

# Newly Discovered Crania of *Nyanzachoerus jaegeri* (Tetraconodontinae, Suidae, Mammalia) from the Woranso-Mille (Ethiopia) and Reappraisal of Its Generic Status

Hailay G. Reda<sup>1</sup> · Ignacio A. Lazagabaster<sup>2</sup> · Yohannes Haile-Selassie<sup>3,4</sup> 

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**Abstract** Suids are among the most common mammalian groups in the Plio-Pleistocene vertebrate fossil record of Africa and the most studied largely due to their significance as biochronological indicators. However, despite their abundance in the fossil record, the remains are mostly isolated teeth and fragmentary crania and mandibles. As a result, disagreements have persisted in terms of their taxonomy and phylogenetic relationships. Here, we present for the first time a detailed description of the cranial anatomy of *Nyanzachoerus jaegeri* based on two crania recovered from middle Pliocene deposits of the Woranso-Mille paleontological study area, Afar region, Ethiopia. Understanding the cranial morphology of this species is particularly significant given the recent reclassification of *Nyanzachoerus jaegeri* to the genus *Notochoerus* based largely on the incisor and symphyseal morphology of specimens from Kanapoi, Kenya. Here, we show that the two genera are clearly distinguished from each other by distinct morphological features of the cranium such as the shape of the braincase, orientation of the zygomatic arches, and premolar/molar ratio, among others. Furthermore, we show that the mandibular and dental morphological features

identified by some workers as characteristic of *Notochoerus* are variable among tetraconodont species and that *Nyanzachoerus jaegeri* best fits within the genus *Nyanzachoerus*.

**Keywords** *Notochoerus* · *Nyanzachoerus jaegeri* · Woranso-Mille · Middle Pliocene · Ethiopia · Taxonomy · Suidae

## Introduction

Suids are among the most common and well-studied elements in Plio-Pleistocene faunal assemblages of Africa and their evolutionary history is better understood compared to other mammalian taxa (White and Harris 1977; Cooke 1978a; Cooke and Wilkinson 1978; Harris and White 1979; Harris 1983; Bishop 1994, 2010, 2011; Fesseha 1999; Kullmer 2008). As a result, they are used for biochronological age determination at sites where ages from radioisotopic dating are unattainable. Although the large number of Plio-Pleistocene fossil suids recovered in Africa since the early 1960s has resulted in the naming of several new genera and species (e.g., Cooke and Ewer 1972; Bishop 1994; Haile-Selassie and Simpson 2013; Boisserie et al. 2014), there are still apparently unresolved taxonomic and phylogenetic issues within the main African suid groups at the subfamily, generic, and specific levels (van der Made 1999; Haile-Selassie 2009; Bishop 2010; Pickford 2013; Boisserie et al. 2014).

According to Harris and Liu (2007), African suids can be grouped in seven subfamilies: Namachoerinae, Schizochocerinae, Kubanochoerinae, Listriodontinae, Cainochoerinae, Tetraconodontinae, and Suinae. However, Pickford (1993, 2007), van der Made (1999), and Orliac et al. (2010) did not recognize Schizochocerinae and Kubanochoerinae and argued that

✉ Yohannes Haile-Selassie  
yhailesselassie@cmnh.org

<sup>1</sup> Department of Anthropology, University of Oregon,  
Eugene, OR 97403, USA

<sup>2</sup> Institute of Human Origins, School of Human Evolution and Social  
Change, Arizona State University, Tempe, AZ 85281, USA

<sup>3</sup> Department of Physical Anthropology, Cleveland Museum of  
Natural History, Cleveland, OH 44106, USA

<sup>4</sup> Departments of Anthropology, Anatomy, Cognitive Sciences, and  
Biology, Case Western Reserve University, Cleveland, OH 44106,  
USA

these groups should most likely be included within the Listriodontinae (van der Made 1999; Orliac et al. 2010). The Listriodontinae and Cainochoerinae dominated the early and middle Miocene of Africa, but the Tetraconodontinae, which were already present in the late early Miocene (Pickford 1993, 2007; van der Made 1999; Bernor et al. 2004), became very abundant during the late Miocene and Pliocene until they went extinct during the early Pleistocene (Pickford 1986). Currently, all modern African suid taxa are members of the subfamily Suinae (Gongora et al. 2011). The subfamily Tetraconodontinae in Africa comprises two genera, *Nyanzachoerus* Leakey, 1958, and *Notochoerus* Broom, 1925, each of which is represented by numerous species (Cooke and Maglio 1972; Cooke 1978a, 1978b; Cooke and Wilkinson 1978; Harris and White 1979; Harris 1983; Bishop et al. 1999; Fesseha 1999; Harris and Leakey 2003; Harris et al. 2003; Cooke 2007; Kullmer 2008), though Leakey (1958) and van der Made (1999), among others, recognized an additional African genus, *Sivachoerus* Pilgrim, 1926. *Nyanzachoerus* was a large and dimorphic group of suids that possessed bunodont third molars and very large premolars (Harris and White 1979). The most derived species in terms of dental morphology is *Ny. jaegeri* Coppens, 1971, which differs from earlier and more primitive nyanzachoeres in having more elongated and hypsodont third molars, more elaborated molars, and relatively smaller premolars. Later tetraconodonts of the genus *Notochoerus* are yet more derived in having longer, more hypsodont, elaborated third molars, smaller premolars, and thinner enamel. Virtually almost all African suid experts agree that *Ny. jaegeri* is the most likely ancestor of the genus *Notochoerus* (White and Harris 1977; Cooke 1978a, 1978b; Harris and White 1979; van der Made 1999; Pickford 1993; Kullmer et al. 2008; Bishop 2010, 2011). In fact, the derived dental morphology of *Ny. jaegeri* has led some researchers to question the generic assessment of *Ny. jaegeri* and to include this taxon within *Notochoerus* (Fesseha 1999; Kullmer 1999, 2008; Harris and Leakey 2003; Harris et al. 2003; Bishop 2010, 2011) contra Harris and White (1979), Pickford (1993), and van der Made (1999), among others. For example, Harris et al. (2003) questioned the generic assignment of *Ny. jaegeri* based on their study of some mandibular specimens from Kanapoi that appeared to share morphological similarities with *Notochoerus* mandibles. As a result, they proposed that *Ny. jaegeri* be better placed as a species within the genus *Notochoerus*. Kullmer (1999) and Fesseha (1999) had suggested this reclassification earlier and Fesseha (1999) also proposed to rename *Ny. kanamensis* as *Notochoerus kanamensis*. While the latter suggestion did not receive much acceptance, Fesseha's (1999) and Kullmer's (1999) reclassification of *Ny. jaegeri*, reverberated by Harris and Leakey (2003) and Harris et al. (2003), was followed in subsequent works (e.g., Kullmer 2008; Bishop 2010, 2011). Harris and White (1979) considered that *Ny. jaegeri* was a likely descendant of an early stock of *Ny.*

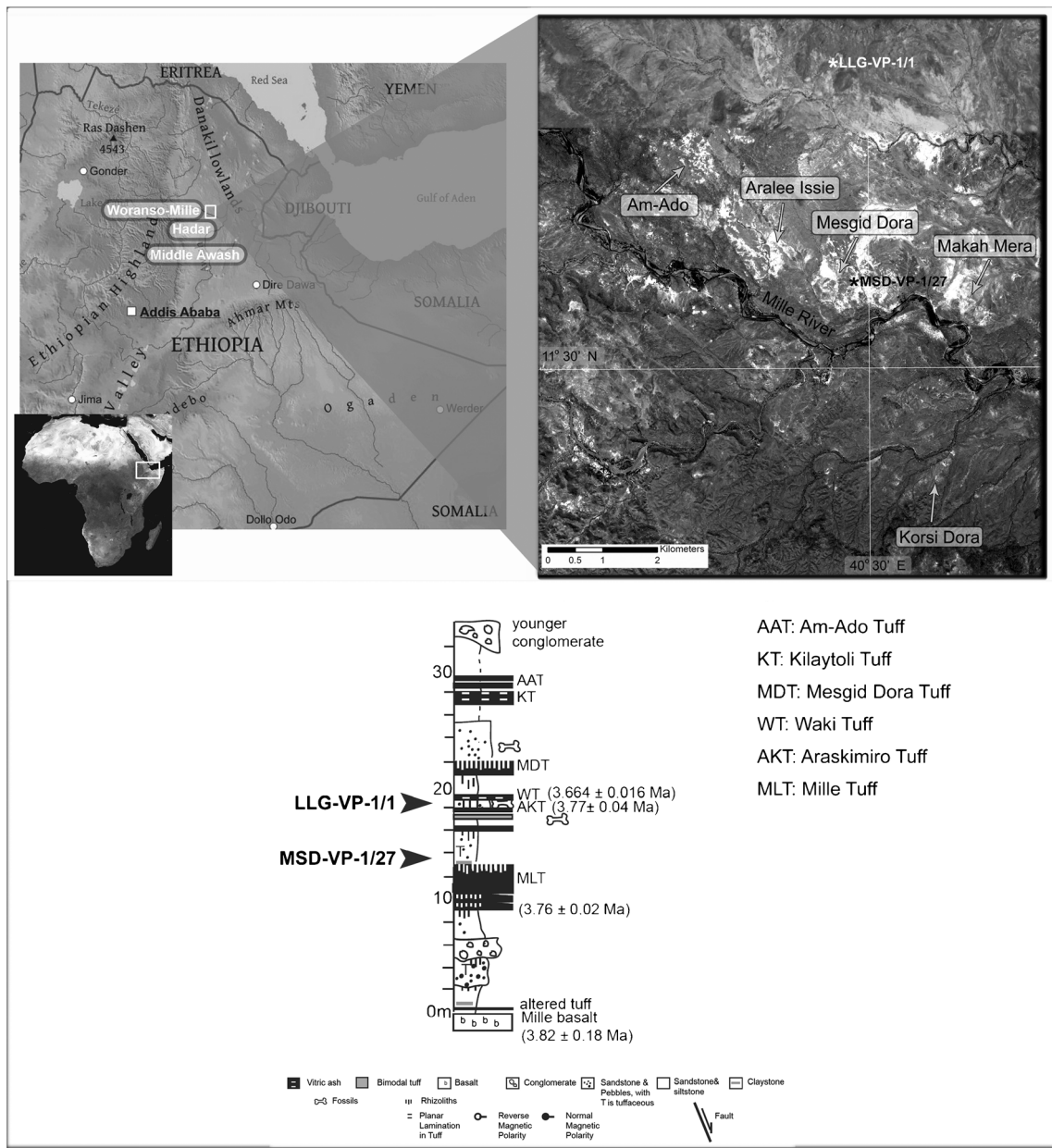
*kanamensis*, even though both taxa are conspecific and contemporaneous for much of their geographical and temporal ranges. Pickford (1993) and van der Made (1999) supported an anagenetic evolutionary lineage *Ny. kanamensis* – *Ny. jaegeri* – *Not. euilus* (Hopwood, 1926). However, van der Made (1999) restricted the name *Ny. kanamensis* to the material from Kanam, the type locality of the species but also of the genus *Nyanzachoerus*. The rest of the material attributed to *Ny. kanamensis* by Harris and White (1979) was previously assigned to *Ny. pattersoni* Cooke and Ewer, 1972, and was referred to the specimens from Kanapoi, Sidi Hakoma Member of the Hadar Formation, and the Lonyumun, Moiti, Lokochot, Tulu Bor, and Lower Burgi members of the Koobi Fora Formation. For van der Made (1999), the difference between this material and the holotype and the rest of *Ny. kanamensis* material from Kanam was large enough to warrant different genus attribution, and he assigned the *Ny. pattersoni* material to *Sivachoerus pattersoni* (Cooke and Ewer, 1972).

The nomenclatural disagreements mentioned above are also apparent within the genus *Notochoerus*. For example, recently, Pickford (2013) argued that the genus *Notochoerus* has to be limited to the type species *Notochoerus capensis* Broom, 1925, because the latter species is a suine. He suggested that the rest of the material traditionally assigned to *Notochoerus* should be reassigned into the genus *Gerontochoerus* Leakey, 1943, a name used to refer to specimens from the Shungura Formation of the Omo Basin, Ethiopia. Pickford (2013) not only resurrected the genus name *Gerontochoerus*, but also divided the previously known *Not. euilus* hypodigm into two species – *G. euilus* and *G. koobiforensis* Pickford, 2013, and subsumed *Notochoerus clarki* White and Suwa, 2004, into *G. euilus* and *Notochoerus harrisi* van der Made, 1998, into *G. scotti*.

With the taxonomy and phylogenetic relationships of Pliocene tetraconodonts now being in a state of flux, our goal in this paper is to specifically examine the reassignment of *Ny. jaegeri* to *Notochoerus* using two newly discovered suid crania from the Woranso-Mille study area, dated to 3.82–3.66 million years ago (Ma) (Fig. 1). This work also represents the first comprehensive description of the cranial anatomy of *Ny. jaegeri*, as there were no previously known complete crania of the species, except for a partial cranium discovered from Kanapoi and initially described by Cooke and Ewer (1972) as *Nyanzachoerus plicatus*, sp. nov.

### Spatial and Temporal Distribution of *Nyanzachoerus jaegeri*

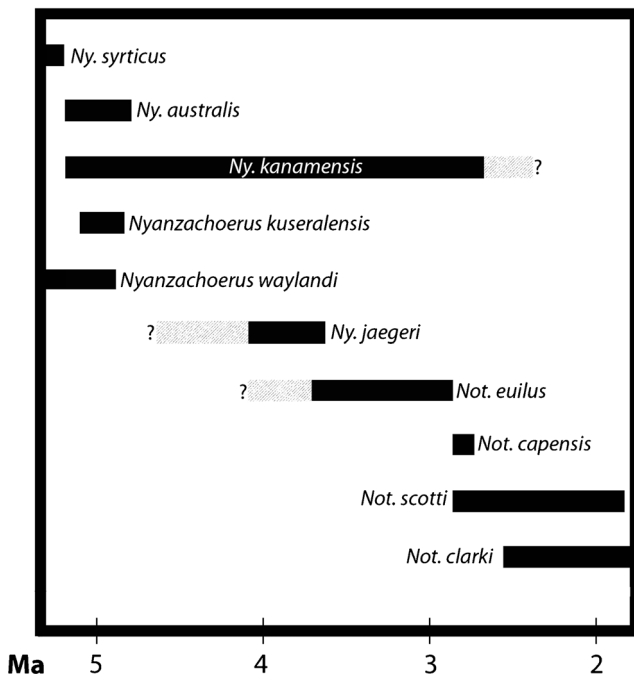
Tetraconodonts first appear in the African fossil record sometime during the late Miocene (Pickford 1986). Their Pliocene record consists of at least ten species in two genera (*Nyanzachoerus* and *Notochoerus*) (Fig. 2) (Harris and White 1979; though see van der Made 1999). *Nyanzachoerus jaegeri*,



**Fig. 1** Location Map of the northern Woranso-Mille study area (top) and a composite stratigraphy, age, and provenience of tetraconodont-bearing localities (below) at Woranso-Mille. Modified from Deino et al. (2010) and Saylor et al. (2016)

the subject of this study, was first recognized by a partial right mandibular corpus with p2-m3, partial left mandibular corpus with p3-m3, two isolated left upper molars, and fragments of an isolated right upper molar, recovered from Hamada Damous, Tunisia (Coppens 1971). Subsequently, Cooke and Ewer (1972) described similar fossil specimens collected from Kanapoi, Kenya, but named a new species, *Nyanzachoerus plicatus*, while they retained the species name *Ny. jaegeri* to refer to the material from North Africa. A few years later, these two names were synonymized (White and Harris 1977; Cooke and Wilkinson 1978; Harris and White 1979) with *Ny. jaegeri* having priority. This species is considered to be a progressive

tetraconodontine and an advanced form of the genus *Nyanzachoerus* (Cooke and Ewer 1972; Cooke and Wilkinson 1978; Harris and White 1979; Kullmer et al. 2008; Bishop 2010, 2011). It has been identified from a number of Pliocene sites in Africa, including the Pelletal Phosphorite Member of Langebaanweg (South Africa; Cooke and Hendey 1992), Mursi Formation of Omo (Ethiopia; Cooke 1978a, 1978b, 2007), Kolle (Chad; Brunet 2001), Chiwondo Beds (Malawi; Kullmer 2008), Lothagam, Ekora, Aterir, the Chemeron Formation, and Kanapoi in Kenya (Cooke and Ewer 1972; Harris and Leakey 2003; Harris et al. 2003), and the Nkondo Formation of the Albertine Rift in Uganda (Pickford 1994). It



**Fig. 2** Temporal distribution of African Pliocene tetraconodonts. Horizontal *black bars* represent securely dated occurrences; *grey bars* represent uncertain identifications or estimated dates of occurrence

has also been recently reported from the Mount Galili Formation (Ethiopia; Kullmer et al. 2008). Based on fragmentary teeth, Bishop (2011) also reported its presence at Laetoli from the Lower Laetolil Beds (4.36–3.85 Ma) and from below Tuff 2 of the Upper Laetolil Beds (3.86–3.79 Ma; Deino 2011). In fact, Harris et al. (2003) had previously suggested that the massive upper molars from Laetoli and assigned to *Not. euilus* should be in fact be attributed to *Ny. jaegeri* due to their similarity with the specimens from Kanapoi. Despite the recognition of the species from numerous Pliocene sites in Africa, the fossil material representing *Ny. jaegeri* was limited to dental and mandibular specimens (Cooke and Ewer 1972; White and Harris 1977; Cooke 1978a; Harris and White 1979). As a result, the cranial morphology of this species is so far virtually unknown.

Based on its fossil record, *Ny. jaegeri* appears to have had a wide spatial distribution, extending from South Africa to eastern Africa, but a limited temporal distribution, restricted to between 4.35 Ma and 3.7 Ma (White 1995). However, there is no clear consensus on the First Appearance Datum (FAD) of this species even though it might go as far back as 5–6 Ma (White 1995; Hill 1995). The species might have been present in the Middle Awash of Ethiopia in sediments older than 4.4 Ma (Haile-Selassie 2009), in the latest Miocene/early Pliocene deposits of Langebaanweg of South Africa (White and Harris 1979; Cooke and Hendey 1992), and in the Tabarin and Chemeron formations of Kenya from deposits that may be as old as 5 Ma (Hill 1995; but see Bishop 2010). While its FAD is uncertain, its Last

Appearance Datum (LAD) has been widely accepted to be at 3.75 Ma based on specimens between the Cindery Tuff and VT-3 (=Wargolo) of the Middle Awash succession (White et al. 1993; White 1995). This date (ca. 3.75 Ma) has been used as the minimum age for Unit 2 of the Chiwondo beds based on the presence of 11 dentognathic specimens assigned to *Ny. jaegeri* (Sandrock et al. 2007; Kullmer 2008). However, it has been long known that many factors affect the determination of FAD and LAD of a species (see White 1995, for further discussions). First and Last Appearance Datums are susceptible to subjective interpretations and establishment of accurate provenience, which render the taxonomy and evolutionary relations more ambiguous. This is particularly of interest in light of the presence of *Ny. jaegeri* specimens in the Woranso-Mille study area from radi isotopically dated deposits that are younger than 3.7 Ma (see Fig. 1).

### On the Generic Affinity of *Nyanzachoerus jaegeri*

The taxonomy and generic affinity of *Ny. jaegeri* has been a subject of interest for the last two decades with some researchers claiming that this species is best placed in the genus *Notochoerus* (Fesseha 1999; Kullmer 1999, 2008; Harris and Leakey 2003). Fesseha (1999) and Harris and Leakey (2003) argued that *Ny. jaegeri* shares derived dental and mandibular features with *Not. euilus*. They indicated that the shape and breadth of the mandibular symphysis, the horizontal arrangement of the lower incisors, and lower canine orientation of *Ny. jaegeri* are important features that resemble *Not. euilus* rather than *Ny. kanamensis* or *Ny. syrticus* (Leonardi, 1954) (Harris and Leakey 2003; see also Bishop 2010). In sharp contrast to *Ny. kanamensis*, the postero ventral border of the symphysis projects below the inferior surface of the corpus, which is long, narrow, and lightly built (Harris and Leakey 2003; Harris et al. 2003). Reduction of the posterior premolars and elaboration of the third molars in *Ny. jaegeri* are also argued to be indicative of its affinity with the genus *Notochoerus* (Fesseha 1999; Harris and Leakey 2003; Harris et al. 2003; Kullmer 2008; Kullmer et al. 2008; Bishop 2010, 2011). Harris and White (1979), on the other hand, recognized *Ny. jaegeri* as a species morphologically and phylogenetically intermediate between *Ny. kanamensis* and *Not. euilus* but included it in the former genus.

Kullmer (1999) further argued for the assignment of *Ny. jaegeri* into the genus *Notochoerus* by looking at notochoerine enamel wear pattern. The lateral pillars of *Ny. jaegeri* molars tend to indicate deep mesial and distal vertical enamel folds as seen in *Not. euilus* (Kullmer 2008; Kullmer et al. 2008; Bishop 2010). Cooke and Ewer (1972) have long-established the complex enamel folding of the molars of *Ny. jaegeri* (= *Ny. plicatus*) compared to *Ny. kanamensis* and *Ny. pattersoni*. As a result, the same authors have suggested the possibility of transferring *Ny.*

*plicatus* (= *Ny. jaegeri*) to a distinct genus due to its smaller third and fourth premolars associated with more complex third molars compared to *Ny. pattersoni* (= *Ny. kanamensis*). However, additional morphological evidence, particularly in relation to cranial anatomy, was required in order to warrant separation at the generic level.

### Institutional and Locality Abbreviations

The following institutions house the specimens studied (cited in text and [Appendix](#)): **KNM** – National Museums of Kenya, Nairobi; **NME** – National Museum of Ethiopia, Addis Ababa. Fossil specimens from the Woranso-Mille have three-letter abbreviation for the locality name, followed by “-VP-” (vertebrate paleontology); **AMA** – Am-Ado; **ARI** – Aralee Issie; **LLG** – Lehaysule Guda; **MKM** – Makah Mera; **MSD** – Mesgid Dora (see Fig. 1 for locations); other locality abbreviations are as follows: **A.L.** – Hadar, Ethiopia; **KNM-ER** – East Rudolf, Kenya; **KNM-KP** – Kanapoi, Kenya.

### Dental Abbreviations

**I1** – upper first incisor; **i1** – lower first incisor; **I2** – upper second incisor; **i2** – lower second incisor; **I3** – upper third incisor; **i3** – lower third incisor; **M1** – upper first molar; **m1** – lower first molar; **M2** – upper second molar; **m2** – lower second molar; **M3** – upper third molar; **m3** – lower third molar; **P2** – upper second premolar; **p2** – lower second premolar; **P3** – upper third premolar; **p3** – lower third premolar; **P4** – upper fourth premolar; **p4** – lower fourth premolar.

### Materials and Methods

The Woranso-Mille specimens included in this study are two relatively complete crania recovered from middle Pliocene deposits that have been radioisotopically dated to 3.82–3.66 Ma (see below for details). One of these crania was initially described by one of us (HGR) as part of a Masters thesis (Reda 2011). Comparative materials from sites outside Ethiopia are mostly those that have been fully published and available in the literature (see below). However, we studied the originals of the Woranso-Mille specimens and other *Nyanzachoerus* and *Notochoerus* specimens recovered from Pliocene sites in Ethiopia housed at the NME. Table 1 provides the list of specimens from Woranso-Mille and those included in the descriptive and comparative analyses. The methods of cranial morphological description, measurement techniques (especially for the length of premolars to molars), and terminologies are adopted from Harris and White (1979) and supplemented with those from Fesseha (1999) and Cooke (2007). The techniques used to measure cranial dimensions follow van der Made (1996) and Driesch (1976).

Comparative cranial samples include both original and published fossil materials of *Ny. jaegeri*, *Ny. kanamensis*, and *Not. euilus* available from various eastern African localities (Table 1) housed at NME and KNM. The designations of these species are based on the traditional and most-commonly accepted taxonomy proposed by Harris and White (1979). The material referred here to *Ny. kanamensis* is what was initially recognized as *Ny. pattersoni* by Cooke and Ewer (1972) and *Sivachoerus pattersoni* by van der Made (1999), while the material referred here as *Not. euilus* is recognized as *Gerontochoerus euilus* or *Gerontochoerus koobiforaensis* by Pickford (2013). The only cranial specimen of *Ny. jaegeri* available for comparison is a badly crushed partial skull from Kanapoi (KNM-KP 251; Cooke and Ewer 1972; Harris et al. 2003). *Nyanzachoerus kanamensis* specimens included in the comparative analysis comprise KNM-KP 264, KNM-KP 239, KNM-KP 30186, A.L. 107–13, and A.L. 137–4. KNM-KP 264 is a damaged skull of an old male individual with an associated but incomplete mandible (Cooke and Ewer 1972; Harris et al. 2003). KNM-KP 239 is an almost complete skull of an adult female individual associated with a mandible, atlas, and damaged thoracic vertebra (Cooke and Ewer 1972; Harris et al. 2003). KNM-KP 30186 is a well-preserved male cranium (Harris et al. 2003). The Kanapoi specimens are dated to between 4.07 and 4.17 Ma (Feibel 2003). The Hadar *Ny. kanamensis* skull A.L. 137–4 is an almost complete specimen of a presumed male with associated atlas vertebra, known from the lower Sidi Hakoma Member SH-2. A.L. 107–13 is a slightly damaged skull of a presumed female from the Upper Sidi Hakoma Member SH-3 (Cooke 1978b). Both skulls were recovered from sediments dated to between 3.4 and 3.22 Ma (Walter and Aronson 1993; Walter 1994).

Comparative crania of *Not. euilus* are mostly from the Hadar Formation and were initially described by Cooke (1978b). These specimens include A.L. 108–3, A.L. 171–1, A.L. 172–1, A.L. 342–9, and A.L. 167–15. A cranium from the Koobi Fora Formation, KNM-ER 3541, is also included in the analysis. A.L. 108–3 is a damaged skull partially retaining the dentition. Similarly, A.L. 171–1 is a damaged skull with both sides of the cheek teeth preserved. A.L. 172–1 is a well-preserved skull with slight damage at the occiput; however, it retains both the right and left cheek teeth. A.L. 342–9 is a young adult skull with associated mandible. The skull is damaged at the occiput and front of the snout. A.L. 167–15 is a damaged skull lacking the snout. However, most of the cheek teeth are present. A.L. 108–3 and A.L. 171–1 were recovered from the Lower (SH-2/3) and Upper (SH-3) Sidi Hakoma members, respectively (Cooke 1978b). However, they are generally within the 3.4–3.22 Ma time range (Walter and Aronson 1993; Walter 1994). The other three *Not. euilus* skulls from Hadar were recovered from the Denen Dora Member, DD-2 (Cooke 1978b) and they are dated to between 3.22 and 3.18 Ma (Walter 1994). The Koobi Fora specimen is a complete cranium associated with postcranial elements

**Table 1** List of the Woranso-Mille and other cranial specimens included in the comparative analysis

Specimen number	Age (Ma)	Site	Taxon
MSD-VP-1/27	3.66–3.82	Woranso-Mille, Ethiopia	<i>Ny. jaegeri</i>
LLG-VP-1/1	3.66–3.82	Woranso-Mille, Ethiopia	<i>Ny. jaegeri</i>
KNM-KP 251	4.17–4.07	Kanapoi, Kenya	<i>Ny. jaegeri</i>
A.L. 107–13	3.4–3.22	Hadar, Ethiopia	<i>Ny. kanamensis</i>
A.L. 137–4	3.4–3.22	Hadar, Ethiopia	<i>Ny. kanamensis</i>
KNM-KP 239	4.17–4.07	Kanapoi, Kenya	<i>Ny. kanamensis</i>
KNM-KP 264	4.17–4.07	Kanapoi, Kenya	<i>Ny. kanamensis</i>
KNM-KP 30186	4.17–4.07	Kanapoi, Kenya	<i>Ny. kanamensis</i>
A.L. 108–3	3.4–3.22	Hadar, Ethiopia	<i>Not. euilus</i>
A.L. 167–15	3.22–3.18	Hadar, Ethiopia	<i>Not. euilus</i>
A.L. 171–1	3.4–3.22	Hadar, Ethiopia	<i>Not. euilus</i>
A.L. 172–1	3.22–3.18	Hadar, Ethiopia	<i>Not. euilus</i>
A.L. 342–9	3.22–3.18	Hadar, Ethiopia	<i>Not. euilus</i>
KNM-ER 3541	3.22–2.9	Koobi Fora, Kenya	<i>Not. euilus</i>

(Harris and White 1979; Harris 1983). It was recovered from unit 2 of the Koobi Fora Formation area 117 (Harris and White 1979; Harris 1983). Harris and White (1979) had biochronologically correlated the *Not. euilus* specimens from unit 2 of the Koobi Fora Formation with the Hadar Denen Dora Member and Omo Shungura Formation Member B. Radiometrically, the sediments are dated to between 4.10 Ma and 3.32 Ma based on the Moiti Tuff and Toroto Tuff, respectively (McDougall 1985). All data generated or analyzed during this study are included in this published article, or available in publications cited in the text.

**Descriptive Methods** The cranial description includes observation of the character states on both right and left sides of an individual so that variations due to taphonomic factors or natural bilateral asymmetry could be documented. For specimens that lack one side of a paired skeletal part like the zygomatic knob of MSD-VP-1/27, description is based only on the preserved side. Cranial character state description is adopted from Cooke and Ewer (1972), Harris and White (1979), and Harris et al. (2003) (see Appendix).

**Linear Measurement Methods** Cranial dimensions of the Woranso-Mille specimens under consideration were measured using manual and digital calipers. Standard measures and measurement techniques were adopted from van der Made (1996) and Driesch (1976). All measurements are reported in millimeters (mm). The manual caliper was largely used to measure cranial dimensions greater than 140 mm and complete tooth rows. Every cranial dimension was measured three times at different days and the difference between these measurements was not statistically significant (1–2 mm). Therefore, what is reported in this study is the mean value of all three measurements. Craniodental measurements of the comparative

specimens listed in Table 1 were taken from published sources (Cooke and Ewer 1972; Cooke 1978b; Harris and White 1979; Harris et al. 2003). Measurements related to lengths such as vertex length, basilar length, palatal length, skull length, and premolar and molar series length were taken along the sagittal axis of the skull. However, cranial dimensions related to breadths such as bizygomatic breadth, muzzle breadth, bicondylar breadth, palatal and premaxillary breadth, are measured along the plane perpendicular to the skull axis. In measuring the cranial metric values, dimensions are taken from the two ends (reference points) of the character state only when a specimen is complete. However, if a specimen is incomplete and only a single point is present and the midline is preserved, the measurement is conducted from one end to a midpoint of the axis and then the result is doubled. For instance, the bizygomatic breadth of MSD-VP-1/27 was calculated using this approach as the left side is not preserved. The cranial morphological features and quantitative values of the Woranso-Mille specimens were compared to those of *Ny. kanamensis* and *Not. euilus* specimens from other Pliocene sites in eastern Africa. Cranial dimensions were compared using descriptive statistics primarily based on the mean values for the three taxa.

### Systematic Paleontology

Suidae Gray, 1821

Tetraconodontinae Lydekker, 1876

*Nyanzachoerus* Leakey, 1958

#### Synonyms

*Sivachoerus* Pilgrim, 1926

*Sivachoerus* (sensu van der Made 1999)

Other synonyms in Harris and White (1979)

**Type Species** *Nyanzachoerus kanamensis* Leakey, 1958

**Included Species** The type species; *Nyanzachoerus devauxi* (Arambourg, 1968); *Nyanzachoerus syrticus* (Leonardi, 1954); *Nyanzachoerus tulotos* Cooke and Ewer, 1972; *Nyanzachoerus australis* Cooke and Hendey, 1992; *Nyanzachoerus kuseralensis* Haile-Selassie, 2009, *Nyanzachoerus waylandi* (Cooke and Coryndon, 1970); *Nyanzachoerus khinzir* Boisserie et al., 2014; *Nyanzachoerus jaegeri* Coppens, 1971.

**Distribution** Late Miocene to late Pliocene of Africa.

**Diagnosis** A genus of the family Suidae that possesses large posterior (third and fourth) premolars in relation to the anterior premolars and in general, simple bunodont molars similar to *Potamochoerus* Gray, 1854, but taller and with thicker enamel; molars have cusps that, when worn, show dentine islands forming a star shape; more derived specimens show a trend towards increased elaboration of the third molars and reduced premolars; incisors wide and large; upper canines oval to flattened oval in transverse section; lower canines verrucose with thin, weakly grooved enamel on two lateral faces; strong sexual dimorphism characterized by larger size, robustness, massiveness of skull, and the presence of large zygomatic knobs in males; robust mandibles, with thick corpus that contrast with the unusually thin bone forming the angle (after Cooke and Ewer 1972, Harris and White 1979; Bishop 2010).

**Remarks** Van der Made (1999) retained the name *Sivachoerus* for the narrow-toothed (especially narrow premolars) specimens from the Western Gregory Rift (including *S. pattersoni* from Hadar and Kanapoi) and restricted the name *Nyanzachoerus* for the material including the type species *Ny. kanamensis* from Kanam, and the material assigned to *Ny. waylandi*, *Ny. cookei* Kotsakis and Inigo, 1980, and *Ny. jaegeri*. Harris and White (1979) recognized the high intra-specific variation within *Nyanzachoerus*, especially within *Ny. kanamensis*, and subsumed *Ny. pattersoni* into this species.

*Nyanzachoerus jaegeri* Coppens, 1971

**Synonyms**

*Notochoerus jaegeri* Fesseha, 1999; Harris and Leakey 2003  
Other synonyms in Harris and White (1979)

**Holotype** Partial right mandibular corpus with p2-m3, partial left mandibular corpus with p3-m3, left M2-M3, and fragments of right M3, from the same individual.

**Type Locality** Hamada Damous, Tunisia.

**Age of Type Locality** “Lower Villafranchian” (Pliocene)

**Temporal Distribution and Other Localities** Pliocene of Africa; Kanapoi, Lothagam, Ekora, Aterir, and the Chemeron Formation in Kenya, the Pelletal Phosphorite Member of Langebaanweg (South Africa), the Chiwondo Beds (Malawi), the Nkondo Formation of the Albertine Rift (Uganda), the Lower and Upper (below Tuff 2) Laetoli Beds (Tanzania), and the Omo Mursi Formation, Mount Galili Formation, and Woranso-Mille in Ethiopia.

**Diagnosis** A progressive species of the genus *Nyanzachoerus* with dental attributes that are intermediate in morphology and size between a more typical *Nyanzachoerus* condition and a more derived tetraconodont condition (genus *Notochoerus*) general skull morphology, number of premolars, number, morphology, and size of incisors, and enamel thickness as in *Nyanzachoerus*. Derived dental characteristics include longer third molars, molars with more enamel folding, and smaller premolars; otherwise general teeth architecture as in *Nyanzachoerus kanamensis*.

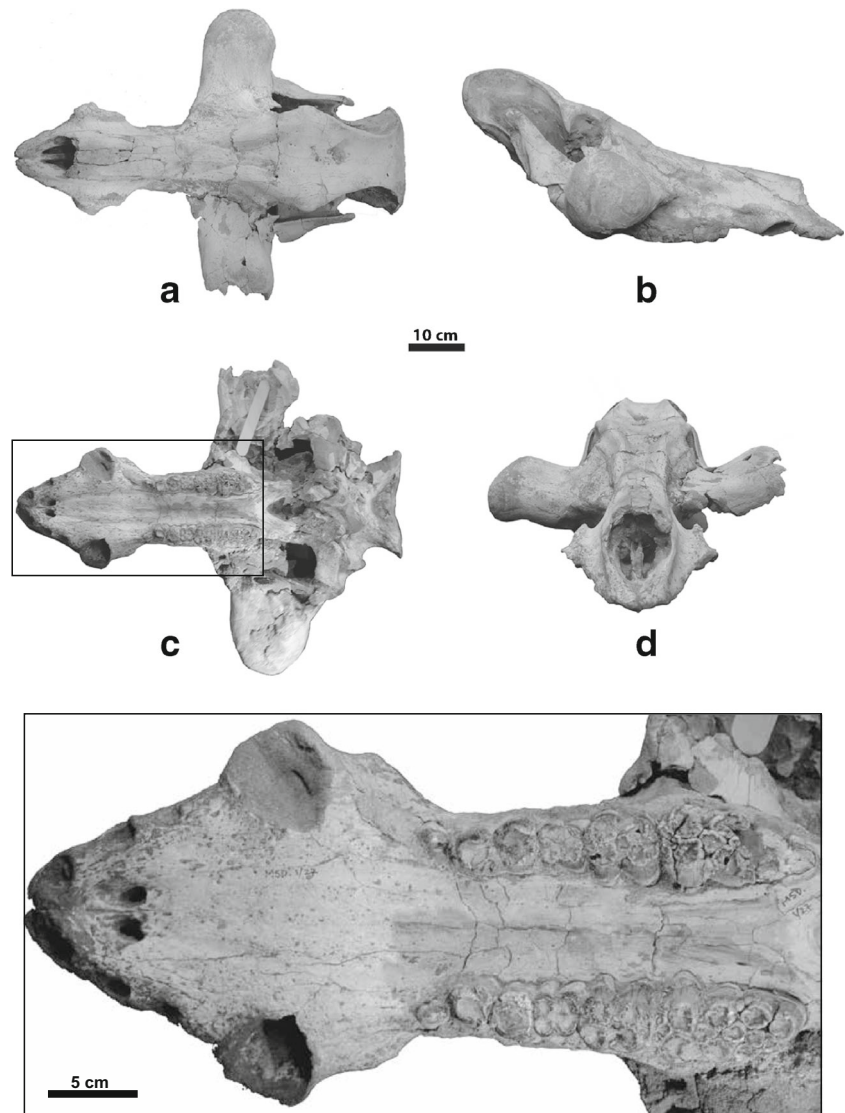
**Remarks** The First Appearance Datum (FAD) of this species is unclear but might go as far back as 5–6 Ma (White and Harris 1979; Cooke and Hendey 1992; White 1995; Hill 1995). The Last Appearance Datum (LAD) is now 3.66 Ma based on the specimens of Woranso-Mille described here.

**Referred Specimens from Woranso-Mille** MSD-VP-1/27, cranium with right and left P2-M3 (Fig. 3); LGG-VP-1/1, cranium with left P3, left M2–3, right P3 and right M2, associated edentulous mandibular fragment, as well as isolated left M2, fragmented left p3, left p2, right i1–i3, left i2, canine fragments, and other molar fragments (Fig. 4).

**Geological Context and age** MSD-VP-1/27 was recovered in situ in a cross-bedded pinkish and poorly consolidated sandstone horizon. Its provenience is well bracketed by the Waki Tuff (WT) above and the Mille Tuff sequence (MLT) below. Both tuffs are radiometrically dated to  $3.66 \pm 0.008$  and  $3.76 \pm 0.02$  Ma, respectively (Deino et al. 2010; Saylor et al. 2016; see Fig. 1). LGG-VP-1/1 was a surface find eroded from a sandstone stratigraphically positioned ca. 10 m below the Kilaytoli Tuff (KT) and ca. 3 m above the WT.

**Preservation** MSD-VP-1/27 is a well-preserved cranium with only a few parts missing (Fig. 3). The postcanine teeth are intact with only slight damage to the left M3. The incisors and canines are also missing although the alveoli are intact. The left zygomatic knob is partially broken but the right side is well preserved and intact. The basicranium is also well preserved, except for the missing left occipital condyle. The cranial vault, the frontal, and nasals are generally in a good state of preservation except for some cracks running along the skull’s longitudinal axis. Few transverse cracks are also apparent, smaller ones on

**Fig. 3** MSD-VP-1/27. **a** dorsal view; **b** right lateral view; **c** ventral view and close-up view of dentition and anterior part (*in square*); **d** anterior view



the cranial vault and wider ones on the frontal and nasals. The anterior end of the nasals is also broken. The occipital region is completely preserved. Towards the front of the cranium, the palate is also well preserved throughout its length. Both the right and left canine flanges are intact. In addition, the right orbital region is excellently preserved whereas the left side is broken at its infero lateral portion. The posterior half of the frontal and parietal are also well preserved. Based on its overall size and the large zygomatic knobs, it appears to be a large male.

LLG-VP-1/1 is relatively well-preserved cranium and associated with an edentulous mandible (Fig. 4). Both specimens were recovered in numerous broken pieces, most of which joined. The left C, P3, M2, and M3, as well as the right P3 and M2 are present. The palate is relatively well preserved except for a transverse crack immediately posterior to the P3s. Most of the basicranium is missing, but the occipital condyles are well preserved. The zygomatic arches are also missing except for some part preserved on the right side. The right orbital area is well

preserved except for some damage along the anterior edge of the orbital ridge. The supra-canine flanges on both sides are present.

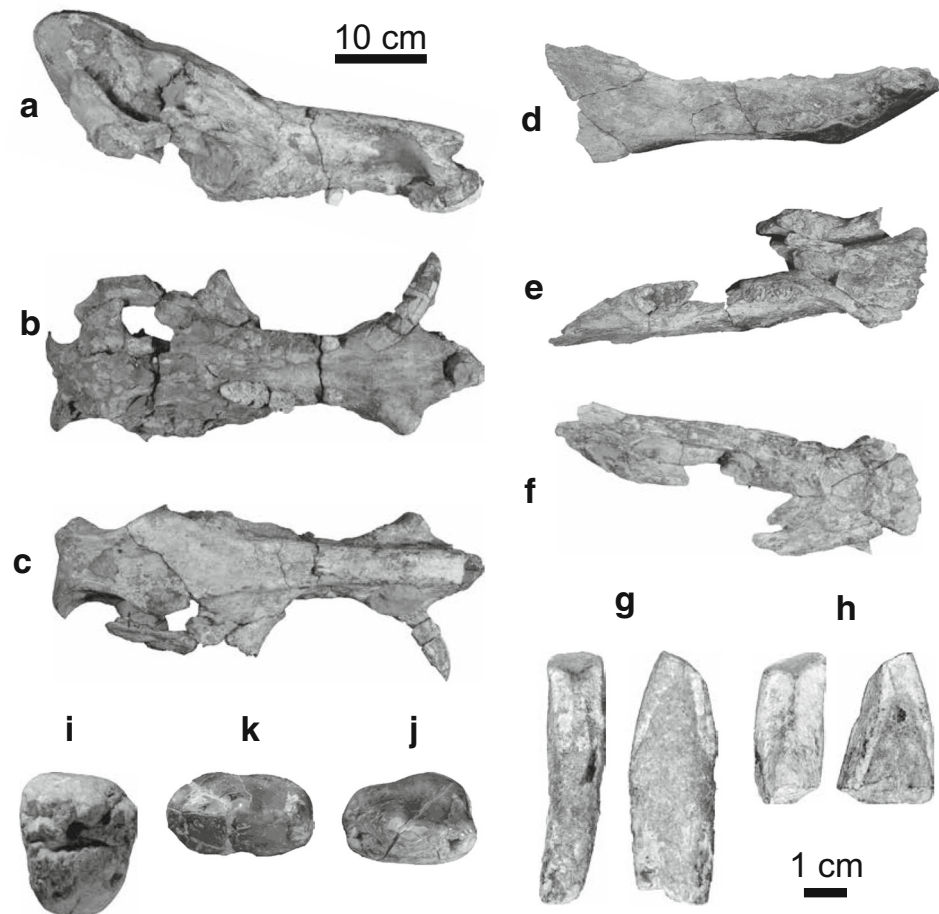
The associated edentulous mandible is relatively well preserved mainly on the right side and the symphysis is intact (Fig. 4). The right corpus has cracks oriented in different directions. There is a major crack running obliquely from the distal edge of the right canine to the symphyseal base at midline. Another transverse crack is present at the base of the ascending ramus. Towards the gonial angle, a longitudinal weak crack is also present. The mandibular condyle is missing. All of the teeth are missing and only the roots of p2–p4 and m3 on the right side are preserved. The left half of the mandible posterior to the canine is missing.

### Comparative Morphological Description

**Crania** Based on a partial cranium from Kanapoi (Kenya) and a few maxillary specimens from elsewhere, Cooke and Ewer



**Fig. 4** Associated cranium, mandible, and incisors of LLG-VP-1/1, and selected dental remains of *Ny. jaegeri* from Woranso-Mille. **a** right lateral view of cranium; **b** ventral view of cranium; **c** dorsal view of cranium; **d** right lateral view of mandible; **e** dorsal view of mandible; **f** ventral view of mandible; **g** right i1 in lingual (*left*) and proximal (*right*) views; **h** left i2 in lingual (*left*) and proximal (*right*) views; **i** AMA-VP-2/38, left P4; **j** MSD-VP-5/26, right P3; **k** MKM-VP-1/146, left P4



(1972), Harris and White (1979), and Harris et al. (2003) compiled a list of important cranial and dental morphological traits of *Ny. jaegeri* (= *Ny. plicatus*) (see Appendix). The single partial cranium from Kanapoi (Cooke and Ewer 1972) provided very little information on the species' cranial morphology.

MSD-VP-1/27 is the largest Pliocene tetraconodont cranium ever found in the fossil record with a vertex length of 646.7 mm and bizygomatic breadth of 526.7 mm (Table 2). LLG-VP-1/1 is only slightly smaller in terms of its vertex length. Both MSD-VP-1/27 and LLG-VP-1/1 show a transversely convex nasal region although it is flattened at midline towards its posterior half in MSD-VP-1/27 whereas it is slightly flat at the anteriormost part in LLG-VP-1/1. Most of the Hadar *Not. euilus* crania exhibit straight and parallel-sided nasals, whereas in *Ny. kanamensis* they appear to be curved upward such as in specimens like A.L. 107–13 (Cooke 1978a). The nasals in the Koobi Fora *Not. euilus* specimens such as KNM-ER 3540 and KNM-ER 3541 are convex posteriorly but bisected by medial depressions anterior to the canine alveoli. This area is virtually flat in *Ny. kanamensis* specimens such as KNM-KP 264 and KNM-ER 3183. This might indicate variability in the morphology of this region among the tetraconodonts. Both LLG-VP-1/1 and MSD-VP-

1/27 have nasals that are broader at the level of the supra-canine flange and progressively taper anteriorly. This is also a condition shared with *Ny. kanamensis* specimens such as A.L. 137–4 and KNM-ER 3183. In *Not. euilus* specimens, such as KNM-ER 3540 and 3541, the nasals are elongated and gently slope antero inferiorly. In MSD-VP-1/27, the nasal wall forming a junction with the maxilla extends from the zygoma to the canine alveolus. Laterally the nasal-premaxilla region is partially ossified. MSD-VP-1/27 also has a slightly broad supra-canine flange with weakly ornamented dorsal ridge, whereas this ridge is sharp in LLG-VP-1/1 but similarly less ornamented. Furthermore, the posterior part of the nasal region is bounded by prominent ridge-like structures emanating from the anterior edge of the orbit and fading immediately posterior to the infraorbital foramen. A supra-canine flange with ornamented dorsal ridge is also present in the Koobi Fora *Not. euilus* specimens KNM-ER 3540 and KNM-ER 3541. The supra-canine flange of the Woranso-Mille specimens continues posteriorly behind the canine alveolus almost to the level of the P2-P3 and their supra-canine gutter is relatively broad as in KNM-ER 3540 and KNM-ER 3541.

The orbital rim is relatively thick in both Woranso-Mille specimens. The posterior portion of the orbit is marked by

**Table 2** Comparative measurements of *Notochoerus eutilus* and *Nyanzachoerus kanamensis* crania from Koobi Fora, Hadar, and Kanapoi, and *Ny. jaegeri* from Woranso-Mille. Measurements for *Not. eutilus* and *Ny. kanamensis* were compiled from Cooke and Ewer (1972), Cooke (1978a), Fesseha (1999), and Harris and Leaky (2003)

Measurement	<i>Not. eutilus</i>										<i>Ny. kanamensis</i>										<i>Ny. jaegeri</i>	
	KNM-ER 3540	KNM-ER 3541	A.L. 172–1	A.L. 171–1	A.L. 342–9	A.L. 108–3	A.L. 167–15	Mean	KNM-KP 264	KNM-KP 30186 M	KNM-KP 239	A.L. 107–13	A.L. 137–4	Mean	MSD-VP- 1/27	LLG-VP- 1/1	Mean					
Vertex length (Max. Length)	–	–	580	610	620	395	620	565	620	–	480	457	580	534.25	646.7	630	638.35					
Basilar length	555	578	496	510	530	320	340	475.57	500	425	440	490	463.75	501.7	–	–	–					
Bizygomatic breadth	331	197	392	380	380	–	–	325	480	400	308	270	345.6	526.7	–	–	–					
Width postorbital processes	–	–	187	175	200	166	230	191.6	–	140	–	147	166	151	177.7	155	166.35					
Parietal constrictions	–	–	50	–	59	49	74	58	76	–	–	72.5	98	82.17	87	80.7	83.85					
Crest breadth/Max.width of occiput	–	–	–	–	–	135	178	156.5	–	136	–	108	155	133	183	148.1	165.55					
Greatest breadth across nasals	–	–	57	77	62	–	–	65.33	71	70	53	–	62	64	70	79.3	74.65					
Muzzle breadth between infraorbital foramen	–	–	65	70	80	–	–	71.67	66	–	48	–	56	56.67	71.3	63.9	67.6					
Canine flange breadth	134	157	163.5	–	–	–	–	151.5	136	–	–	136	169.3	164.2	166.75	–	–					
Palatal length	–	–	369	–	320	152	205	261.5	352	–	301	305	327.75	372.3	–	–	–					
Breadth of Palate at M3-M3	–	–	46.7	51.5	59	46.7	53.7	51.52	40	–	33	35	43	37.75	41.2	38.2	39.7					
Breadth of Palate at P3-P3	–	–	53.1	58	79	–	67.3	64.35	73	–	52.5	40.2	71.5	59.3	66.3	66.6	66.45					
Premaxilla breadth at I3-I3	–	–	–	–	–	–	–	–	95	–	69	–	76	80	81.8	74.8	78.3					
Diastema I1-P3	–	–	175	–	–	–	–	–	–	–	–	–	–	177.2	170.3	173.75	–					
Diastema C-P3	–	–	74	–	–	–	–	–	–	–	–	–	–	61.3	51.2	56.25	–					
Diastema I3-P2	–	–	–	–	–	–	–	–	101	–	72	–	–	86.5	110.2	120.3	115.25					
Diastema C-P2	–	–	–	–	–	–	–	–	35	–	39.5	–	49	41.17	49.4	41.3	45.35					
Length of pre-molar series	–	–	29.8	31.5	–	–	33	31.43	68	–	51.9	50.3	56.5	56.68	54.9	50.0	52.45					
Length of M1-M3	–	–	111.6	119.1	–	129	131.7	122.85	99.1	–	95.2	92	105.5	97.95	118.3	–	–					
Length of P2-M3	–	–	–	–	–	–	–	–	161	–	147	142	162	153	175	164.5	169.75					
Length of P3-M3	–	–	141.4	150	–	–	164	151.8	–	–	–	–	–	160.7	154.6	157.65	–					
Length of P3-P4	–	–	–	–	–	–	–	–	–	–	–	–	–	41.5	38.8	40.15	–					
Length of molar series	–	–	–	–	–	–	–	–	–	–	–	–	–	117.1	113.8	115.45	–					
Dental length	–	–	–	–	–	–	–	–	–	–	–	–	–	358.5	340.0	349.25	–					
Condylbasal length	–	–	–	–	–	–	–	–	–	–	–	–	–	525	–	–	–					
Premolar-Prosthion	–	–	–	–	–	–	–	–	–	–	–	–	–	185.8	175.9	180.85	–					

**Table 2** (continued)

Measurement	<i>Not. euilus</i>						<i>Ny. kanamensis</i>				<i>Ny. jaegeri</i>						
	KNM-ER 3540	KNM-ER 3541	A.L. 172-1	A.L. 171-1	A.L. 342-9	A.L. 108-3	A.L. 167-15	Mean	KNM-KP 264	KNM-KP 30186 M	KNM-KP 239	A.L. 107-13	A.L. 137-4	Mean	MSD-VP-1/27	LLG-VP-1/1	Mean
Short skull length	-	-	-	-	-	-	-	-	-	-	-	-	-	-	329.7	-	-
Max. Palatal breadth	-	-	-	-	-	-	-	-	-	-	-	-	-	-	121.2	115.6	118.4
Estimated Bicondylar width	-	-	-	-	-	-	-	-	-	-	-	-	-	-	82.7	-	-
Breadth of Palate at P3-P3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	42.0	49.2	45.6
Diastema I1-P2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	161.7	158.2	159.95
Mim. width of orbits	-	-	-	-	-	-	-	-	-	-	-	-	-	-	47.3	-	-

large postorbital processes in MSD-VP-1/27, while the process is smaller in LLG-VP-1/1. The area between the orbits is strongly concave in both Woranso-Mille specimens. This concavity extends posteriorly across the frontals and top of the braincase. *Nynzachoerus kanamensis* specimens such as A.L. 107–13 also show slight concavity between the orbits. However, the frontal area and top of the braincase of *Not. euilus* are flat (Cooke 1978a) even though KNM-ER 3541 shows a domed frontal region but without any sign of concavity. On the other hand, the frontal bone in A.L. 172–1 is marked by two depressions on either side of the sagittally-oriented ridge-like structure at the midline. In the two Woranso-Mille crania, the concave frontal bone is continuous with the top of the cranial vault with relatively little interruption. In LLG-VP-1/1, the frontal region between the orbits is bound by pronounced ridges running from the anterior edge of the orbit towards the posterior part of the nasals.

The large size and globular shape of the zygomatic knob of MSD-VP-1/27 indicate that this specimen more likely belonged to a male. It is more massive than male *Not. euilus* specimens such as A.L. 172–1. Its zygomatic protuberance diverges from the sagittal axis at right angles like KNM-KP 264, A.L. 107–13, and other Hadar *Ny. kanamensis* specimens. There is also a similarity in the origin of the root of the zygoma among MSD-VP-1/27, LLG-VP-1/1, and *Ny. kanamensis* specimens such as KNM-KP 264 and A.L. 172–1 where in almost all cases the zygoma originate immediately behind the infraorbital foramina.

Maximum width of the cranial vault in MSD-VP-1/27, LLG-VP-1/1, A.L. 137–4, A.L.172–1, and A.L.108–3 is at the postorbital processes and narrows towards the nuchal crest. The narrowing trend in *Not. euilus* specimens is sharp while slight tapering is apparent in the Woranso-Mille specimens. The parietal constriction is relatively broader in the Woranso-Mille *Ny. jaegeri* specimens and positioned more centrally on the cranial vault whereas *Not. euilus* has very narrow and posteriorly positioned parietal constriction (Cooke 1978b). The top of the braincase of the Woranso-Mille specimens is strongly concave along the sagittal length. It is also smoothly concave in *Ny. kanamensis* specimens such as KNM-KP 264 and A.L. 107–13. Likewise, a slight depression of this region is seen in KNM-KP 239 and A.L. 137–4. The presence of this depression in the Hadar *Ny. kanamensis* specimens was initially considered as an artifact of preservation (Cooke 1978b), although it was later proved to be a real cranial feature of the genus *Nyanzachoerus*. In sharp contrast, the top of *Not. euilus* crania such as KNM-ER 3541, A.L. 172–1, and A.L. 108–3 is flat. The naso-frontoparietal angulation is pronounced in MSD-VP-1/27, LLG-VP-1/1, KNM-KP 239, KNM-KP 30186, and KNM-ER 3183. Even though the angulation seems more pronounced in the males, as noted in MSD-VP-1/27 and KNM-KP 30186, even presumably female individuals of *Ny. kanamensis* such as A.L. 137–4, still

have slightly higher angulation than in *Not. euilus* males such as KNM-ER 3541 and A.L. 172–1.

The position of the temporal lines coincides with the lateral edges of the cranial vault in both of the Woranso-Mille *Ny. jaegeri* specimens. This condition is also seen in the *Not. euilus* specimen KNM-ER 3541. However, there is a strong difference in the shape and size of the temporal fossae where the *Ny. jaegeri* specimens have deeply excavated fossae, as does the *Ny. kanamensis* specimen A.L. 137–4, while KNM-ER 3541 and other *Not. euilus* specimens (e.g., A.L. 172–1 and A.L. 108–3) have generally very shallow fossae. However, edges of the cranial vault hang over the temporal fossae in almost all specimens regardless of the genus. On the parietal bones of MSD-VP-1/27, there are two transversely oriented foramina positioned superiorly. The right foramen is broad and shallow whereas the left is narrow and deep. Conversely, LLG-VP-1/1 has the foramen only on the left side.

The supraoccipital is laterally expanded below the nuchal crest and tapers towards the foramen magnum. This is a common feature in all three taxa. The occipital condyles in MSD-VP-1/27 are positioned midway between the plane of orbit and the palatal plane as in KNM-ER 3541 and KNM-KP 239. However, they are relatively small compared to those of the latter specimens. The angle between the parietal and supraoccipital region in MSD-VP-1/27 and LLG-VP-1/1 is acute (30°–35°). It is less acute (40°–47°) in *Ny. kanamensis* specimens, such as A.L. 107–13 and A.L. 137–4, and is much higher in *Not. euilus* crania, where it is 65°–70° in specimens such as A.L. 172–1.

The palate is relatively elongated in both Woranso-Mille specimens compared to *Ny. kanamensis*. It is expanded at the level of the canine alveoli and narrows anterior and posterior to it. Some *Ny. kanamensis* specimens such as KNM-KP 239 and KNM-KP 264 also show this feature. The shape of the palatonarial border is V-shaped in MSD-VP-1/27. This border also appears to have been V-shaped in LLG-VP-1/1, judging from the preserved parts of the notch. The notch is much narrower in KNM-KP 239, slightly broader in A.L. 137–4, and much broader in A.L. 172–1, indicating variability of this feature in tetracondonts. In MSD-VP-1/27, LLG-VP-1/1, A.L. 137–4, KNM-ER 3541, and A.L. 172–1, the position of the palatonarial notch is far posterior than the distal edge of the M3. The greater palatine foramina and incisive foramina are also present in MSD-VP-1/27. The greater palatine foramina are positioned between the first pillars of the M3 in this specimen. The incisive foramina are also very large and positioned at the I2 level. The palate of MSD-VP-1/27 is generally shallow.

It is obvious from the cranial comparative descriptions above that the two Woranso-Mille crania share more characters with *Ny. kanamensis* than with *Not. euilus*. However, compared to *Ny. kanamensis*, in addition to their absolutely much larger size, the Woranso-Mille crania have relatively and absolutely smaller premolars and M3s that have extra

pair of pillars and more complicated talons (see below for further discussions on dental metrics).

**Mandibles** MSD-VP-1/27 and LLG-VP-1/1 have associated mandibles although both of them lack teeth. However, the preserved roots show that p2 was present. The overall robusticity of these two mandibles is comparable to *Nyanzachoerus* mandibles where the corpus is inflated below the molars and premolars and associated with very wide retromolar sulcus. The symphysis of LLG-VP-1/1 is superiorly concave as in other *Nyanzachoerus* and early *Not. euilus* mandibles. One of the mandibular features that Harris et al. (2003) used to reassign *Ny. jaegeri* to *Notochoerus* is related to the morphology of the symphysis. Harris et al. (2003:75) stated that the symphysis of ‘*Notochoerus*’ *jaegeri* is “distinctly spatulate and flattened at the widest point across the canine alveoli.” Indeed, the specimens that they are referring to resemble *Not. euilus* rather than *Ny. kanamensis*. In fact, LLG-VP-3/60, a 3.66–3.76 Ma complete mandible with dentition of an early *Not. euilus* from the Woranso-Mille (Lazagabaster et al. in prep.) is morphologically (dental and mandibular) indistinguishable from the two Kanapoi mandibles (KNM-KP 30178 and KNM-KP 30452) referred to *Notochoerus jaegeri* by Harris and Leakey (2003). Further, the Kanapoi cranium KNM-KP 30617 is morphologically more similar to *Not. euilus* crania than it is to the *Ny. jaegeri* specimens from Woranso-Mille. The ‘drooping’ and posteriorly angled zygoma and minimal nasal to frontoparietal angulation in KNM-KP 30617, the slender mandibular corpora, and narrow but elongated third molars of KNM-KP 30178 and KNM-KP 30452 all indicate a closer affinity with *Not. euilus*. The inferred geological age of these specimens may have influenced their previous taxonomic assignment to *Ny. jaegeri* as their morphology would suggest a placement in *Not. euilus*. Thus, the Kanapoi specimens may very well represent the earliest representatives of *Not. euilus* and push back the FAD of the species to ca. 4.2 Ma.

**Dentition** African Pliocene tetracondonts show a general trend towards a decrease in overall size and number of premolars and increase in the third molar length. However, assignment of isolated teeth to a specific taxon has always been challenging. Hence, isolated teeth, particularly premolars and lower incisors, are not separately discussed in this paper. However, upper and lower incisors upper third molars are briefly discussed below due to their relevance to the taxonomic assignment of the Woranso-Mille specimens.

**Upper Incisors** The number of upper incisors appears to distinguish *Ny. jaegeri* from *Not. euilus*. MSD-VP-1/27 and LLG-VP-1/1 both have pairs of three incisors as judged from the alveoli of MSD-VP-1/27 and inference from the broken parts in LLG-VP-1/1. The same number of incisors is also

noted from the upper incisor sockets of KNM-KP 264. However, only a single pair of upper incisors is present in *Not. euilus* specimens such as KNM-ER 3540 and 3541 and the Hadar *Not. euilus* specimens.

**Lower Incisors** LLG-VP-1/1 is associated with isolated Li2 and Ri1-i3. The right first lower incisor is mesio-distally compressed (18.6 mm at the base) but very thick linguo-labially (12.8 mm at the base). The advanced wear does not allow for visualization of the lingual crests, but there is a well-developed non-occlusal lingual facet on the endocristid (the crest in the middle), like those that develop in modern taxa like *Sus* Linnaeus, 1758, and *Potamochoerus* (Lazagabaster 2013). The left second lower incisor has a well-developed endocristid with an incipient non-occlusal lingual facet. The postcristid (the distal crest) is visible but there is no sign of a precristid (the mesial crest) at this stage of wear. As the first lower incisor, the second lower incisor is very wide linguo-labially (20.7 mm at the base) but more compressed mesio-distally (13.8 mm at the base). Contrary to *Sus*, *Potamochoerus*, or *Kolpochoerus* van Hoepen and van Hoepen, 1932, where the labial side tends to have a longer (or higher) surface of enamel, in these incisors the lingual and labial sides are of equal length. *Notochoerus euilus* incisors, like those from Hadar, are significantly reduced, simpler, and more circular in cross-section. They have a smooth lingual enamel surface with crests that are not well developed and are usually very worn and covered in cementum. The preserved right third lower incisor of *Ny. jaegeri* is more asymmetrical and much smaller (13.2 mm bucco-lingually and 11.8 mm mesio-distally) than the first and the second lower incisors.

**Upper Third Molars** First lateral pillar pairs of the M3 are separated from the anterior cingulum by a smaller median cusp. The anterior cingulum is less rugose than in *Not. euilus* and has subsidiary cusps that are also less complex. MSD-VP-1/27 and LLG-VP-1/1 M3s have both endostyle and ectostyle at the trigon/talon junction, a feature also seen in the Kanapoi specimens (Cooke and Ewer 1972). The endostyle and ectostyle are present siding the posterior median of the trigon in other *Ny. jaegeri* specimens (Harris and White 1979). Like the *Ny. jaegeri* specimens from other sites, the M3s recovered from the Woranso-Mille show a single median pillar separating the trigon from the talon, as opposed to the *Not. euilus* condition where the M3s usually contain double median pillars.

The talon comprises a large single lingual pillar, a terminal pillar, and smaller labial cusplets of variable number. *Nyanzachoerus jaegeri* M3s have a single large lingual pillar separating the trigon from the terminal pillar whereas there are two or more prominent lingual pillars in *Not. euilus*. The specimens MSD-VP-1/27 and LLG-VP-1/1

show an incipient third pillar pair, while it is well developed in the Kanapoi specimens (Cooke and Ewer 1972). The Woranso-Mille M3s show slight lateral bulging on their lateral pillars as in the Chiwondo Beds *Ny. jaegeri* (Kullmer 2008) while *Not. euilus* has flat lateral pillars. Overall, the major lateral pillars, including the terminal pillars, are very large and robust in MSD-VP-1/27 and LLG-VP-1/1. They have moderate crown height and are less hypsodont than *Not. euilus*. The enamel of the M3 is generally rough in texture but slightly smooth in MSD-VP-1/27 and LLG-VP-1/1. Occlusally, the enamel surfaces of the Woranso-Mille *Ny. jaegeri* are convoluted and have a general irregular outline as in the *Ny. jaegeri* specimens from other sites (Harris and White 1979). This appears to be different from the strong mesial and distal vertical folds reported for *Ny. jaegeri* specimens from the Chiwondo Beds (Kullmer 2008) and Mount Galili Formation (Kullmer et al. 2008).

### Comparative Cranial Metrics

Cranial measurements of MSD-VP-1/27 and LLG-VP-1/1, individual measurements of the comparative specimens of *Ny. kanamensis* and *Not. euilus*, and mean values are provided in Table 2. The mean vertex length of the two Woranso-Mille crania (638 mm) is longer than the mean for both *Ny. kanamensis* (534 mm) and *Not. euilus* (565 mm). Similarly, the bizygomatic width of *Ny. jaegeri* from the Woranso-Mille (526.7 mm) is larger than the average values of *Ny. kanamensis* (345 mm) and *Not. euilus* (325 mm). The ratio of vertex length to bizygomatic breadth for the two Woranso-Mille specimens (1.23) is lower than the average ratio of both *Ny. kanamensis* (1.55) and *Not. euilus* (1.74). In terms of the width across the postorbital processes, *Ny. jaegeri* has an intermediate value (166 mm) between *Ny. kanamensis* (151 mm) and *Not. euilus* (191 mm). On the other hand, the average parietal constriction value for *Ny. jaegeri* is ca. 83 mm, closer to the value of *Ny. kanamensis* (82 mm). *Notochoerus euilus* has a much lower value (58 mm) in this regard. The maximum breadth across the nasals is slightly higher in *Ny. jaegeri* (74 mm) by about 10 mm than the two comparative species. The breadth of the muzzle at the infraorbital foramina is slightly less than the values for *Not. euilus* (71 mm). *Nyanzachoerus kanamensis* appears to have a narrow muzzle right below the infraorbital foramina (56 mm). The palatal length of *Ny. jaegeri* from Woranso-Mille (MSD-VP-1/27 = 372 mm) is higher than the values for *Ny. kanamensis* (327 mm) and *Not. euilus* (261 mm). The breadth of the palate at the P3 and M3 levels is comparable with 45 mm and 40 mm, respectively, whereas in *Not. euilus*, the tooth rows converge more posteriorly. For the latter species, the average breadth at the P3s and M3s is 64 mm and 51 mm, respectively.

## Comparative Dental Metrics

Dental measurements of the Woranso-Mille specimens were taken by the authors on the original specimens housed in the Paleoanthropology Laboratory of the National Museum of Ethiopia and are provided in Tables 3 and 4. Dental measurements of *Ny. kanamensis* non-Woranso-Mille *Ny. jaegeri*, and *Not. euilus* used in Fig. 5a-d were compiled from various publications including Cooke and Ewer (1972), Cooke (1978a), Fesseha (1999), Harris et al. (2003), Kullmer et al. (2008), Reda (2011), and Pickford (1994, 2013). Scatter plots of the length and breadth of upper and lower third molars of the three Pliocene tetraconodonts are presented in Fig. 5a and b, respectively (see Tables 5 and 6 for statistical summaries of the dental measurements used in the comparative analysis). Fig. 5a shows that the basal length of *Ny. kanamensis* lower m3s are generally shorter than in *Ny. jaegeri* and *Not. euilus*. In terms of the length-breadth relationship, *Ny. kanamensis* also clusters outside the range of the latter two species. There is, unsurprisingly, substantial overlap between *Ny. jaegeri* and *Not. euilus* both in terms of length and length-breadth relationship. In Fig. 5b, similar relationships are seen for the M3s. However, it is also apparent, at least from the

distribution of the *Ny. jaegeri* specimens, that there is probably a taxonomic misidentification of specimens and/or inaccurate published measurements. For example, the two “*Ny. jaegeri*” data points that fall within the *Ny. kanamensis* cluster in Fig. 5b are the left and right M3s of KNM-KP 225 identified by Harris et al. (2003) as “*Not. jaegeri*.” Cooke and Ewer (1972) assigned KNM-KP 225 (right M3) to “*Ny. plicatus*” (= *Ny. jaegeri*) and reported length and breadth measurements of 68.0 mm and ca. 30.0 mm, respectively, for this specimen, which fall within the observed range of *Ny. jaegeri*. Although both m3 and M3 length-breadth ratios appear to distinguish *Ny. kanamensis* from *Ny. jaegeri* and *Not. euilus*, they do not distinguish the latter two species in a significant way (see Fig. 5a and b). What appears to be taxonomically more informative in terms of dental measurements is the ratio of the combined third and fourth premolar length to the third molar length (Fig. 5c and d). In this ratio, there seems to be minimal or no overlap between the three tetraconodont species. *Nyanzachoerus kanamensis* is significantly distinguished from *Ny. jaegeri* and *Not. euilus*, and even *Ny. jaegeri* and *Not. euilus* are separated; the differences observed among these species are statistically significant ( $p < 0.001$ , Student’s two-tailed t-test).

**Table 3** Metric values of the upper dentition of *Nyanzachoerus jaegeri* from Woranso-Mille

Specimen no.	BL	BR	BL/BR	BL*BR	HT	TRIG	HT/BR
Upper Third Premolars							
MSD-VP-1/27	19.71	20.38	0.97	401.69			
LLG VP-1/1	23.20	21.70	1.07	503.44			
Upper Fourth Premolars							
AMA-VP-2/38	19.29	21.84	0.88	421.29			
ARI-VP-1/311	19.18	20.51	0.94	393.38			
ARI-VP-1/98	17.18	17.99	0.95	309.07			
MSD-VP-1/27	20.48	23.96	0.85	490.7			
Upper First Molars							
MSD-VP-2/59	19.3	18.76	1.03	362.07			
MSD-VP-1/27	18.3	19.93	0.92	364.72			
Upper Second Molars							
MSD-VP-5/5	31.69	28.75	1.1	911.09			
MSD-VP-1/27	28.07	28.61	0.98	803.08			
LLG VP-1/1	31.40	28.00	1.12	879.20			
Upper Third Molars							
AMA-VP-2/56	55.7				23.68		
ARI-VP-3/241					27		
ARI-VP-1/291					21.97		
ARI-VP-1/430	62.19	35.59	1.75	2213.34	11.62	34.19	0.33
MKM-VP-1/274		34.5					
MSD-VP-1/9					15.91		
MSD-VP-1/27	65.86	34.79	1.89	2291.27	13.76	33.14	0.4
LLG VP-1/1	61.6	33.9	1.82	2088.24	22.6+	36.1	

BL Basal length, BR Maximum breadth, HT Height, TRIG Trigon/id length

**Table 4** Metric values of the lower dentition of *Nyanzachoerus jaegeri* from Woranso-Mille

Specimen no.	BL	BR	BL/BR	BL*BR	HT	TRIG
Lower First Incisors						
LLG VP-1/1	12.84	18.6	0.69	238.82	23.1+	
Lower Second Incisors						
LLG VP-1/1	13.81	20.72	0.67	286.14		
Lower Third Incisors						
LLG VP-1/1	13.2	11.8	1.12	155.76	15.1+	
Lower Second Premolars						
LLG VP-1/1	9.12	6.64	1.37	60.56		
Lower Third Premolars						
ARI-VP-3/222	23.42	15.14	1.55	354.58		
MSD-VP-2/188	22.43	14.51	1.55	325.46		
MSD-VP-5/26	24.22	16.53	1.47	400.36		
Lower Fourth Premolars						
MKM-VP-1/146	18.93	16.6	1.14	314.24		
MKM-VP-1/261	22.21	19.08	1.16	423.63		
MSD-VP-2/105	17.4	16.62	1.05	289.19		
MSD-VP-2/187	19.8	16.33	1.21	323.33		
MSD-VP-5/26	21.69	17.92	1.21	388.68		
Lower First Molars						
ARI-VP-3/132	20.63	17.81	1.16	367.42		
ARI-VP-1/477	17.92	14.75	1.21	264.32		
Lower Second Molars						
MKM-VP-1/261	29.08	20.92	1.39	608.35		
Lower Third Molars						
MSD-VP-2/38						20.3
MSD-VP-2/177						16.64

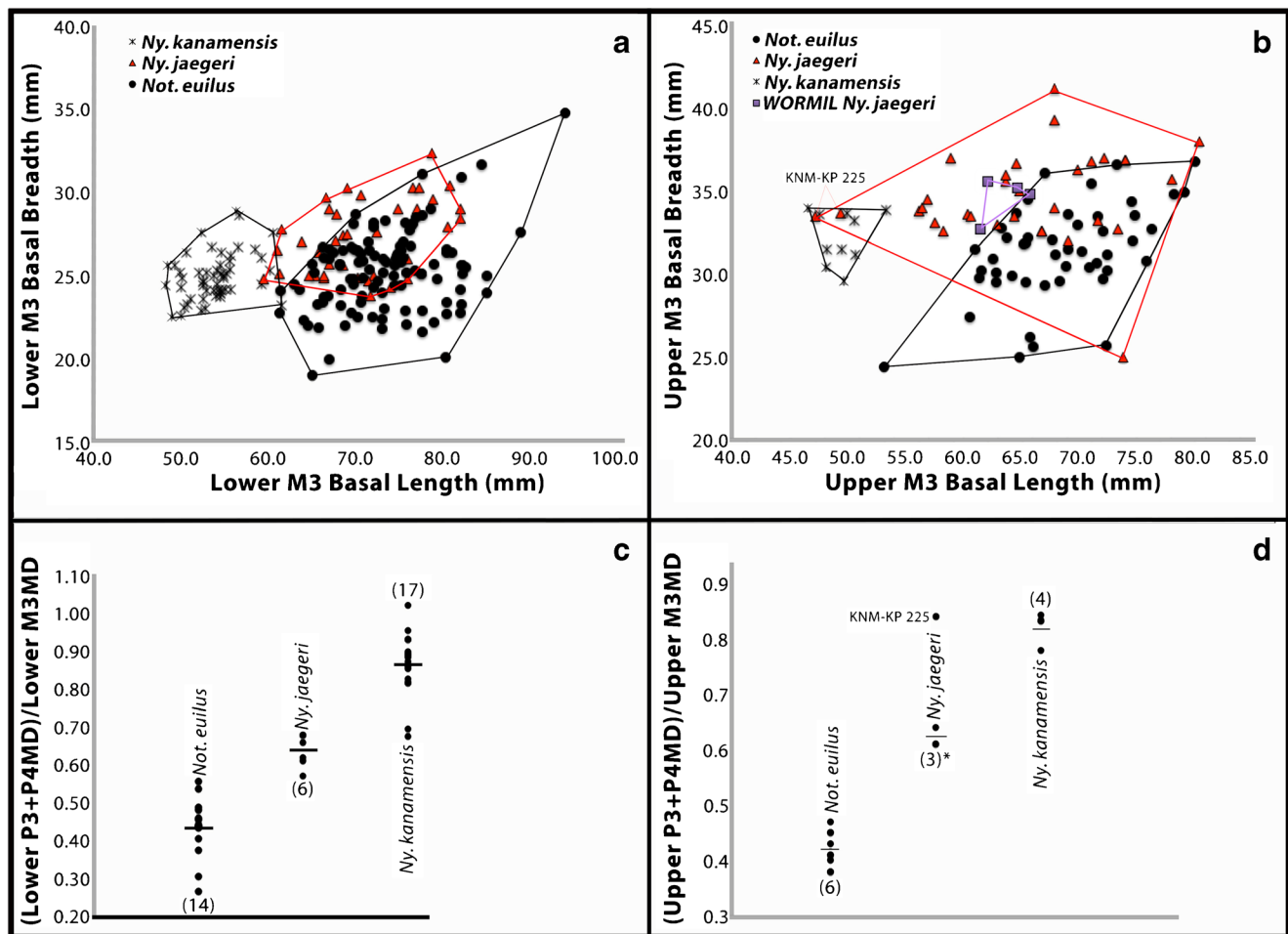
BL Basal length, BR Maximum breadth, HT Height, TRIG Trigon/id length

## Discussion

*Nyanzachoerus jaegeri* is a crucial taxa to understand the late evolution of the Tetraconodontinae because it displays intermediate dental attributes between the more primitive *Nyanzachoerus* and later, more derived *Notochoerus*, including longer and more plicated third molars, and smaller premolars. It is not surprising, therefore, that several authors have opted to include this species within the more derived genus, *Notochoerus* (Fesseha 1999; Kullmer 1999, 2008; Harris and Leaky 2003; Harris et al. 2003; Bishop 2010, 2011). Harris et al. (2003) reclassified *Ny. jaegeri* into the genus *Notochoerus* based on: (1) the longer and less robustly constructed mandibular corpus of the Kanaopi *Ny. jaegeri* specimens (KNM-KP 30178 and KNM-KP 30452) compared to those of *Ny. kanamensis* and *Ny. syrticus*, (2) the breadth and flatness of the mandibular symphysis, (3) the horizontal arrangement of the lower incisors, and (4) lower canine orientation resembling those of *Not. euilus* rather than *Ny. kanamensis* and *Ny. syrticus* (Harris and Leakey 2003; Bishop 2010). Kullmer (1999) also added that the enamel

pattern with strong mesial and distal vertical folding and the reduction in premolar size are typical of *Notochoerus* (Fesseha 1999; Kullmer 2008). However, no cranial characters were quantified for this reclassification of *Ny. jaegeri* into *Notochoerus* mainly due to the lack of complete *Ny. jaegeri* crania. MSD-VP-1/27 and LLG-VP-1/1, complete crania from the Woranso-Mille, allow us to test the validity of the generic reassignment of *Ny. jaegeri* by comparing the crania of *Ny. jaegeri*, *Ny. kanamensis*, and *Not. euilus*.

Comparison of the available crania of the three species provides evidence for a strong affinity of *Ny. jaegeri* with *Ny. kanamensis* rather than with *Not. euilus*. Several cranial characters corroborate the similarity between *Ny. jaegeri* and *Ny. kanamensis*. For example, the orbits are placed low on the skull and their shape is oval in both taxa. The top of the cranial vault is concave in *Ny. jaegeri* and *Ny. kanamensis* but generally flat in *Not. euilus*. Angulation of the nasal to frontoparietal is strong in both *Ny. jaegeri* and *Ny. kanamensis* compared to *Not. euilus*. The complete *Ny. jaegeri* cranium from the Woranso-Mille also highlights the presence of strongly excavated temporal fossae as in *Ny.*



**Fig. 5** Bivariate plots: **a** m3 mesiodistal length to buccolingual breadth. **b** M3 mesiodistal length to buccolingual breadth. Univariate plots: **c** The ratio of p3 + p4 mesiodistal length to m3 mesiodistal length. **d** The ratio of P3 + P4 mesiodistal length to M3 mesiodistal length. Note that KNM-KP

225, identified by Harris and Leakey (2003) as *Not. jaegeri*, falls within the distribution of *Ny. kanamensis* in 5.b and 5.d. We suspect that this discrepancy is due to either inaccurately reported measurements or taxonomic misidentification

*kanamensis*. On the other hand, *Not. euilus* generally possesses very weak temporal fossae. Relative breadth of the parietal constriction is also comparable in the Woranso-Mille crania and *Ny. kanamensis*, whereas it is less constricted in *Not. euilus*. Further, the zygomatic knob in MSD-VP-1/27 is more massive than in *Not. euilus*.

In addition, both *Ny. jaegeri* and *Ny. kanamensis* retain three upper incisors and three upper premolars whereas *Not. euilus* commonly has a single pair of upper incisors and two pairs of upper premolars (though there are exceptions within *Not. euilus*, at least from Hadar). Furthermore, the premolars of *Ny. jaegeri* are not reduced in size as much as in *Not. euilus* and as a result, the premolar-molar length ratio is comparable in *Ny. kanamensis* and *Ny. jaegeri*. The premolars of *Not. euilus* are reduced in size compared to the nyanzachoeres. The associated lower incisors of *Ny. jaegeri* are more similar to *Ny. kanamensis* in size and morphology, and very different from those of *Not. euilus*,

which are comparatively reduced and morphologically simpler.

Despite the similarities in overall cranial shape and topography between the Woranso-Mille crania and *Ny. kanamensis*, MSD-VP-1/27 and LLG-VP-1/1 differ from *Ny. kanamensis* in a number of ways that are taxonomically significant. First, the Woranso-Mille crania are the largest crania ever discovered in the Pliocene tetraconodont fossil record of Africa. They fall outside the range of *Ny. kanamensis* cranial dimensions (see Table 2). Moreover, the relative and absolute size of the P3 and P4, the size and morphology of the M3s, and the P3-P4 length to the M3 length ratio clearly distinguish the Woranso-Mille specimens from *Ny. kanamensis* (Fig. 5).

Generally, the craniodental morphological attributes and metric data suggest closer affinities of *Ny. jaegeri* with *Nyanzachoerus*. Some of the dentognathic attributes of *Ny. jaegeri* are more derived and intermediate between *Nyanzachoerus* and *Notochoerus*, like the length and



**Table 5** Statistical summary of dental measurements used in the metric analysis. All measurements for non-Woranso-Mille specimens were compiled from Cooke and Ewer (1972), Cooke (1978a), Fesseha (1999), Harris et al. (2003), Kullmer et al. (2008), Reda (2011), and Pickford (1994, 2013). All measurements are in mm

	<i>Not. euilus</i> <sup>a</sup>		<i>Not. euilus</i> <sup>b</sup>		<i>Ny. jaegeri</i> <sup>a</sup>		<i>Ny. jaegeri</i> <sup>b</sup>		<i>Ny. kanamensis</i> <sup>b</sup>	
	MD	BL	MD	BL	MD	BL	MD	BL	MD	BL
UPPER DENTITION										
P3										
<i>n</i>	9	9	22	22	1	1	10	10	20	19
Mean	17.8	15.7	15.5	15.4	–	–	22.5	20.2	21.9	19.8
Range	(15.9–21.8)	(12.8–17.2)	(13.3–17.9)	(12.6–17.8)	19.7	20.4	(19.1–24.2)	(18.4–22.2)	(19.9–23.9)	(16.3–22.6)
Stdv	1.7	1.5	1.5	1.5	–	–	1.5	1.3	1.1	1.5
P4										
<i>n</i>	11	11	28	28	4	4	10	10	21	22
Mean	15.5	17.1	13.9	17.0	19.1	21.1	18.5	21.9	18.8	22.4
Range	(13.3–20.3)	(15.0–21.7)	(11.0–16.6)	(14.4–19.7)	(17.2–20.5)	(18.0–24.0)	(15.9–22.3)	(19.2–25.0)	(15.9–22.3)	(19.2–25.9)
Stdv	1.1	1.3	1.4	1.3	1.4	2.5	1.9	1.6	1.3	1.5
M3										
<i>n</i>	6	6	48	48	4	4	36	36	10	10
Mean	72.6	33.0	68.5	31.3	63.6	34.6	65.2	34.7	49.4	32.3
Range	(65.3–79.3)	(29.6–35.0)	(53.2–80.2)	(24.4–36.8)	(61.6–65.9)	(32.7–35.6)	(47.2–80.6)	(25.0–41.2)	(46.6–53.4)	(29.6–34.0)
Stdv	5.0	2.0	5.5	2.9	2.1	1.3	7.4	2.7	1.9	1.6
LOWER DENTITION										
p3										
<i>n</i>	8	7	32	27	3	3	21	21	36	36
Mean	21.8	13.7	19.1	12.7	23.3	15.4	24.6	17.1	24.5	19.6
Range	(20.6–22.9)	(12.6–14.5)	(15.3–22.9)	(9.6–15.3)	(22.4–24.2)	(14.5–16.5)	(20.4–30.0)	(11.1–23.7)	(20.5–28.3)	(15.3–24.5)
Stdv	0.9	0.7	2.1	1.2	0.9	1.0	2.7	3.1	1.8	2.0
p4										
<i>n</i>	6	6	60	59	5	5	21	21	38	35
Mean	18.4	15.5	16.5	14.4	20.0	17.3	22.7	18.8	21.7	19.8
Range	(16.3–19.6)	(13.3–16.5)	(12.8–20.5)	(11.5–17.3)	(17.4–22.2)	(16.3–19.1)	18.1–33.5)	(15.3–23.0)	(18.0–26.4)	(16.3–22.8)
Stdv	1.3	1.3	1.7	1.3	2.0	1.2	3.6	2.2	1.9	1.5
m3										
<i>n</i>	6	8	103	103	–	–	39	39	53	53
Mean	74.2	26.1	73.5	25.2	–	–	70.9	27.3	53.8	24.9
Range	(70.0–82.3)	(23.6–28.7)	(61.3–94.1)	(19.0–34.8)	–	–	(59.4–82.0)	(23.8–32.4)	(48.1–61.5)	(22.5–28.9)
Stdv	4.9	2.3	6.2	2.4	–	–	6.2	2.2	3.1	1.4

<sup>a</sup> Woranso-Mille specimens only

<sup>b</sup> Non-Woranso-Mille specimens

elaboration of the third molars and the size of the premolars. There is no compelling cranial morphological evidence to transfer *Ny. jaegeri* to *Notochoerus* except for some subtle features related to the mandibular symphyseal shape, which appear to be variable even within *Ny. jaegeri* and *Not. euilus*. Therefore, we propose to keep this species within the *Nyanzachoerus* hypodigm. In spite of the much argued taxonomic relationships within the Tetraconodontinae, this attribution is compatible not only with Harris and White (1979) but also with van der

Made (1999). Early tetraconodontines share similar craniodental adaptations, and this is true regardless of the division of *Nyanzachoerus* into two genera (*Nyanzachoerus* and *Sivachoerus*) by van der Made (1999) and it is also true for *Ny. jaegeri*. It is only with the appearance of *Notochoerus* that the dentition, but especially the skull, exhibit considerable morphological change. This is a further reason to maintain the genus *Notochoerus* sensu Harris and White (1979) and keep *Ny. jaegeri* within *Nyanzachoerus*.

**Table 6** Summary statistics of the ratio of combined third and fourth premolar mesiodistal length to the third molar mesiodistal length. Measurements were compiled from references cited in Table 5. All measurements are in mm

(P3 + 4MD)/M3MD	n	Mean	Range	Stdv
LOWER				
<i>Not. euilus</i>	16	0.43	(0.27–0.56)	0.08
<i>Ny. jaegeri</i> *	–	–	–	–
<i>Ny. jaegeri</i>	6	0.64	(0.57–0.68)	0.04
<i>Ny. kanamensis</i>	17	0.87	(0.68–1.02)	0.09
UPPER				
<i>Not. euilus</i>	9	0.42	(0.38–0.47)	0.03
<i>Ny. jaegeri</i> *	1	–	0.61	–
<i>Ny. jaegeri</i>	4	0.62	(0.61–0.64)	0.02
<i>Ny. kanamensis</i>	4	0.82	(0.78–0.84)	0.02

\*Woranso-Mille specimens only

If in fact *Ny. jaegeri* is the ancestor of *Not. euilus*, its intermediately derived dentition suggests that dental changes preceded the cranial changes in this lineage. This modular evolution needs an ecological explanation because the fossil record shows that both ancestor and daughter species were conspecific and contemporaneous at Woranso-Mille. What were the different ecological and/or dietary niches occupied by these species? The derived dentition of *Notochoerus* has been traditionally related to the incorporation of more grasses in its diet (Harris 1983; Harris and Cerling 2002). The paleodietary analysis of the suids from Kanapoi (Ungar et al. accepted) revealed differences in the dental microwear signal between *Ny. jaegeri* and *Ny. kanamensis*, with *Ny. jaegeri* occupying the grazing spectrum (more similar to extant warthogs and giant forest hogs) but also overlapping with *Ny. kanamensis*. This suggests that tetraconodont diets were already enriched in grasses before 4.0 Ma. Further exploration of the paleoecology of these taxa (e.g., dental microwear analysis) and a better understanding of the relationship between suid dental morphology and diet should shed some light on this issue.

## Conclusion

African Pliocene tetraconodonts have been a subject of numerous studies and rigorously used in biochronological age determinations. Despite the rarity of paleontological sites sampling the entire Plio-Pleistocene eastern African fossil suid record in a single geological sequence, the combination of successions such as those in the Lower Omo Basin (Cooke 2007), Koobi Fora (Harris 1983; Cooke 2007), Kanapoi (Cooke and Ewer 1972; Harris et al.

2003), and the Middle Awash (White 1995) preserve most of what we know of the suid Plio-Pleistocene evolutionary history. However, there are still some crucial time gaps that are lacking in the fossil record. This is one of the reasons why the phylogenetic relationships and taxonomy of some taxa are still in a state of flux. The Woranso-Mille paleontological study area samples one of these gaps (3.4–3.8 Ma ago) and, in addition to the material described here, it has also yielded more complete specimens of *Not. euilus* that might help to solve some of the issues mentioned above.

This paper presents, for the first time, a detailed description of the cranial morphology of *Ny. jaegeri*. Comparison of the craniodental morphology of two partially-complete crania, MSD-VP-1/27 and LLG-VP-1/1, with those of *Ny. kanamensis* and *Not. euilus*, clearly shows that *Ny. jaegeri* and *Ny. kanamensis* are more similar to each other in their cranial anatomy than either is to *Not. euilus*. For example, the two Woranso-Mille crania are similar to *Ny. kanamensis* in the fronto-parietal region being transversely concave, postorbital constriction being positioned more posteriorly, and in the way the zygomatic protuberance diverges from the sagittal axis, among others. However, the Woranso-Mille crania differ from *Ny. kanamensis* by being much larger in overall size, having relatively and absolutely smaller premolars, and more complicated M3s. The similarities between *Ny. kanamensis* and the Woranso-Mille specimens assigned to *Ny. jaegeri* have strong implications on the recent transfer of *Ny. jaegeri* to the genus *Notochoerus*. Based on the morphology of the Woranso-Mille specimens, *Ny. jaegeri* is best placed in the genus *Nyanzachoerus* than *Notochoerus*. The chronological age of the Woranso-Mille specimens suggests recalibration of the Last Appearance Datum (LAD) of *Ny. jaegeri* to at least ca. 3.66 Ma. In relation to this, it is also important to note that *Not. euilus* specimens have been recovered from Woranso-Mille deposits dated to older than 3.66 Ma (Lazagabaster et al. in prep). This has broader implications on the mode of transition from *Ny. jaegeri* to *Not. euilus*, which may have been cladogenetic rather than phyletic as has been previously thought.

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**Appendix**

**Table 7** Cranio-dental character states of *Nyanzachoerius jaegeri* and their expressions compiled from Harris and White (1979), Cooke and Ewer (2003), and Harris and Leakey (2003). Note that the new specimens from Woranso-Mille document some cranial morphological features of the species that were not known previously

Element	Character state	Expression <sup>a,b,c</sup>	Expression in Woranso-Mille specimens (this study)
Rhinarium	Relative width Degree of tapering Ossification	nr nr nr	– – –
Supracanine flange	Relative width Presence/absence of dorsal ridge Ornamentation of dorsal ridge Continuity of ridge Relative width of supra canine gutter	relatively broad slight dorsal ridge present weakly carinated continues backward behind canine alveolus relatively broad	relatively broad strong dorsal ridge present weakly carinated continues backward behind canine alveolus relatively broad
Nasal region	Convexity Relative width Medial sagittal depression Extension of nasal wall overhanging the maxilla	laterally convex (in males) narrower than in <i>Ny. tulatos</i> or <i>Ny. kanamensis</i> . Maximum expansion level with supra canine flange flattened towards the midline zygoma-canine alveolus laterally ossified	Wider than in <i>Ny. kanamensis</i> . Expanded at supracanine flange level slightly concave toward midline
Orbital region	Nasal-premaxillar ossification Shape of orbit Position of orbit Orbital rim thickness Posterior portion of orbit Frontal bone between orbits Divergence from sagittal axis Relative size and shape of boss Position of zygomatic knob Root of zygoma orientation of temporal process of zygoma	zygoma-canine alveolus laterally ossified oval low on the skull relatively thick marked by large post orbital processes strongly concave at 90° shape similar to <i>Not. evitius</i> but larger at ventrolateral edge starts behind the infraorbital foramen nr	laterally ossified oval low on the skull relatively thick marked by large post orbital processes strongly concave at 90° very large and globular posterior to M3 starts behind the infraorbital foramen runs superoposteriorly ending at the level of the superior margin of the orbit
Cranial vault	Maximum width Bone thickness Shape Angle of nasal-frontoparietal region Position of temporal lines Temporal fossa parietal constriction Supraoccipital lateral expansion	at postorbital process narrow toward nuchal crest very thick strongly concave on the midline strong angulation coincides with lateral edges of cranial vault deeply excavated broad expand below nuchal crest and taper towards the foramen magnum midway between palatal and orbital plane	at postorbital process narrow toward nuchal crest very thick strongly concave on the midline strong angulation coincides with lateral edges of cranial vault deeply excavated broad expand below nuchal crest and taper towards the foramen magnum midway between palatal and orbital plane; positioned more anteriorly than in <i>Ny. kanamensis</i>
Occipital region	Position of occipital condyles	nr	nr
Nuchal planum	Orientation	nr	nr
Palate	Relative length Relative width Shape of palatomarial border Position of palatomarial border Position of posterior palatine foramina Position of incisive foramina	relatively long wide at the canine alveoli gothic arched/ about V-shaped well behind level of M <sup>3</sup> between first pillars of third molars nr	relatively long wide at the canine alveoli V-shaped well behind level of M <sup>3</sup> between first pillars of third molars at the level of the second incisor

nr no record

<sup>a</sup> Harris and White (1979)

<sup>b</sup> Cooke and Ewer (1972)

<sup>c</sup> Harris and Leakey (2003)

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