant and certainly not of species value, a conclusion also reached by Boisserie et al. (2014). All these populations are quite similar to each other, the m3s from the Hadar Formation being only slightly longer than those from the earlier sites. Besides this slight difference in m3 length, the relative proportions of the premolars are also similar, showing that this species underwent little evolutionary change with time. The Lothagam teeth are slightly shorter, and the Nkondo ones are clearly smaller, warranting distinction of the form from the Western Rift as *Ny. waylandi* (Pickford, 1989, 2014). The holotype of *Ny. kuseralensis* Haile-Selassie, 2009 from the Kuseralee Mb of the Middle Awash is of similar size. Its m3 was said to have only two pairs of pillars, but a third pair is in fact as fully formed as in the holotype of *Ny. waylandi*, and we follow Boisserie et al. (2014), who discussed the issue in detail, in regarding both names as synonymous.
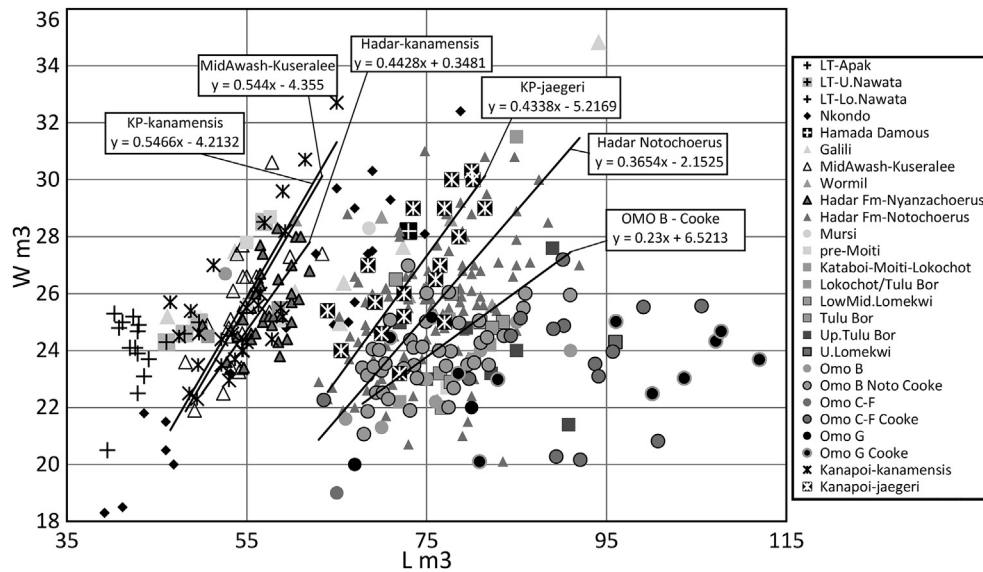
Figure 4. Scatterplot of length vs. width of m3s in various samples of species assigned to *Nyanzachoerus* and *Notochoerus*. Most measurements are our own, except for Galili (Kullmer et al., 2008), Nkondo (Pickford, 1994; with some corrections), WorMil (Gebreyesus, 2011), and a few measurements from Harris (1983), White and Suwa (2004), and Fessaha (1999). In addition, for the Omo Shungura Fm, we added measurements digitized from graphs in Cooke (1976). Cooke did not mention how he took his measurements, so they may be slightly over estimated, but this is unlikely to significantly alter the comparisons. Some regression lines (reduced major axis) are also indicated.

The right cloud includes specimens assigned to *No. jaegeri* and other *Notochoerus*. The former taxon can be distinguished by its relatively broader teeth (both the width of p3 and that of m3 are smaller relative to m3 length), while the teeth of *Notochoerus* become increasingly narrow with time. Delimitation of species within this large cloud is obviously difficult. Even in a single site such as Kanapoi, the size range is large, and choosing a specimen at both ends of it might suggest the occurrence of two distinct species, such as was done by identifying *No. euilus* at this site. On the basis of tooth morphology, *No. euilus* can easily be descended from *No. jaegeri*, and the long snout with a straight dorsal profile of the holotype of *Ny. plicatus* (Cooke and Ewer, 1972: their Pl. 13A-B) and the zygomatic bony knob KNM-KP 242 (Cooke and Ewer, 1972: their Pl. 27C-D) definitely resemble *Notochoerus*.

Another issue is the possible origin of *No. jaegeri* from *Ny. kanamensis* or from some other *Nyanzachoerus* with short molars. It is interesting to observe that while there are some outliers, there is clearly no continuum between the two main clouds, and the regression lines of *Ny. kanamensis* and *No. jaegeri* at Kanapoi (and other sites) are clearly distinct, so that a gradual, direct evolution of *Ny. kanamensis* into *No. jaegeri* can probably be rejected. The only intermediate forms are the group of large size from Nkondo (group 2 of Pickford, 1994). Pickford (1994) called it *Ny. jaegeri* but the very large premolars rule out this identification; this group 2 looks more like an enlarged version of *Ny. kanamensis*, although there is an incipient fourth pair of cuspids on m3, almost matching that of *No. jaegeri*. Because the premolars decreased in size and the molars became narrower from *No. jaegeri* to *No. euilus* (if these species are really a lineage), it is conceivable that *No. jaegeri* arose from such a form, although group 2 shows no trend in this direction. The Woranso-Mille skull described by Gebreyesus (2011) as *Ny. jaegeri* is very different from that of *Notochoerus*, and it is indeed hard to believe that the species it represents is ancestral to this genus. We have not seen this material, whose description appeared only in a Master's thesis, but it looks to us that this skull might in fact be a derived version of a *kanamensis*-like form: the ante-premolar portion is quite short, the choanae located not far behind M3, the tooth row is located anteriorly, and P4 is large (as at Nkondo). All

these features are very different from those of KNM-KP 30617 and similar to *Nyanzachoerus* sensu stricto. If we are right, this material does not belong to *No. jaegeri* and does not contradict the inclusion of this species in *Notochoerus*.

3.2. Ecology of Nyanzachoerus and Notochoerus at Kanapoi

Because of their large size and abundance, *Nyanzachoerus* and *Notochoerus* can be inferred to have played a greater role in the Kanapoi ecosystem than modern suids in present-day Africa. The only possible predators of adult individuals were the saber-toothed felid *Homotherium* and perhaps the leopard-size *Dinofelis petteri*. We can imagine that they were able to thrive in the open, without the need to hide from these carnivores, especially if they lived in relatively large groups. The large size of the zygomatic bony expansions, whose display certainly played a role in agonistic behavior, also suggests life outside dense vegetation. On the basis of postcranial ecomorphology, Bishop et al. (1999) concluded that *Ny. kanamensis* inhabited intermediate habitats and *Notochoerus* closed ones, but this is hard to reconcile with the longer, more hypsodont teeth of the latter.

Cooke and Ewer (1972) and Cooke (1985) attempted some dietary interpretations from the cranial functional anatomy of *Nyanzachoerus*. One may hypothesize that the enlarged premolars were used to process tough food and that they were no longer needed in *Notochoerus* when its diet changed, also involving lengthening of the third molars and perhaps slightly increased hypsodonty. It is noticeable, however, that most premolars of *Ny. kanamensis* are little worn and that they seem to start being in full use only after the m1s and m2s are worn out. These authors also observed that the broad mandibular symphysis, the moderately developed rostral muscles, and the relative proportions of the temporalis and masseter muscles are intermediate between *Potamochoerus* and *Phacochoerus*, suggesting less rooting than in the former genus, but less grazing than in the latter.

Figure 5 shows the $\delta^{13}C$ values of the tooth enamel of suids of the *Nyanzachoerus-Notochoerus* group. Using the identifications provided by the authors, we distinguished those with short third
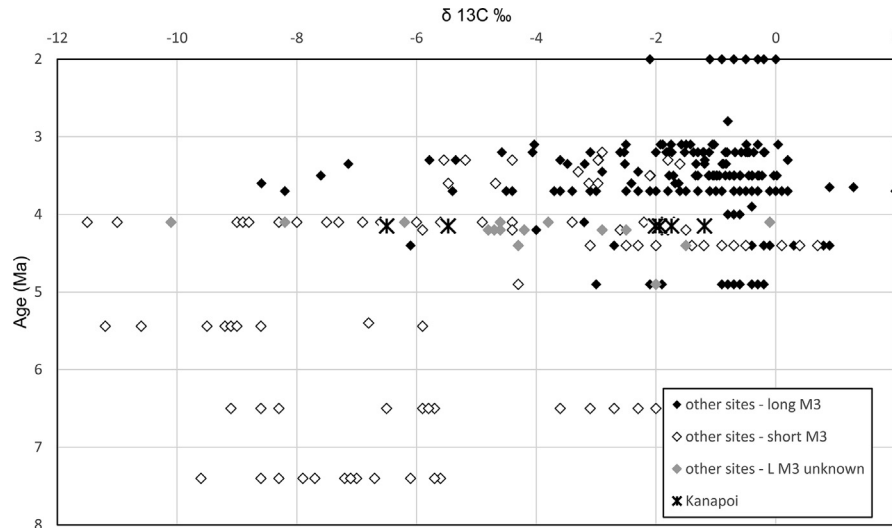
Figure 5. δ ^{13}C values of dental enamel of Central and Eastern African fossil Suidae of the *Nyanzachoerus-Notochoerus* group. Data (see SOM Table 1) from Zazzo et al. (2000), Harris et al. (2003), Levin et al. (2008), White et al. (2009), Kingston (2011), Uno et al. (2011), Bedaso et al. (2013), Boisserie et al. (2014), Drapeau et al. (2014), and Cerling et al. (2015).

molars (*Ny. kanamensis, Ny. tulotos-syrticus-australis*) from those with long ones (*No. jaegeri* and other *Notochoerus*), but this distinction is impossible for many specimens as isotope analyses are, regrettably, often conducted on fragments. In addition, it is likely that many of the identifications are not reliable, given the similarities between the various taxa. Given these reservations, the first obvious conclusion, in agreement with the observations of Harris and Cerling (2002), is that very few of them were pure browsers and that there is a general trend towards incorporation of more C$_4$ grasses in the diet. It is also clear that, on the whole, suids with long third molars were more grazers than those with short ones, but the correlation is far from perfect, as there are *Ny. kanamensis* that were grazers and some *Notochoerus* that were not. At Kanapoi, both grazers and mixed feeders coexist, but the material is too incomplete for species identification. Given the large overlap of

isotopic values in other sites of the 4.5−3 Ma time range, it is likely that the diets of these species also overlapped at Kanapoi, as also suggested by the similarities of their dentitions.

One of the most significant features of the Kanapoi suid assemblage is the absence of *Kolpochoerus*, which we regard as significant, given the large number of collected specimens. According to Brunet and White (2001), this genus makes its first appearance in the region at c. 4.4 Ma in the Middle Awash, but they also described older material from Kossom Bougoudi in Chad, and Pickford (2012) described (as *Dasychoerus*) a similar form from Wadi Natrun in Egypt. Still, the genus remains absent from many early Pliocene East African sites, including Galili (Kullmer et al., 2008) and the whole Turkana basin below the Tulu Bor tuff. This certainly lends support to the hypothesis of Pickford (2012) that the genus is of northern origin and derives from (or is identical with)

Table 2
Relative abundance of three suid groups of some Late Miocene to Pliocene African sites.[a]

Age (Ma)		*Notochoerus*	*Nyanzachoerus*	*Kolpochoerus*
3.2	Omo A-B-Usno	11	2	3
3.2	Hadar	100	33	54
3.3	Turkana: Tulu Bor-Lomekwi	21	0	x
3.3	Chad: Koro Toro	1	0	3
3.5	Lothagam: Kayumung	0	1	0
3.5	Kanam West	0	2	1
3.6	Wormil	4	1	16
3.7	Laetoli	7	2	6
3.7	Turkana: Moiti-Lokochot-Kataboi	1	2	0
4	Mursi	1	1	0
4.1	Kanapoi	19	31	0
4.2	Galili	4	4	0
4.2	Turkana: pre-Moiti	1	2	0
4.4	Aramis	7	37	17
4.4	Lothagam: Apak	0	2	0
4.5	Chad: Kollé	3	5	0
5	Nkondo	9	14	0
5.2	Middle Awash: Kuseralee	0	25	0
5.3	Chad: Kossom Bougoudi	0	2	10
5.8	MidAwash: Asa Koma	0	3	0
6	Lothagam: Upper Nawata	0	4	0
7	Lothagam: Lower Nawata	0	14	0

[a] *No. jaegeri* is grouped with *Notochoerus* because of its long third molars. Ages are approximate. Numbers are based upon the number of measurable m3s, except for Chadian sites (all specimens). Data from Harris et al. (1983), Harris and Leakey (2003), Fara et al. (2005), Kullmer et al. (2008), Haile-Selassie (2009), White et al. (2009), Bishop (2011), Gebreyesus (2011), Haile-Selassie and Simpson (2012), Drapeau et al. (2014), and our own observations. x = presence, but number of specimens unavailable or no measurable tooth.

the Eurasian *Dasychoerus*. We can imagine that in the early Pliocene of Ethiopia and Uganda these early *Kolpochoerus* were unable to compete with small *Nyanzachoerus* (*Ny. waylandi, Ny. kuseralensis*) and that it is only with the disappearance of these small species (extinction or evolution into larger forms) that *Kolpochoerus* became so successful. However, this tentative interpretation does not hold for the Turkana Basin, where no small *Nyanzachoerus* is known.

During the whole Pliocene, *No. jaegeri* and *No. euilus* progressively replaced *Nyanzachoerus* (Table 2). The first representatives of *Notochoerus* appear at Nkondo (assuming that the date of 5 Ma is correct) and perhaps Aramis and Kollé (but this material still has to be published). The shift in relative abundance mainly takes place between c. 4 and 3.3 Ma. It may have to do with climate change but is very progressive throughout the Pliocene.

4. Conclusions

The current collection of Pliocene Kanapoi Suidae consists of at least 120 distinct specimens (individuals), most of these identified as *Nyanzachoerus kanamensis*, and the remaining ones as *Notochoerus jaegeri*. These two species are closely related and may constitute an ancestor-descendant evolutionary relationship, although establishing the exact nature of this transition remains a key problem in African Pliocene suid evolution. Thus, the Kanapoi fauna samples only one of the subfamilies (and one tribe) of suids: the Tetraconodontinae. Contemporaneous suids present elsewhere in Africa, most notably *Kolpochoerus*, remain absent from the collection, probably for biogeographical reasons (rather than insufficient sampling). Suids along with other mammals play a prominent role in environmental and ecological reconstructions of Pliocene African sites. The stable isotopic signature of Kanapoi suids indicates that both *Nyanzachoerus kanamensis* and *Notochoerus jaegeri* were mixed feeders (following the dietary classification of Cerling et al., 2015), suggesting that the habitats shared by these species with early *Australopithecus* were mosaics of grassy and woody vegetation. These data are included in a broader paleoecological discussion of Kanapoi elsewhere in this volume.

Acknowledgments

Appendix A. Supplementary Online Material

Supplementary online material related to this article can be found at http://dx.doi.org/10.1016/j.jhevol.2017.05.004.

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