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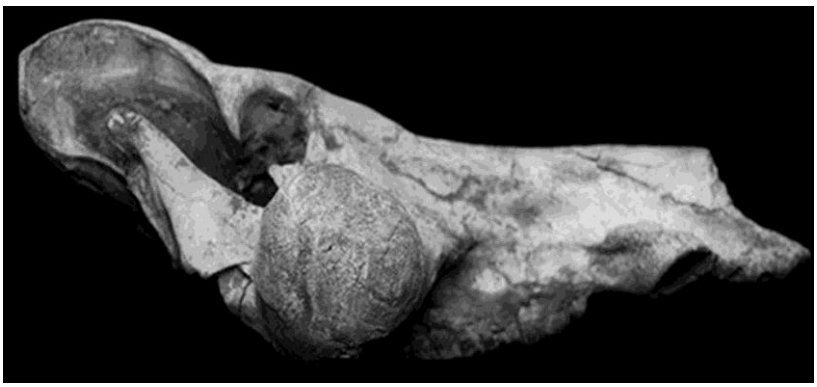
THE ORIGIN AND EVOLUTION OF *NOTOCHOERUS EUILUS* (SUIDAE): FOSSIL EVIDENCE FROM WORANSO-MILLE, CENTRAL AFAR, ETHIOPIA



A THESIS SUBMITTED TO THE SCHOOL OF GRADUATE STUDIES OF ADDIS ABABA UNIVERSITY IN PARTIAL FULFILLMENT OF THE REQUIRMENTS FOR THE DEGREE OF MASTER OF SCIENCE IN PALEONTOLOGY AND PALEOENVIRONMENT

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The Origin and Evolution of *Notochoerus euilus* (Suidae): Fossil evidence from Woranso-Mille, Central Afar, Ethiopia.

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ABSTRACT

Members of the Family Suidae (Artiodactyla, Mammalia) are among the most studied in the Plio-Pleistocene vertebrate fossil record of Africa. However, a number of disagreements remain in terms of their taxonomy and phylogenetic relationships. There were also some disagreements in relation to the tempo and mode of evolution of *Notochoerus euilus*. The contemporaneous presence of both *Nyanzachoerus jaegeri* and *Notochoerus euilus* in the Pliocene Woranso-Mille site, Central Afar, Ethiopia, has allowed a better understanding of the phylogenetic relationships between the two taxa. The fossil evidence from the Woranso-Mille indicates that *Not.euilus* appeared as early as 3.76 Ma and *Ny. jaegeri* persisted until about 3.72 Ma. This means that both *Ny.jaegeri* and primitive *Not.euilus* have co-existed between 3.76-3.72 Ma. Morphological and metric comparisons of the Woranso-Mille *Not.euilus* specimens with those from the slightly younger Hadar and Koobi Fora localities clearly show that the Woranso-Mille specimens are more primitive. There is now strong evidence for the possibility of a cladistic mode of origin for *Not.euilus*. However, the cranial and dental morphological similarities still maintain their ancestral-descendant relationships. Furthermore, some workers reassigned *Ny.jaegeri* into genus *Notochoerus* based on description of complete mandibles from Kanapoi (KNM-KP 30178 and KNM-KP 30452). However, the argument was not supported by cranial characters, mainly due to the lack of complete crania of *Ny. jaegeri*. A detailed description and comparison of a newly discovered complete cranium of the species from the Woranso-Mille site suggests that *Ny. jaegeri* best fits into the genus *Nyanzachoerus*.

Key words: *Notochoerus euilus, Nyanzachoerus jaegeri,* Woranso-Mille, Ethiopia, Phylogeny, Cladistics.

Chapter 1: Introduction

1.1 Background

African fossil Suidae are common elements in the Plio-Pleistocene faunal assemblages of Africa (White and Harris, 1977; Cooke, 1978a; Cooke and Wilkinson, 1978; Harris and White, 1979; Harris, 1983; Fesseha, 1999; Kullmer, 2008; Bishop, 1994, 2010, 2011). They have been used as one of the most important mammalian groups for biochronological age determinations at sites where other dating methods such as radiochronology are unattainable. In addition, the family has also been recognized as an important taxonomic group in testing hypotheses of evolutionary biology (Harris and White, 1979). As a result, they have been a focus of rigorous study by many researchers for several decades, particularly after the publication of Louis Leakey's survey of the east African Suidae in 1958. Since then, a substantial amount of fossil suids comprising more complete specimens have been discovered (Cooke and Ewer, 1972; Bishop, 1994). These new fossil samples of suids led researchers to create several new species and genera which later became subjects of a number of taxonomic revisions. However, there remains no clear agreement to date on these issues (Cooke and Wilkinson, 1978; Cooke, 1978a; Harris and White, 1979; Fesseha, 1999; Van der Made, 1999). This is largely due to the fact that many generic and specific names were created based on subtle cranial and dental differences resulting in an artificial proliferation of named suid taxa (Leakey, 1958; Van der Made, 1999).

The African suids are generally represented by two subfamilies: Tetraconodontinae and Suinae (Cooke, 1978a,b; Cooke and Wilkinson, 1978; Harris and White, 1979; Harris, 1983; Bishop et al., 1999; Geraads, 2004; Pickford, 2006; Bishop, 2010). The origin of the Tetracondontinae is traced back to the Eurasian Miocene suids (Cooke and Wilkinson, 1978; Pickford, 1986, 2006; Fesseha, 1999; Van der Made, 1999; Harris and Leakey, 2003). The subfamily comprises two genera, *Nyazanchoerus* and *Notochoerus*, that are represented by a number of species (Cooke and Maglio, 1972; Cooke, 1978a,b; Cooke and Wilkinson, 1978; Harris and White, 1979; Harris, 1983; Bishop et al., 1999; Fesseha, 1999; Harris and Leakey, 2003; Cooke, 2007; Kullmer, 2008).These two genera are also a subject of contentious phylogenetic and taxonomic classifications particularly in relation to *Nyanzachoerus jaegeri* and *Notochoerus euilus*. Some consider a lineal continuation (ancestor-descendant relationship) between *Notochoerus euilus* and *Nyanzachoerus jaegeri* (White and Harris, 1977; Harris and White, 1979; Bishop, 1999; Van der Made, 1999) while others suggest a cladogenetic event where *Notochoerus euilus* branched off from the *Nyanzachoerus jaegri*

stock (Cooke, 1978a). The species *Nyanzachoerus jaegri* is considered by some researchers as one of the species of *Notochoerus* (Fesseha, 1999; Harris and Leakey, 2003; Kullmer, 2008; Bishop, 2010, 2011) in addition to renaming *Nyanzachoerus kanamensis* as *Notochoerus kanamensis* (Fesseha, 1999).

Disagreements among workers of the African suid taxonomy and phylogenetic relationships are related to several factors, although the poor preservation of fossil specimens and lack of adequate sample size remain the most crucial. Subjectivity in the description and functional interpretation of morphological features and polarization of character states (primitive vs. derived) in cladistic analyses are also problems worth mentioning. Additional disagreements also emanate from Researchers' differences in taxonomic philosophies and recurrent paradigm shifts. Furthermore, factors related to inter- and intra-specific variation, sexual dimorphism, geographic and ontogenetic variations are also important sources of taxonomic inconsistencies. The taxonomy and phylogenetic relationships of the genera and species of the family Suidae have been affected by most, if not all, of these factors.

In almost all cases, the discovery of new fossil materials adds new data relevant to address various existing taxonomic issues although they don't answer all of the existing questions. New fossils are important particularly when they sample taxa from temporally continuous stratigraphic sequences and/or previously little known time frames in the fossil record. Although paleontological sites sampling the entire Plio-Pleistocene eastern African fossil suid record are rare, successions such as in the Lower Omo Basin (Cooke, 2007), Koobi Fora (Cooke, 2007; Harris, 1983),Kanapoi (Harris et al., 2003; Cooke and Ewer,1972) and the Middle Awash (White, 1995), albeit some gaps, preserve most of the suid Plio-Pleistocene evolutionary history. The Woranso-Mille paleontological study area, located in the central Afar region of Ethiopia, is one good example for sampling one of these gaps (3.4 – 3.8 Million years ago) that is poorly understood in the entire African vertebrate evolutionary history. Among fossil specimens of numerous mammalian taxa recovered from this site are diverse suid taxa extremely significant to address some of the major issues in African Pliocene tetraconodonts, particularly in relation to the taxonomy and phylogenetic relationships of *Nyanzachoerus jaegeri* and *Notochoerus euilus*.

The main focus of this thesis is described below and utilizes the rich, and previously undescribed, middle Pliocene suid fossil material from the Woranso-Mille site of the Afar region of Ethiopia. The suid hypodigm from the Woranso-Mille includes, among others, a well-preserved and complete cranium of *Nyanzachoerus jaegeri*, a species whose complete cranial morphology has been hitherto unknown from other Pliocene sites. The comparative

description of the new cranium by itself generates new data and constitutes a major contribution to the Pliocene paleontology of Africa

1.2 Objectives

Three major objectives are broadly proposed here. These objectives will be met by first conducting a complete description and proper taxonomic assignment of the Woranso-Mille suid fossil material to the lowest possible taxonomic level. The next objective is to address the origin and evolution of the species *Notochoerus euilus* which is far from being fully understood. The new fossil material from the Woranso-Mille sheds new light on this issue. This work further re-evaluates the evolutionary concepts related to the mode and tempo of *Notochoerus euilus*. Finally, the relationships between *Not.euilus* and *Ny.jaegeri* will be addressed in light of the new cranial descriptions of the latter species.This will also bear a better understanding on the generic status of the *Ny.jaegeri*,presumed ancestor of *Not.euilus*.

Description and taxonomic determination of the suid material from the Woranso-Mille is part of the main objectives of the research work. While focusing on the description of the original fossil material from the Woranso-Mille study area, it also includes in the discussion comparative cranial and dental materials of *Nyanzachoerus kanamensis, Nyanzachoerus jaegri* and *Notocheorus euilus* from other localities in Africa.

1.3 Organization of the Chapters

The paper has comprised of seven chapters.Background and objectives of the study are included under the first chapter. The origins and evolutionary history of African tetraconodonts has been a subject of interest for many decades. Chapter 2 summarizes some of this work with particular emphasis on *Nyanzachoerus jaegeri* and *Notochoerus euilus*. The main focus of this study is the fossil suid material from the Woranso-Mille study area whose context is described in Chapter 3. The Woranso-Mille study area was discovered in 2004 and has thus far yielded numerous suid remains including a complete cranium of the taxon *Nyanzachoerus jaegeri*. The Woranso-Mille suid specimens considered in this study are radiometrically dated to between 3.82 Ma -3.57 Ma (Deino et al., 2010). It is evidently known that the temporally and spatially diverse African fossil suid hypodigms are largely dominated by isolated dental remains. Complete crania are relatively rare or even unknown for some taxa. However, researchers have utilized different descriptive and metric measurement methods in order to study the available fossil material and extrapolate maximum data. Chapter 4 describes some of these methods in addition to the methods utilized in this study. This

chapter further presents the original and comparative materials used in this study. The bulk of this work lies in the comparative description of the Woranso-Mille Pliocene suid remains presented in Chapter 5. Accordingly,the cranio-dental materials of the Woranso-Mille have been described in detail and thier metric values have also been analyzed. The data extracted from the complete cranium is compared with *Ny.kanamensis* and *Not.euilus* skulls. Based on these features, the *Ny.jaegeri* generic status has been re-evaluated and this is discussed in chapter six. Similarly, the chapter has considered the dental morphological features and metric values to determine the mode and tempo of evolution of the *Not.euilus* and the phylogenetic relatioships between *Ny.jaegeri* and *Not.euilus*. In general, conclusions have been drawn from the research findings about the origin and evolution of *Not.euilus* and this is presented in the last chapter. Furthermore, the taxonomic placement of *Ny.jaegeri* as well as explanation related to the relationships between the *Ny.jaegeri-Not.euilus* lineage is included.

Chapter 2: Evolutionary History of African Tetraconodonts (Suidae)

2.1 Introduction to African Suids

Since the publication of Leakey's survey of the eastern African Suidae and the naming of *Nyanzachoerus kanamensis* (Leakey, 1958), a substantial amount of material including more complete specimens have been recovered from different localities in the region, expanding the temporal and spatial range of suid taxa (Cooke and Ewer, 1972; Bishop, 1994). The fossil record shows that African suids underwent multiple adaptive radiations during the Pliocene and Pleistocene epochs (White and Harris, 1977; Cooke, 1978a; Harris and White, 1979; Pickford, 2006). However, while their evolutionary history is reasonably well documented after 3.5 Ma, earlier taxa are less understood primarily because of limited sample size and uncertain provenance (Harris and Leakey, 2003).

African fossil Suidae have been grouped into five generic associations: *Nyanzachoerus, Notochoerus, Mesochoerus, Phacochoerus,* and *Metridiochoerus* by Cooke and Maglio (1972). White and Harris (1977) and Harris and White (1979) recognized 16 suid species in 7 genera including modern Sub-Saharan representatives, whereas Cooke (1978a) suggested 21 species in 9 genera. Harris and White (1979) further reorganized the African Plio-Pleistocene suids into three lineages: *Nyanzachoerus-Notocoerus, Metridiochoerus-Phacochoerus,* and *Mesochoerus-Hylochoerus*. Fesseha (1999), while accepting the first two lineages, modified Harris and White's *Mesochoerus-Hylochoerus* lineage and recognized *Kolpochoerus-Potamochoerus* and *Hylochoerus* as a single lineage. There was always some agreement on the *Nyanzachoerus-Notochoerus* lineage being the most dominant suid lineage during the Pliocene of Africa (White and Harris, 1977; Cooke, 1978a; Harris and White, 1979; Bishop, 1999). However, there was never an agreement in terms of how many suid species should be recognized during the Plio-Pleistocene of Africa. Cooke (1978a) stressed that the taxonomic discrepancy, especially between him and White and Harris (1977), was semantic. Later, Cooke (2007) suggested that the differences among researchers, in terms of the number of taxa, are in part due to the differences in the definition of a species in a paleontological context.

Suid fossil record has been considered as important in testing concepts of evolutionary biology regardless of the taxonomic discrepancies (White and Harris, 1977; Cooke, 1978a; Harris and White, 1979). In terms of the tempo and mode of evolution of the Pliocene African suids, Cooke (1978a) emphasized on branching of daughter species from a parent stock as the

dominant way of speciation, indicating contemporaneous existence of the parent and daughter species. As a result, he criticized the phylogenies developed by White and Harris (1977) for oversimplifying classification of the African Suidae. White and Harris (1977) and Harris and White (1979) argued that the mode of evolution is largely phyletic and hence possible to reconstruct continuous morphological evolutionary changes in a lineage. Van der Made (1999) completely opposes cladistic origination as a mechanism for the emergence of African suid taxa. He rather proposes all the species as chronospecies of single origin changing overtime. Regardless of the mode of speciation, however, a plethora of species names have been created in the last few decades to refer to African Plio-Pleistocene fossil suids collected from different localities sampling different time frames. This has resulted in a number of taxonomic and phylogenetic revisions of African Plio-Pleistocene suids (Cooke and Ewer, 1972; Cooke, 1978a; Cooke and Wilkinson, 1978; Harris and White, 1979; Bishop, 1994; Van der Made, 1999; Cooke, 2007). One of the problems is usually associated with the lack of good control of the exact temporal and spatial distribution of suid taxa. Some suid species are better known across time and space than others. For example the temporal and spatial distribution of *Ny.jaegeri* and *Not.euilus* is relatively well understood.

Species recognition among African suids is largely based on the third molar morphology as it serves as a substrate for variation due to selective pressure related to dietary adaptation and its plentiful abundance. Species recognition is also supplemented by other dental and cranial characters (White and Harris, 1977; Cooke, 1978a,b; Harris and White, 1979; Cooke, 2007; Kullmer et al., 2008; Bishop, 2010, 2011). However, White (1995) cautions that the third molar should not be solely considered as the best element to determine African suid speciation. An important aspect of the African Pliocene suids is, understanding their phylogenetic relationships. In fact, the paleontological work on the African suids is dominated by phylogenetic and taxonomic considerations (White, 1995).

2.2 African Tetraconodonts

Tetraconodonts constitute one of the two subfamilies of the mammalian family Suidae. They are common elements in the Plio-Pleistocene African faunas and their evolutionary history has been assessed rigorously (White and Harris, 1977; Cooke, 1978a; Cooke and Wilkinson, 1978; Harris and White, 1979; Harris, 1983; Kullmer, 2008; Bishop, 1994, 2010, 2011). They are also among the most abundant taxa in eastern African Plio-Pleistocene fossil sites and the most significant mammalian taxa in biochronological age determination. As a result, they have been a subject of numerous discussions and publications (Cooke and Maglio,

1972; Cooke and Wilkinson, 1978; Harris and White.1979; Harris, 1983; Cooke, 1978a, 2007; Geraads, 2004; Kullmer, 2008; Bishop, 1994, 2010). Based on current taxonomy, two tetraconodont genera (*Nyanzachoerus* and *Notochoerus*) are recognized in Africa. Both genera are known from a number of species that existed from the late Miocene to the early Pleistocene. There are at least seven recognized species of the genus *Nyanzachoerus* (*Ny. devauxi,Ny. syrticus, Ny. Kuseralensis, Ny. waylandi, Ny. australis, Ny, kanamensis, and Ny. jaegeri*) and four species belonging to *Notochoerus (Not.scotti ,Not.capensis, Not.euilus* and *Not. clarki*). However, some researchers (for example, Fesseha, 1999; Harris and Leakey, 2003; Kullmer et al., 2008) place *Nyanzachoerus kanamensis* and *Nyanzachoerus jaegeri* to the genus *Notochoerus* although this is not universally accepted.

African tetraconodonts are believed to have migrated from Eurasia and their oldest fossil record in Africa comes from the Late Miocene (Wilkinson, 1976 in Bishop, 1994; Cooke and Wilkinson, 1978; Pickford, 1986, 2006; Fesseha, 1999; Van der Made, 1999; Harris and Leakey, 2003; Harris et al., 2003; Bishop, 2010, 2011). They are represented in Africa by two genera: *Nyanzachoerus* and *Notochoerus* (Cooke, 1978a,b; Harris and White, 1979; Cooke and Hendey, 1992; Fesseha, 1999; Harris and Leakey, 2003; Harris et al., 2003; Geraads, 2004; Kullmer et al., 2008; Bishop, 1994, 2010, 2011). But they went extinct in the early Pleistocene with the disappearance of *Notochoerus scotti* in the fossil record (White, 1995; White and Suwa, 2004; Cooke, 2007; Bishop, 1994, 2010). The genus *Notochoerus* is largely believed to have evolved from *Nyanzachoerus jaegeri* (Cooke and Ewer, 1972; White and Harris, 1977; Cooke, 1978a; Harris and White, 1979; Cooke, 2007). However, some researchers have recently suggested that the latter should be reclassified as *Notochoerus jaegeri* and represents the earliest representative of the genus (Harris and Leakey, 2003; Kullmer, 2008; Kullmer et al., 2008; Bishop, 2010, 2011). Fesseha (1999) further transfers *Nyanzachoerus knamensis* to the genus *Notochoerus.*

2.2.1 Overview of Tetraconodont Cranial Morphology

The published cranio-dental morphological features of *Not. euilus*, *Ny.kanamnesis* and *Ny.jaegeri* are described below. These features are also summarized under Tables 6-9.

2.2.1.1 Cranial morphology of *Nyanzachoerus kanamensis*

Ny.kanamensis was first described by Leakey (1958) based on a left mandibular corpus (M15882) with canine and p3-m3 recovered from Kanam West. Cooke and Ewer (1972) on the other hand described materials from Kanapoi and assigned them to a new species

Ny.pattersoni considering slight differences from Leakey's species (e.g., the stouter premolar of the latter species). However, Harris and White (1979) considered *Ny. Pattersoni* as a junior synonym of *Ny. Kanamensis*. This species is sexually dimorphic and somewhat larger than *Ny. Syrticus* (= *Ny.tulotos*) (Harris, 1983). As a result, males have larger cranium with more massive zygomatic knobs.

Males have possessed supracanine flanges and located on top of the canine alveolus (Harris and White, 1979). Cooke and Ewer (1972) have noted the absence of this character in females. However, even the male flanges are not generally well-developed (Cooke and Ewer, 1972). The flange is less prominent in size and its rugosity than in *Ny. Syrticus* (Harris and White, 1979). Furthermore, this feature is variable such that it is more developed in the Hadar than in the Kanapoi specimens (Cooke, 1978b).

As compared to *Ny. syrticus*, the *Ny.kanamensis* males have wider nasal region (Harris and White,1979).There is variation in the breadth of the nasals between male and female *Ny.kanamensis* where it is wider in the former (Harris and White, 1979). The nasals are virtually flat and tapering anteriorly (Harris and White, 1979; Harris, 1983) although they are up-curved in the Hadar specimens (Cooke, 1978b). Nasals reach their maximum width level to the canine alveolus (Cooke, 1978b; Harris, 1983). However, there is variation in the nasal width between the Koobi Fora and Kanapoi specimens where the former specimens have wider nasals (Harris, 1983). The muzzle of the species is generally narrow (Cooke and Ewer, 1972).Both the nasal-maxillary and naso-premaxillary junctions form a slight thickening (Harris and White, 1979; Cooke and Ewer, 1972). The narrowest part of the maxillary area is noted between the infraorbital foramina (Cooke, 1978b).

The zygoma diverges smoothly as compared to *Ny.syrticus* (Harris and White, 1979). The extra inflation of the zygoma is present on the anterior external part (Cooke, 1978b). The root of the zygomatic arch begins behind the infraorbital foramen (Cooke and Ewer, 1972). Lateral edge of the zygomatic boss is equivalently rugose like the *Ny. syrticus* (Harris and White, 1979).

Majority of the cranial vault of the species is less known. Based on the description of the retained parts, male *Ny.kanamensis* materials have possessed less pronounced supraorbital ridges than the *Ny.syrticus* specimens (Harris and White, 1979). The occipital condyles are relatively higher above the occlusal plane (Cooke and Ewer, 1972). The braincase between the temporal lines is flattened or smoothly concave (Cooke and Ewer, 1972). However,

description of the Hadar material indicates the presence of a depression on top of the braincase (Cooke, 1978b). This feature was regarded at first as an artifact but was later recognized in several skulls and assumed to be a real feature of the genus (Cooke,1978b).The parietal constriction of the species is broad (Cooke,1978b).

The palate is relatively wider than in *Ny.syrticus* and forms a U-shaped palatonarial border placed behind the level of the third molars (Harris and White, 1979). Cooke (1978b) has noticed broadly rounded palatine notch with a little gothic shape. The palate becomes wider anteriorly towards the enlarged canines (Cooke and Ewer, 1972).The palatine grooves has shown greater divergence as they extend anteriorly (Harris and White, 1979).

Ny.kanamensis is known to have three pairs of upper incisors (Cooke and Ewer, 1972; Harris and White, 1979; Fesseha, 1999). In addition, it has three or four pairs of upper premolars where the first is smaller and button like placed midway between canine and second premolar (Harris and White, 1979; Harris, 1983; Fesseha, 1999). This tooth is variably retained (Cooke and Ewer, 1972; Harris and White, 1979; Fesseha, 1999).

2.2.1.2 **Cranial morphology of *Nyanzachoerus jaegeri***

Cranial features of *Ny. Jaegeri* are less well-known due to lack of complete crania in the fossil record. Its known cranial characters were documented mainly from cranial fragments discovered at different localities. This species is sexually dimorphic with males possess an evident zygomatic knobs (Harris and white, 1979; Harris and Leakey, 2003). Based on description of the partial cranium, the species is described to have larger and more elongated crania than in other *Nyanzachoerus* species (Harris and White, 1979; Harris and Leakey, 2003).

The Supracanine flange is not well known like many of other cranial features but KNM-KP 251 has shown a slight dorsal ridge (Harris and White, 1979). As compared to the *Ny. syrticus* or *Ny. kanamensis* the species shows narrower nasal region (Harris and White, 1979). In fact, the whole configuration of the snout is an elongated and narrowed version of *Ny.kanamensis* (Cooke and Ewer, 1972).The nasals are flattened on the midline but curving downwards (Cooke and Ewer, 1972).The nasal forms a junction with the maxilla from the zygoma to the canine alveolus (Harris and White, 1979).

Harris and White (1979) have examined the lack of well preserved *Ny. jaegeri* zygoma and were unable to make valid interpretations regarding this character. They have noted the

similarity in jugal expansion between this taxon and the female *Ny.kanamensis* based on the observation of KNM-KP 257. Furthermore, isolated bosses were noted by the same authors from KNM-KP 242 and conclude the feature is similar to *Not. euilus* except the size where the former is having larger boss. The root of the zygoma starts just behind the infraorbital foramen (Cooke and Ewer, 1972).

Like many other cranial features, cranial vault morphology of the taxon *Ny.jaegeri* is also less known. However, Harris and White (1979) have recognized the presence of less prominent supraorbital ridges in males.

There are three pairs of upper premolars although the number of upper incisors are unknown for this species (Harris and White, 1979; Cooke and Ewer, 1972). As noted above, many of the cranial features are poorly known for this species. Therefore, the complete cranium discovered from the Woranso-Mille generates enormous data relevant to completely understand the cranial morphology of *Ny. jaegeri*.

2.2.1.3 Cranial morphology of *Notochoerus euilus*

Cranial features of *Not.euilus* are relatively well documented from a number of specimens as opposed to *Ny.jaegeri* and *Ny.kanamensis* species, which are less known. *Not. euilus* is generally known to have deep, narrow and elongated cranium with sexually dimorphic zygomatic knob (Harris and White, 1979; Harris, 1983; Harris and Leakey, 2003; Harris et al., 2003; Bishop, 2011). However, some of its cranial features resemble *Ny.kanamnesis* and *Ny.jaegeri* (Cooke, 1978b). The species has a narrow rhinarium and the premaxilla tapers in front of the canines (Harris and white, 1979) and slightly expanding at the canine alveoli (Harris, 1983). There is a sign of strong indentation on the premaxilla behind the upper incisors (Harris, 1983).KNM-ER 3541has indicated the ossification of the nasal cartilage (Harris and White, 1979; Harris, 1983). However, Harris (1983) is uncertain if this is the real feature of the species.

The supracanine flange is broad with ornamented ridge on its dorsolateral border (Harris and White, 1979). The flange extends shortly in front of the canine alveolus (Harris and White, 1979). The width of the flage diminishes posteriorly and curves to merge with the root of the zygoma (Cooke, 1978b; Harris, 1983). As compared to *Nyanzachoere* species the supracanine flange of male *Not.euilus* is less developed (Harris, 1983). The taxon is known to possess a broader supracanine gutter (Harris and White, 1979; Harris, 1983).

Nasals of *Not.euilus* are elongated with a slight anterior slanting (Harris and White, 1979; Harris, 1983). Even though the nasals are transversely convex, they are bisected by a depression superiorly in front of the canine alveolus (Harris and White, 1979; Harris, 1983). The Hadar specimens, however, differ in that the nasals are straight and parallel sided (Cooke, 1978b).The nasal-maxillary junction forms a ridge which becomes pronounced posteriorly (Harris and White, 1979; Harris, 1983).

Orbits are circular and positioned relatively elevated on the skull (Cooke, 1978b; Harris and White, 1979; Harris, 1983). It is marked by strong postorbital processes (Harris and White, 1979; Harris, 1983). The orbit is surrounded by a thickened rim (Harris and White, 1979). The frontal bones between the orbits is slightly domed (Harris, 1983). However, it is gently concave as is seen in the Hadar specimens (Cooke, 1978b). The zygomatic region shows strong knobs in males (Harris and White, 1979; Harris, 1983). These knobs are at right angles to the axis of the skull when viewed dorsally and drooping on the anterior view (Cooke, 1978b). The root of the zygoma begins just behind the infraorbital foramen (Cooke, 1978b).

The cranial vault is generally with variable shape. It can be virtually flat but may be slightly concave (Harris and White, 1979; Harris, 1983). However, KNM-ER 220 has a slightly convex vault while KNM-ER 3540 is slightly concave (Harris, 1983). The angulation between the nasal and the frontoparietal region is low (Harris and White, 1979; Harris, 1983). The vault is widest between the orbits and gradually tapers towards the nuchal crest (Harris and White, 1979; Harris, 1983).The parietal constriction is narrow for this taxon (Cooke, 1978b).The temporal lines are weakly represented and coincides with the lateral edges of the cranial vault (Harris and White, 1979; Harris, 1983). These lines overhang the temporal fossae (Harris and White, 1979; Harris, 1983). The temporal fossa is described as deeply excavated based on the Koobi Fora materials (Harris, 1983). However, the fossae is weakly developed in the Hadar samples.The supraoccipital expands laterally for a short distance below the nuchal crest and tapers gradually towards the foramen magnum (Harris, 1983). Harris (1983) has also noticed the location of the occipital condyles as midway between the palatal plane and plane of orbits. The young adult skull from Hadar, A.L. 108-3, shows that the occipital condyles are not highly elevated above the palatal plane (Cooke, 1978b).

The palate is narrow and the molar rows are arranged in a straight sided manner (Harris and White, 1979; Harris, 1983). Palatonarial border is located behind the upper third molar

talon (Harris and White, 1979; Harris, 1983). Harris and White (1979) have also noted that it is farther back than in *Nyanzachoerus jaegeri*.

Not.euilus is known to possess only a single pair of upper incisors in adults (Harris and White, 1979; Harris, 1983; Fesseha, 1999). Cooke (1978b) has also confirmed the presence of a single pair of upper incisors and no traces are noted for other incisors. There are only two pairs of upper premolars in adults (Cooke, 1978b; Harris and White, 1979; Harris, 1983; Fesseha, 1999).

2.3 The *Nyanzachoerus jaegeri-Notochoerus euilus* lineage

The *Nyanzachoerus jaegeri-Notochoerus euilus* lineage represents one ancestor-descendant relationship among the African Tetraconodonts. This lineage is revealed based on the dental and mandibular features which suggest they are closely related (White and Harris, 1977; Cooke, 1978b; Cooke and Wilkinson, 1978; Harris and White, 1979; Bishop, 1994; Kullmer, 2008; Kullmer et al., 2008). In fact, some researchers have suggested recognizing *Ny. jaegeri* as a species of *Notochoerus* (For example, Harris and Leakey, 2003). The naming and evolutionary history of each species is described below.

2.3.1 *Nyanzachoerus jaegeri*

Nyanzachoerus jaegeri was accepted as the most advanced form of the genus *Nyanzachoerus* (Cooke and Ewer, 1972; Harris and White, 1979; Bishop, 2010, 2011). It was initially recognized by a partial mandibular corpus with p3-m3 from Hamada Damous, Tunisia (Coppens, 1971). It is considered as the progressive species of the tetraconodontines (Cooke and Wilkinson, 1978; Harris and White, 1979; Harris and Leakey, 2003; Kullmer et al., 2008). Similar materials collected from eastern Africa were assigned to *Nyanzachoerus plicatus* while the materials from North Africa were relegated under *Nyanzachoerus jaegeri* (Cooke and Ewer, 1972). Later, these two taxonomic names were recognized as synonymous (White and Harris, 1977; Cooke and Wilkinson, 1978; Harris and White, 1979) and both are considered to belong to *Nyanzachoerus jaegeri* due to name priority

According to Coppens (1971) and Harris and White (1979), *Nyanzachoerus jaegeri* is known from the Pliocene of Africa at sites such as Hamada Damous - type area (Tunisia), Langebaanweg (South Africa), Mursi Formation of Omo (Ethiopia), Chiwondo Beds (Malawi), and from Lothagam, Ekora, Aterir, the Chemeron Formation, and Kanapoi in

Kenya (Cooke and Ewer, 1972; Harris and Leakey, 2003). The species has also been recently reported from the Mount Galili formation, Ethiopia (Kullmer et al., 2008). Bishop (2011) recently reported the presence of the species from the lower Laetoli beds as well as the upper Laetoli beds below tuff-2 ranging from 4.36 - 3.79 Ma (Deino, 2011). However, the specimen composition consists of few fragmentary ones. Harris and Leakey (2003) have also suggested earlier that the massive upper molars of *Notochoerus euilus* specimens from Laetoli should be attributed to *Nyanzachoerus jaegeri* after comparing them with the Kanapoi samples. Some specimens have also been reported from the Langebaanweg Pelletal Phosphorite member (PPM) as having similar features with the *Ny. jaegeri* specimens recovered from Kanapoi (Cooke and Hendey, 1992).

However, the overall fossil material representing *Nyanzachoerus jaegeri* is limited to dental and mandibular specimens and lacks complete cranial material (Cooke and Ewer, 1972; White and Harris, 1977; Cooke, 1978a; Harris and White, 1979). Although the species has wide spatial distribution, its temporal range appears to be restricted to between 4.35 Ma and 3.99 Ma in the Mursi Formation (Bishop, 1994, 2010). The fossil record of *Nyanzachoerus jaegeri* from Tabarin and the Chemeron Formation is dated to between 4.3 and about 4.0 Ma (Bishop, 2010). The Chiwondo specimens exhibit typical characteristics of the species, which predates the transitional time (ca.3.75Ma) towards *Notochoerus euilus* (Kullmer, 2008; Sandrock et al., 2007). It is possible that the First Appearance Datum (FAD) of this species went as far back as 5-6 Ma though within a million year error range and its Last Appearance Datum (LAD) to be at 3.75 Ma (White, 1995). Kullmer (2008) spreads the temporal range of *Nyanzachoerus jaegeri* from the upper most Miocene to the Lower Pliocene. Harris and White (1979) have also mentioned the presence of a transitional form of the species from *Nyanzachoerus kanamensis* at the Pelletal Phosphorite Member, Langebaanweg. However, many factors affect the determination of the first and last appearance datum of the species (White, 1995). The FAD and LAD are viable to subjective interpretations, preservation and depositional factors, which render the taxonomy and evolutionary relations more ambiguous.

Some researchers have recently started renaming *Nyanzachoerus jaegeri* as *Notochoerus jaegeri*. Fesseha (1999) and Harris and Leakey (2003) argued that *Nyanzachoerus jaegeri* should be placed into the genus *Notochoerus* because it shares derived dental and mandibular features with the latter genus. They further argue 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 *Notochoerus euilus* rather than *Nyanzachoerus kanamensis* or *Nyanzchoerus syrticus* (Harris and Leakey, 2003; Bishop, 2010). In sharp contrast to *Nyanzachoerus kanamensis*, the postero-ventral border of the symphysis projects down below the inferior surface of the corpus, which is long, narrow, and lightly built (Harris and Leakey, 2003; Harris et al., 2003). The reduction of the posterior premolars and elaboration of the third molars allying it 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 the species (*Ny. jaegeri*) as morphologically and phylogenetically intermediate between *Nyanzachoerus* and *Notochoerus* but included it in the former genus.

Kullmer (1999) further strengthened the assignment of the *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 *Notochoerus euilus* (Kullmer, 2008; Kullmer et al., 2008; Bishop, 2010). Cooke and Ewer (1972) have long-established the complex enamel folding of the molars of *Nyanzachoerus plicatus* (= *Ny. jaegeri*) compared to *Nyanzachoerus kanamensis* and *Nyanzachoerus pattersoni*. As a result, the same authors have suggested the possibility of transferring *Nyanzachoerus plicatus* (= *Ny. jaegeri*) to a distinct genus due to its smaller third and fourth premolars compared to *Nyanzachoerus pattersoni* (= *Ny. kanamensis*). However, it required more complete fossil material to warrant separation at a generic level.

Overall, advanced *Nyanzachoerus jaegeri* and early *Notochoerus euilus* have strong dental similarities such that it is often too difficult to distinguish them at the species level (Cooke, 1978b; Harris, 1983; Van der Made, 1999; Bishop, 1994, 2010). As a result of these strong morphological relations, the ancestry of the genus *Notochoerus* undoubtedly lies within the genus *Nyanzachoerus* and more specifically within the progressive form of *Nyanzachoerus jaegeri* (White and Harris, 1977; Cooke, 1978 a, b; Harris and White, 1979; Bishop, 1994; Fesseha, 1999). However, as explained above, the similarities have brought some doubt whether these two species are really distinct even at the species level (Van der Made, 1999). Despite the fact that advanced *Nyanzachoerus jaegeri* and early *Notochoerus euilus* have strong morphological similarities, features such as lower hypsodonty of the third molars and lateral pillar bulginess, relatively larger premolar size as well as the enamel complexity set the *Nyanachoerus jaegeri* apart from the advanced *Notochoerus euilus* (Harris, 1983; Kullmer, 1999; Kullmer et al., 2008).

2.3.2 ***Notochoerus euilus***

Hopwood (1926) initially coined the species name '*euilus*' to refer to a right third molar talonid (M12613A) from the Kaiso Formation of Uganda as *Hylochoerus euilus*. Leakey (1965) later reassigned this specimen to *Notochoerus euilus* in addition to other specimens from eastern Africa. This species is the best known and ubiquitous species of the genus during the middle Pliocene of northern and eastern Africa (White and Harris, 1977; Harris and White, 1979; Harris, 1983; Harris et al., 1988; Fesseha, 1999; Ward et al., 1999; Harris and Leakey, 2003; White and Suwa, 2004; Sandrock et al., 2007; Cooke, 1978b, 2007; Kullmer, 2008; Kullmer et al., 2008; Bishop, 1994, 2010, 2011). This species has also been documented from Makapansgat, South Africa (Ewer, 1958a), although Harris and White (1979) recognized the specimens recovered from this site as *Notochoerus capensis*. *Notochoerus euilus* has also been identified from Mount Galili Formation, Ethiopia, by three specimens (Kullmer et al., 2008). The species was also reported from the Chiwondo Beds of Malawi although the third molars are mostly weathered (Schrenk et al., 2002; Kullmer, 2008). It has also been documented from the Lower Laetoli beds (Bishop, 2011).

According to Bishop (1994, 2010), the oldest well-dated specimens of *Notochoerus euilus* are known from the Koobi Fora Formation area 250 and dated to 3.89 Ma. On the other hand, White (1995) recognized ca. 3.75 Ma as the FAD of the taxon. However, the species might have appeared as early as ca.4.35 Ma (Behrensmeyer et al., 1997) or 4.36 Ma, based on specimens recovered from Laetoli (Bishop, 2011; Deino, 2011). The oldest stratigraphic appearance of the species in the Albertine Rift of the Warwire Formation is reported to be ca. 4.0 Ma (Pickford, 1994 in Cooke, 2007). Specimens assigned to the species from Lower Lomekwi, are dated to between 4.1 - 3.36 Ma while those from the Middle Lomekwi are dated to 3.36 - 2.52 Ma (Harris et al., 1988). The LAD of the taxon is documented in the upper member G of the Shungura Formation dated to ca. 2.32 Ma (Harris and White, 1979; Bishop, 1994; White, 1995; McDougall and Brown, 2008). The most reliable LAD is considered to be the transition from Member B to Member C in the Omo Shungura Formation at 2.85 Ma (Kullmer, 2008). *Notochoerus euilus* is known in the Hadar Formation, Ethiopia, up until the deposition of the BKT-2 dated to ca. 2.9 Ma (Fesseha, 1999). The species in general is well-known in the fossil record for ca. 1-million years, had a wide spatial distribution in eastern Africa (Harris and White, 1979; Bishop, 1994; White and Suwa, 2004; Cooke, 2007), and probably disappeared around 2.7 Ma (Cooke, 2007), .

Ancestor-descendant relationship between *Nyanzachoerus jaegeri* and *Notochoerus euilus* is widely accepted (White and Harris, 1977; Cooke, 1978 a, b; Cooke and Wilkinson, 1978; Harris and White, 1979; Harris, 1983; White, 1995; Fesseha, 1999; Cooke, 2007; Kullmer et al., 2008; Bishop, 1994, 2010, 2011). White and Harris (1977) and Harris and White (1979) did not suggest any temporal overlap between these two taxa. Cooke (1978a), on the contrary, preferred to regard the taxon as a derived branch from within the *Nyanzachoerus jaegeri* stock. However, Bishop (2011), based on fragmentary fossils from Laetoli, argues that the two taxa might have overlapped between 4.36 and 3.79 Ma. In general, it appears that *Notochoerus euilus* is a progressive version that evolved from *Nyanzachoerus jaegeri* through an increase in length and height of the third molars as well as reduced size of the premolars (Cooke, 1978 a, b; Harris and White, 1979; Harris, 1983; White, 1995; Fesseha, 1999; Kullmer, 1999, 2008; Kullmer et al., 2008; Bishop, 2010, 2011). The progressive change is also noticed in the molar enamel morphology in *Not. euilus* where there are strong mesial and distal vertical folds, which result in having higher structural complexity than in *Nyanzachoerus jaegeri* (Kullmer, 1999). *Notochoerus euilus* is also known to have deep, narrow and elongated cranium (Harris and White, 1979; Harris and Leakey, 2003).

Notochoerus euilus is generally considered as conservative and has a wide range of third molar size (Harris and White, 1979; Harris, 1983; Bishop, 1994, 2010). The species has been regarded as the primitive form of the genus *Notochoerus* (Harris and White, 1979). The primitive forms of *Notochoerus euilus* are common in the middle Pliocene (White et al., 1984 in White and Suwa, 2004). Accordingly, early forms of the species have been recovered from Galili, Kaiyumung and Member A to B of the Shungura formation (Kullmer et al., 2008). Similarly, *Not. euilus* materials known from the lower Sidi Hakoma Member exhibit massive cheek teeth which have some overlap with the *Ny.jaegeri* features (Cooke, 1978b). On the other hand, later forms of the species have come from Kaiso, Usno, Kubi Algi, upper part of the Koobi Fora section, the upper Hadar sequence and the Shungura Formation persisting to Member G (Harris and White, 1979).

2.4 Environmental adaptations of *Nyanzachoerus jaegeri* and *Notochoerus euilus*

Changes in the environments of Africa during the Pliocene are reflected in the evolution and distribution of the Suidae (Bishop, 2010). The late Pliocene evolution in eastern Africa was affected by cumulative ecological consequences and variable climatic conditions (Behrensmeyer et al., 1997). Between 5 and 7 Ma, it has been suggested that there was a significant expansion of grasses in the tropical environments and hence the late Miocene tetraconodontines have started to exploit these habitats (Harris and Cerling, 2002; Pickford, 2006; Levin et al., 2008). Cooke (2007), on the contrary, pointed out that the environment at about 2.8-2.5 Ma was a closed habitat from ecological perspectives. According to him, the environment was changed after the specified time to an open habitat. Some ecomorphology-based analyses contradict adaptation of the African tetraconodontines to open habitats but rather preferred closed vegetation (Bishop, 1994; Bishop et al., 1999). Stable carbon isotope evidence from the Tugen Hills suggests feeding ranging from mixed C3/C4 to exclusive C4 diets of the Tugen Hills suids (Bishop et al., 1999). Generally, from about 4.3- 0.7 Ma a variety of habitats were present in eastern Africa and the evidence indicates a variety of closed and intermediate habitat preferences by the suids (Bishop, et al., 1999).

Teeth can serve as guide to determine diet as well as habitat of extinct suids (Cooke and Wilkinson, 1978). The increase in size and complexity of the third molars of suids is related to mastication where low crowned taxa exploit less abrasive materials than more hypsodont ones (Ewer, 1958b; Cooke, 1978b; Cooke and Wilkinson, 1978; Harris and White, 1979; Van der Made, 1999; Harris and Cerling, 2002; Cooke, 2007). The third molars became progressively larger in the *Nyanzachoerus*-*Notochoerus* lineages because of the incorporation of grasses in their diet over time (Harris and Cerling, 2002).The change in cranial anatomy also goes parallel with the dental morphological changes (Ewer, 1958b; Harris and White, 1979). Pickford (2006) also hypothesized the evolution of hypsodonty, polylophid third molars covered with cement and eventually becoming rootless is mainly related with expanding grazing behavior of these taxa. In connection with this, he pointed out the change of African paleovegetation from the Miocene onwards to expanding grasslands. The postcranial anatomy of *Nyanzachoerus jaegeri* specimens from the Tugen Hills indicates that the species was a mixed feeder (Bishop, 1999). Kullmer (1999) emphasized the upper Miocene and early Pliocene *Nyanzachoerus* suids possessing brachyodont dentition. They are assumed to adapt to a soft and/or omnivorous diet. However, the isotopic analysis conducted by Harris and cerling (2002) accompanied with the analysis of the molar morphology of the

Kanapoi materials has indicated the tendency of the species towards grazing behavior. Further isotopic evidence from Gona supports the grazing behavior of early Pliocene *Nyanzachoeres* (Levin et al., 2008).

Analysis of the postcranial locomotor ecomorphology of *Notochoerus euilus* has also shown that it preferred a closed habitat (Bishop, 1994; Bishop et al., 1999). This analysis was mainly conducted by analyzing the ecomorphology of the relatively complete postcranial elements of KNM-ER 3541 (Bishop, 1994). On the other hand, stable carbon isotope analysis conducted on other specimens of the species from Kanapoi and Koobi Fora indicate that the species was consuming predominantly tropical grasses (Harris and Cerling, 2002). At South Turkwell, Kenya (4.0- 3.5 Ma) *Notochoerus euilus* was probably living in a mosaic of habitats dominated by bushland (Ward et al., 1999). Kullmer (2008) has remarked the permanent water supply in the Chiwondo Beds provided a suitable habitat for the evolution of *Notochoerines* in the Malawi Rift, indicating the species' preference of well-watered habitat. All of these inferences indicate that there is no single habitat preference inferred for *Not. euilus* based on multiple lines of evidence but rather ranged from closed habitat to tropical grasses to bushland.

Larger body size, large tusks, elevated cranial region and orbit, maxillary deepening and reduction of the role of temporal muscles in *Notochoerus euilus* are considered as adaptations to more open habitat and consumption of very harsh diet (White and Harris, 1977; Cooke and Wilkinson, 1978; Harris and White, 1979; Harris, 1983). Kullmer (1999) agrees that *Notochoerines* generally have numerous morphological manifestations to abrasive diet although *Notochoerus euilus* is recognized as possessing relatively low crowned molars which also enable it to inhabit a closed environment (Cooke, 2007). However, Bishop et al. (1999) and Bishop (1999) argued that in the Pliocene suid species there is no strong link between hypsodonty and preference for open habitats.

The Woranso-Mille localities provide both *Ny.jaegeri* and *Not.euilus* where the context of these fossils is presented in the next chapter.

Chapter 3: Geological and Geochronological Context of the Woranso- Mille Tetraconodonts

Research in the Woranso-Mille paleontological site has been traced back to the early 1970s.At that time a group of geologists and paleontologists formed an International Afar Research Expedition (IARE) to conduct paleontological surveys and exploration in the Afar Rift (Haile-selassie et al., 2007). The team has included in his survey some parts of the Woranso-Mille paleontological site such as Am-ado (previously known Ahmado by the team),Maguaytu and Adaytole. These areas are bounded by the Mt. Gura-Ale in the north and northern fork of the Bedena River in the south. Furthermore, the team has designated four localities from Am-Ado and collected about 400 vertebrate fossil remains (Haile-selassie et al., 2007). Some localities have also been determined from the Maguaytu and Adaytole areas. The fossils collected from these localities are housed at the national Museum of Ethiopia. However, the provenance of these vertebrate fossil remains is poorly known and they are generally less studied (Haile-selassie et al., 2007).

Thirty years after the expedition by the team, another paleontological survey and exploration has been conducted in the fall 2002 in the north and central Afar. In the years 2003 and 2004 further paleontological survey was carried out by Dr. Yohannes Haile-selassie in the area bounded by the Bati-Mille road in the south and the old Mille- Chifra road in the north. Accordingly, five new fossiliferous localities were discovered in the upper Mille basin (Haile-selassie et al., 2007). The fossiliferous areas include Aralee-issie, Megid-Dora, Burtele and Makah Mera. In addition, the localities have furnished vertebrate fossil remains important in biochronological dating (for instance *Nyanzachoerus jaegeri*) and hominid fossil remain was discovered (Haile-selassie et al., 2007). In the following year, research co-directed by both Dr. Yohannes Haile-selassie and Dr. Bruce Latimer was conducted. As a result, further new localities were discovered and more vertebrate fossil specimens were recovered and grouped under 23 mammalian species (Haile-selassie et al., 2007). Similarly, geological and paleontological work continued in 2006. Hence, geological samples were collected for radiometric dating, petrographic and paleomagnetic analysis. In addition, seventeen localities have been designated (Haile-selassie et al., 2007). The localites have yielded about 1000 vertebrate fossil remains and 20 hominid fossil specimens (Haile-selassie et al., 2007). Furthermore,research work in the area is still on progress on an annual basis usually from end of Juanuary to the beginning of March.

3.1 Location of the Study Area

The Woranso-Mille site, located in the central Afar region of Ethiopia, is one of the newest paleontological sites in eastern Africa (Fig. 3.1). Two relatively large rivers, Woranso (seasonal) and Mille (perennial) transect the study area, hence, the name Woranso-Mille. It is about 360 km northeast of Addis Ababa, the capital of Ethiopia. The research site is demarcated by Mille, Chifra, and Kasagita towns. The Woranso-Mille is the northernmost hominid-bearing paleontological site in the Afar Rift (Fig. 3.1).

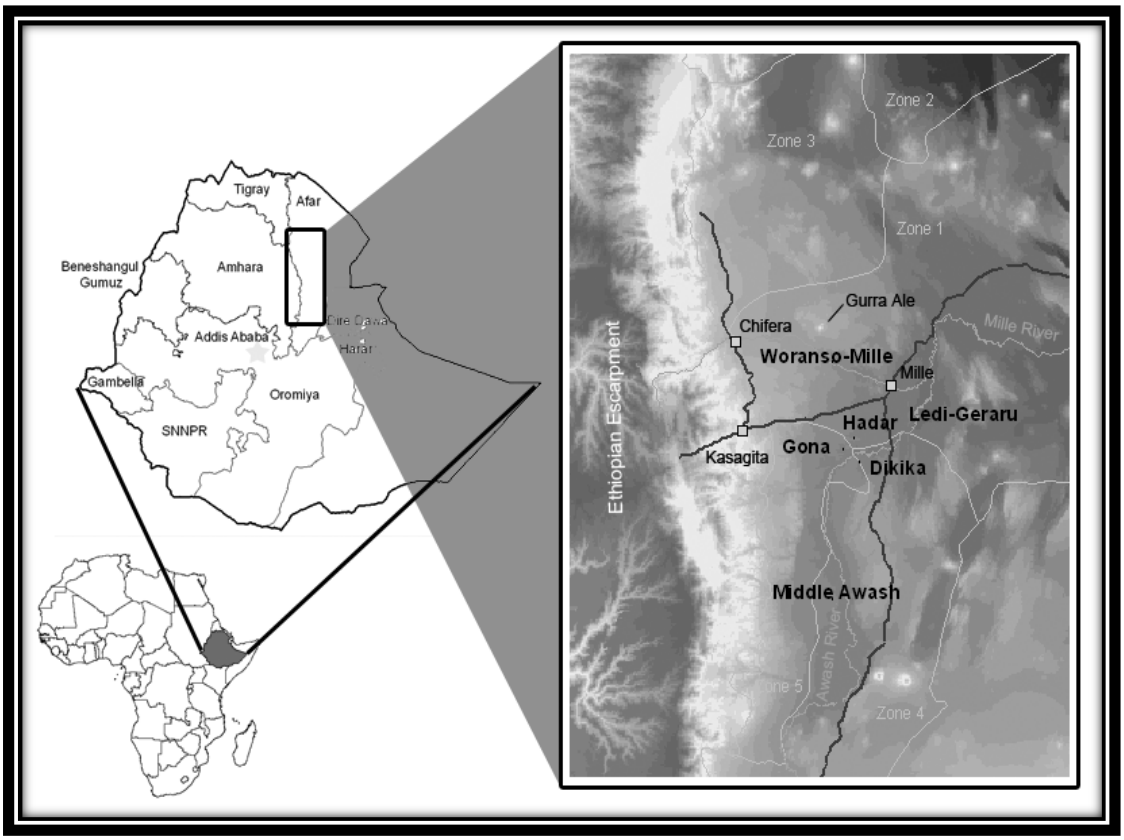


Figure 3.1. Map showing the location of the Woranso-Mille Study area and other paleontological sites in the Afar region of Ethiopia. Figure modified from figure 3.1 in Melillo (2011:40).

The Hadar paleontological site, where the famous "Lucy" was found, is situated ca. 40 Kilometers south of Woranso-Mille. To the southeast of the study area and adjacent to Hadar is another fossil site, the Dikika paleontological site. Further to the south are sites such as Gona and the Middle Awash (Fig. 3.1). The area is inhabited by the Afar. They are primarily pastoralists and depends their life almost totally upon their livestocks. The area is covered by wide plain of land with scattered bushes mainly acacia trees and gullery forest following the

river course.It is is dry and very hot reaching about 40^0 c during the time between end of January and beginning of March.

3.2 Geology and Geochronology

The lithostratigraphy mainly includes fluviatile sedimentary rocks interbedded with primary and reworked tuffs, and basalt flows. The sedimentary rocks are primarily siltstone, sandstone and conglomerate. Basaltic lava underlies the entire strata of the region (Deino et al., 2010; Haile-Selassie et al., 2007). A refined stratigraphic sequence is not currently available for the entire study area.

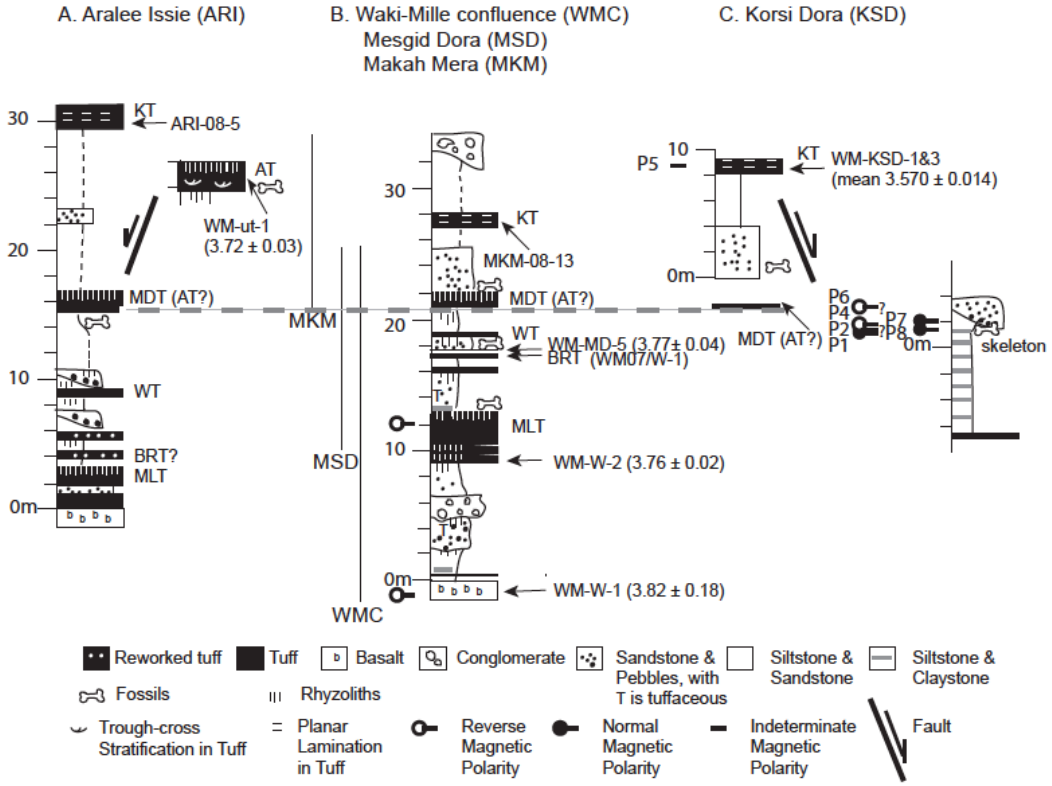


Figure 3.2. Stratigraphy, age, and provenience of fossils at Woranso-Mille (Deino et al., 2010).

However, a composite section comprising the Waki-Mille Confluence (WMC), Aralee Issie (ARI), Mesgid Dora (MSD) and Makah Mera (MKM) areas form a thickness of more than 32 meters (Fig. 3.2).

The WMC, ARI, MSD and MKM combined sections also provide a composite stratigraphic sequence for the 3.57 – 3.82 Ma time span (Deino et al., 2010). Most of the tuffs are well exposed at the lower units both at the WMC and MSD. At WMC, in the northwestern part of the study area, a basalt flow underlies the sequence. This basaltic lava is overlain by

siltstone, sandstone, conglomerate and a few thin unnamed tuff deposits. The sedimentary unit is, in turn, overlain by multiple tuffs interbedded with tuffaceous sandstone and siltstone. The tuffs recognized at the WMC exposure are also present at the MSD section. These tuffs are arranged from bottom to top as follows: the Mille tuff (MLT), Basalt-Rhyolitic tuff (BRT), Waki tuff (WT), and Mesgid Dora tuff (MDT) (Deino et al., 2010). Makah Mera (MKM) is another fossiliferous area where the deposits are slightly younger than at WMC and MSD. The lowest tuff in this section is the MDT, which is overlain by sandstone and siltstone. The younger and widely spread tuff (Kilaytoli tuff, KT) rests above this sedimentary unit. On top of KT another sedimentary sequence is composed of siltstone, sandstone and capped by unconformably lying conglomerate horizon. Aralee Issie (ARI), located north of WMC comprises the most complete stratigraphic section ranging from the basal basalt to the KT (Deino et al., 2010). At Korsi Dora (KSD), the locality where the hominid partial skeleton *Kadanuumuu* (KSD-VP-1/1) was found, only a small sequence, containing a succession of sandstone, siltstone and KT on top, is exposed (Deino et al., 2010).

3.3 Paleontology

The Project has collected more than 4,800 fossil specimens of diverse taxa including those of early hominids. Suids comprising of 16% (n=769) of the total collected fossil sample with more than 242 specimens definitively identified as tetraconodonts. These specimens were collected from spatially and temporally well-defined fossiliferous horizons. Some of the hominid fossils have been published (Haile-Selassie, 2010; Haile-Selassie et al., 2010a, b). The most recent publication is on the discovery and interpretation of 'Kadanuumuu', a 3.58 Ma hominid partial skeleton (Haile-Selassie et al., 2010b). Furthermore, a publication related to bovids has also been provided (Geraads, et al., 2009). However, detailed research is still on progress for other faunal remains including the present work on fossil suids.

Fossil suid samples which are considered in this study are extracted mainly from four major fossiliferous horizons such as Am-Ado (AMA),Aralee Issie (ARI),Mesgid Dora (MSD) and Makah Mera (MKM).They are primarily important because these localities provide fossils which help analyze the transitional morphologies between *Nyanzachoerus jaegeri* and *Notochoerus euilus* and hence the origin of the latter species. In addition, the complete cranium of the *Nyanzachoerus jaegeri* which provides valuable evidence to test the taxonomic assignment of the species is also recovered from one of these localities, MSD. These fossiliferous horizons are well dated and known to range between 3.76-3.57Ma the

time where there is scare faunal assemblage in the African fossil record. Apart from the temporal importance, it is also helpful to document the spatial distribution of the two taxa.

Fossils collected from the Woranso-Mille are catalogued indicating the locality name, locality number and specific specimen number. For instance, the complete cranium MSD-VP-1/27 is explicitly informative that the locality from which the specimen is recovered is Mesgid Dora (MSD). The numbers respectively specify that the specimen is discovered from the first locality and it is the twenty-seventh from that particular locality. The 'VP' stands for Vertebrate Paleontology. Accompanied with this information, the GPS location and provenance of the fossils are also included during the collection time.

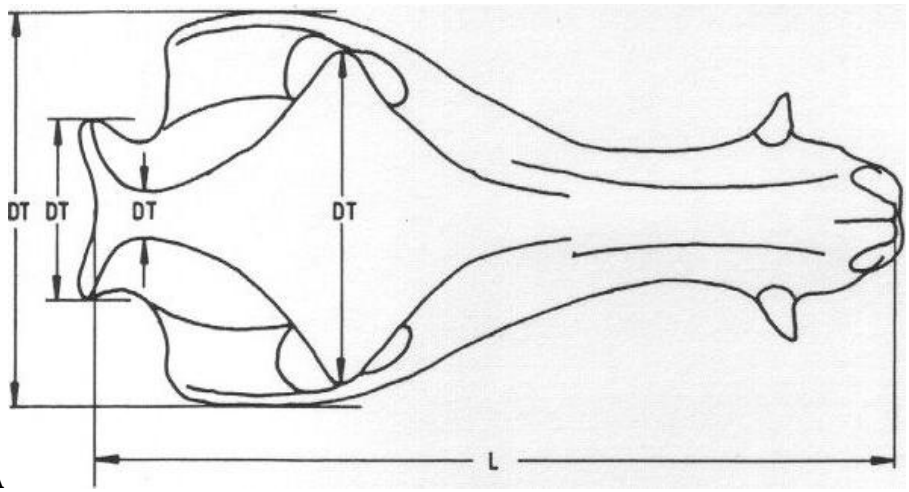
Chapter 4: Methods and Materials

This chapter outlines the materials that have been investigated and the methodological approaches used in this thesis. The methodology section explains how morphological characters are described, how measurements of characters that can be quantified were taken, and the comparative methods. Cranial and dental morphological character states and measured dimensions are adopted from previous works and summarized in Tables 2-5. However, due to the variability of terminologies and measurement techniques used by various authors in the past, a brief review is appropriate in order to clarify which methods are used in this thesis (see below). The methods section explains how the Woranso-Mille dental and cranial samples were described, measured, and compared to determine their taxonomic affinity. The measuring devices used in this study are also indicated. In addition, the methods and softwares used to manipulate the metric data collected from the Woranso-Mille materials are presented. Having performed the morphological description and measurements, the results are compared with previously published datasets. Details of the comparative procedure are also discussed in the methods section below.

Original specimens from the Woranso-Mille included in this study are listed in Table 1. The composition of the Woranso-Mille materials considered in the study and the comparative material from other sites are also briefly discussed below. Finally, a brief introduction to the localities of the Woranso-Mille paleontological site that yielded the fossil samples is presented.

4.1 Methods

The present study implements both qualitative and quantitative analysis of the *Ny. jaegeri* and *Not. euilus* fossil specimens from the Woranso-Mille study area and dated to between 3.6 and 3.8 Million years old. The morphological and metric data collected from the Woranso-Mille specimens were compared to published data for *Ny. kanamensis*, *Ny. jaegeri* and *Not. euilus* from other Pliocene sites in eastern Africa. In this study, *Ny. pattersoni* is considered as a junior synonym of *Ny. kanamensis* following the synonymy proposed by Harris and White (1979). The morphological description and metric measurements of the Woranso-Mille cranio-dental specimens were taken from the original



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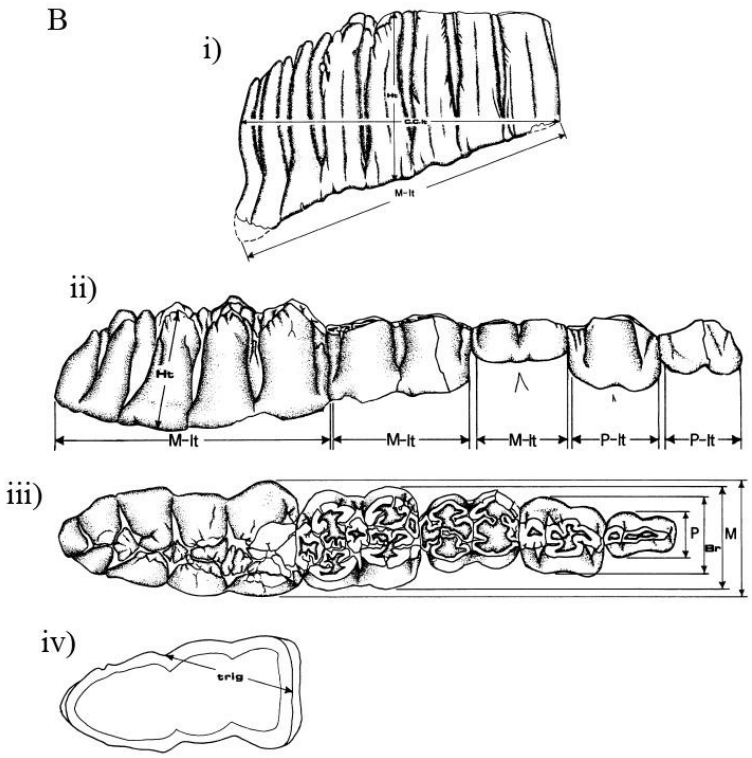


Figure 4.1 **A**. Cranial dimensions (from Van der Made, 1996). 'L' is length; 'DT' is transverse diameter (width) at various osteometric points.

B. Diagram showing various linear dental measurements (from Harris and White, 1979). **i)** Basal length of third molar. **ii)** Basal lengths of molars and premolars. **iii)** Breadth of molars and premolars. **iv)** Trigon/id length of third molar.

specimens. The methods of cranial and dental morphological description, terminologies, and dental measurement techniques are adopted from Harris and White (1979), supplemented with some additional methods from Fesseha (1999) and Cooke (2007). Table 5 summarizes various

dental dimensions measured by Harris and White (1979), Fesseha (1999) and Cooke (2007). The techniques used to measure dimensions of the cranium follow Van der Made (1996) and Driesch (1976) (See Table 4). Both the cranial and dental dimensions measured in this work are also shown in Figure 4.1 A, B.

4.1.1 Review of Previous Methods

In the measurement of cranial dimensions there is relatively similar way of addressing the metric values. However, there are discrepancies among different workers studying suids in terms of cusp terminology and points of references for various dental dimensions. For example, Kullmer et al. (2008) reported measurements of dental specimens from Galili as length (l) and width (w) corresponding to the mesiodistal and buccolingual dimensions, respectively. However, they failed to explain how and at what reference points these measurements were taken. On the other hand, Kullmer (2008) used different terminology (occlusal length and occlusal breadth) to refer to the mesiodistal and buccolingual dimensions, respectively. The latter implies that the measurements were taken near the occlusal surfaces of the teeth. Bishop (2011) used different terms where the dimension along the sagittal axis of the tooth is the mesiodistal length (MD length) and the buccolingual breadth (BL breadth) is the transverse dimension. Although Bishop's (2011) measurement techniques followed the scheme developed by Harris and White (1979), her terminology varied significantly. Harris and White (1979) apply the term length (L) to refer to the maximum antero-posterior distance at the cervical enamel line along the mesiodistal axis and breadth (B) to refer to the maximum breadth taken perpendicular to the mesiodistal crown axis of the crown enamel rim. Harris (1983) and Harris et al. (2003) referred to the mesiodistal dental dimensions as antero-posterior length (ap) and the buccolingual breadth as the transverse width (tr). However, this time there was no indication for the exact points of reference for these dimensions. More specifically in the description of the Koobi Fora materials by Harris (1983), occlusal surface length (oc ap) was used instead of antero-posterior length (ap) implying that the antero-posterior length was taken on the occlusal surface, different from the method used in Harris and White (1979). There are also cases where the antero-posterior length and transverse width values of the left and right sides of the same individual were reported as separate teeth (e.g. Kanapoi; Harris et al., 2003) and Lothagam (Harris and Leakey, 2003)). Harris and Leakey (2003) also reported two transverse width measurements for each molar they measured from Lothagam.

Fesseha (1999) applied the terms basal length (BL length) and maximum width (W) to refer to the mesiodistal and buccolingual dimensions of the Hadar dental materials, respectively. The basal length is measured in a horizontal plane along the antero-posterior dimension near the crown/root junctions. However, a third molar with no visible root because of developmental stages is measured at the apparent crown base. The basal lengths of the dentition were measured on the buccal side. However, it was not stated whether this was done for upper or lower molars. Similarly, the maximum width is measured close to the crown base perpendicular to the antero-posterior dimension of the tooth.

Measurement of height of the third molars is also highly variable. Some workers do not indicate on which molar pillar (cusp) the measurement was taken (e.g., see Harris, 1983). Other researchers don't even measure this character state because of cusp height variability due to wear and developmental stages (Fesseha, 1999). The crown height of specimens from Laetoli has been measured and the values were taken from the talon/id of less worn molar pillars (Bishop, 2011). Contrary to the above, some researchers measure crown height for both first and second pillars accompanied with the wear stages (Kullmer, 2008).

The discrepancy in measurement techniques and terminology may lead to inconsistencies in the results obtained by different researchers. On the other hand, taxonomic analysis based on statistical analysis of these published data may also lead to an unnecessary proliferation of taxonomic names and underestimate geographic variations. This may further affect the analysis of inter- and intraspecific variations because of sexual dimorphism in a single species. Therefore, the combined treatment of all the published data with significant variability in the methodology should be dealt with great caution. Taking this into account, the descriptive methods, measurement techniques and terminology used in this study are described below.

4.1.2 Descriptive Methods

A large number of Plio-Pleistocene fossil suids have been described from eastern Africa. These descriptions incorporate a number of cranial and dental character states whose composition depends on the preservation and completeness of the specimens under consideration. After carefully analyzing the nature of the Woranso-Mille suid material considered in this study, the character states listed in Tables 2 and 3 were compiled. Although these character states were complied in order to describe the most complete specimens, some fragmentary materials have also been described in reference to and compared with the complete ones.

The description includes observation of the character states on both the right and left sides of an individual so that variations due to taphonomic factors or natural bilateral asymmetry could be documented. For instance, associated right and left third molars of a single individual may have variable features such as the presence of double median pillars separating the trigon from the talon on one side and the other side with a single median pillar. Both teeth may also vary in their talon complex: one side with single lateral pillar pair and two pillar pairs on the other side. On the other hand, for specimens which have missed one side of their paired body parts like the zygomatic knob of MSD-VP-1/27 (see comparative description), description is based only on the preserved side.

Every specimen included in the description was photographed in different views (occlusal, lateral/buccal, and lingual) and well organized using adobe photo shop CS3.These are presented in Plates 1-13.

4.1.3 Metric Methods

Cranial and dental dimensions of the Woranso-Mille specimens under consideration were measured using manual and digital calipers and all measurements are reported in millimeters (mm). The manual caliper was largely used to measure cranial dimensions greater than 140mm and whole tooth rows. Individual teeth were measured using a digital caliper. There was no significant difference in the values gauged using the two calipers. The observed difference was about 0.5mm. Every cranial and dental character was measured three times at different days and the difference between these measurements was not statistically significant (1-2mm). Therefore, what is reported in this study is the average value of all three measurements.

Cranial and dental dimensions measured in this study are listed in Tables 4 and 5, respectively. Measurements related to lengths such as vertex length, basilar length, palatal length, skull length, and premolar and molar series are taken along the sagittal axis of the skull. 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 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 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 since the left side is not preserved.

Dental measurement techniques used in this study follow Harris and White (1979), Fesseha (1999), and Cooke (2007). Accordingly, the basal length (BL) is the maximum distance from the anterior to the posterior end of the tooth and that is taken at the cervico-enamel line along the mesiodistal crown axis. This minimizes differences in the values due to the change in the length of the tooth as a result of progressive occlusal wear. The basal length measurements were taken on both the labial and lingual sides and the labial one is reported here while the breadth of the tooth is measured perpendicular to the mesiodistal crown axis and the occlusal plane. This value was measured at the maximum crown shoulder of the enamel. Crown height and trigon/id length were measured only for the third molars. The height is determined from the first major talon/id pillar and usually measured from the cervico-enamel line to the apex of the tooth parallel to the pillar axis. In addition, the wear stage of the tooth has been mentioned. Similarly, the trigon/id lengths have been measured as the minimum distance from anterior cervico-enamel line to the trigon/id-talon/id junction. An average value is reported for the measurements taken from both right and left sides of the same individual.

In addition to the primary measurement values of both the cranial and dental specimens, some ratios have also been calculated. For instance, the ratio of the vertex length to the bizygomatic breadth and ratio of molar to premolar series are reported. The molar to premolar series ratio was computed only when the individual retains the entire cheek teeth row. Moreover, dental proportions such as basal length to the maximum breadth (BL/BR), and areas of the individual tooth (BL*BR) have also been incorporated. The hypsodonty index (HI), i.e., the ratio of height of the third molar versus its maximum breadth, is determined following Cooke (2007). Univariate and bivariate analysis of the metric values was conducted using SPSS (statistical package for social sciences) version 17.0.

4.1.4 Comparative Methods

Both the cranial and dental morphological features and quantitative values of the Woranso-Mille materials are compared with *Ny. jaegeri* and *Not.euilus* specimens from other Pliocene eastern African localities such as Hadar, Koobi Fora, Kanapoi, Galili, Chiwondo Beds, Lothagam and Laetoli. Cranial and dental character states observed in the Woranso-Mille specimens were compared to published morphological attributes of *Ny. kanamensis*, *Not. euilus*, and *Ny. jaegeri*. Accordingly, the metric values of the skulls and the molar to premolar series proportions of the three species were analyzed using univariate and bivariate methods. However, the majority of the metric values of the skulls were compared with simple

descriptive statistics primarily considering the mean values. The basal length to maximum breadth of the molars and premolars was compared graphically with the help of bivariate scatter plot. However, the bivariate graphical analysis of the height versus maximum breadth of the third molars was restricted only to the Woranso-Mille *Ny.jaegeri* and *Not.euilus* materials. Furthermore, the univariate graphical comparison of the ratio of height to maximum breadth of the third molar is limited to the *Ny.jaegeri* versus *Not.euilus* specimens collected from the study area.

4.2 Materials

4.2.1 The Woranso-Mille Materials

The Woranso-Mille suid fossil collection includes a complete cranium, MSD-VP-1/27, assigned here to *Ny. jaegeri*. This is the only known complete cranium of the species thus far and hence its cranial anatomy is described in detail. However, the collection is largely dominated by abundant isolated dental remains. As a result, the bulk of this study deals with description of the dentition primarily focusing on the upper and lower permanent cheek teeth: third and fourth premolars and all molars. Incisors and canines are rarely included in the description only if they are associated with the third molars. In addition to the complete dental remains, some fragmentary specimens were included when they appear to have distinctive features. Deciduous teeth and postcranial remains were not included in this study. This is largely because isolated deciduous teeth are difficult to assign to a species unless they are clearly associated with a taxonomically diagnostic skeletal element. Postcranial remains are also rare in the collection of the project and have no refined taxonomic assignment. The Woranso-Mille fossil suid specimens considered in this work are listed in Table 1. The original fossil specimens are housed at the National Museum of Ethiopia, where this study was conducted.

Specimens from the Woranso-Mille paleontological site were recovered from temporally and spatially well-defined fossiliferous horizons at multiple localities of the study area. These localities include Mesgid Dora (MSD), Makah Mera (MKM), Am-Ado (AMA), and Aralee Issie (ARI), among many others. The localities which yielded the fossil suids considered in this study are temporally bracketed to between 3.8 and 3.6 Ma (Deino et al., 2010).

4.2.2 **The Comparative Materials**

Comparative samples include both original and published fossil materials from various eastern African localities. Original specimens studied here include Hadar *Not. euilus* material, particularly the skulls. Published cranial and dental materials from Hadar, Kanapoi, Koobi Fora, Lothagam, Laetoli, Galili, and Chiwondo Beds were included in the comparative analysis. Based on this, relatively complete cranial specimens of both *Not. euilus* and *Ny. kanamensis* from various localities were the most important comparative materials.

Ny.kanamensis specimens used in the comparative analysis comprise of 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 and Leakey, 2003). However, KNM-KP 239 is almost complete skull of an adult female individual associated with a mandible, atlas, and damaged thoracic vertebra (Cooke and Ewer, 1972; Harris and Leakey, 2003). KNM-KP 30186 is a well preserved male cranium (Harris and Leakey, 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 presumed male with associated atlas vertebra, known from the lower Sidi Hakoma Member SH-2. A.L. 107-13 is slightly damaged skull of presumed female from the Upper Sidi Hakoma Member SH-3 (Cooke, 1978b). Both skulls are recovered from sediments dated to between 3.4 and 3.22 Ma (Walter and Aronson, 1993; Walter, 1994).

Comparative skull specimens for *Not.euilus* are mostly from the Hadar Formation. These specimens include A.L. 108-3, A.L. 171-1, A.L. 172-1, A.L. 349-2 and A.L. 167-15. A single complete specimen 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 articulated with

postcranial skeletal elements (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) has 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).

Chapter 5: Comparative Description of the Woranso-Mille Tetraconodonts

In this chapter, tetraconodont cranio-dental material from the Woranso-Mille is described in detail. These materials are metrically and morphologically compared with published specimens of *Ny.kanamensis* and *Not.euilus*. A complete cranium of *Ny. jaegeri* was previously unknown in the fossil record. However, one complete cranium has been recovered from the Woranso-Mille study area and its detailed description is presented here. In the morphological description, an attempt is made to document the inter- and intra-specific variation in both *Ny. jaegeri and Not. euilus*. Furthermore, the tempo and mode of changes in the dental size, particularly in relation to the hypsodonty of the third molars, from *Ny. jaegeri* to *Not. euilus* are discussed. This chapter has two major parts: the cranial and dental descriptions for both *Ny.jaegeri* and *Not.euilus* supplemented by comparative metrics.

5.1 Description of the Woranso-Mille Material

5.1.1 *Nyanzachoerus jaegeri*

Class MAMMALIA
Order ARTIODACTYLA Owen, 1848
Family SUIDAE Gray, 1821
Subfamily TETRACONODONTINAE Lydekker, 1876
Genus *NYANZACHOERUS* Leakey, 1958
Species *Nyanzachoerus jaegeri* Coppens, 1971

Referred Specimens: MSD-VP-1/27, cranium with right and left P2-M3; MSD-VP-5/5, right upper second molar; MSD-VP-2/59, right upper first molar and upper deciduous fourth premolar; MSD-VP-2/188, right lower third premolar; MSD-VP-2/187, left lower fourth premolar; MSD-VP-5/26, right lower third premolar and left lower fourth premolar; ARI-VP-1/311, right upper fourth premolar; ARI-VP-3/222, right lower third premolar; ARI-VP-1/477, left lower first molar; ARI-VP-1/98, right upper fourth premolar; ARI-VP-1/430, left upper third molar; AMA-VP-2/56, left upper third molar and associated molar fragments; AMA-VP-2/38, left upper fourth premolar; MKM-VP-1/261, right and left lower fourth premolars, left lower second molar, and mandibular as well as additional molar fragments; MKM-VP-1/146, left lower fourth premolar.

Localities and Age: Specimens from Aralee Issie (ARI), Am-Ado (AMA), Mesgid Dora (MSD) and Makah Mera (MKM) were collected from sediments that are radiometrically dated to between 3.82 ± 0.18 Ma and 3.57 ± 0.014 Ma.

5.1.1.1 ***Comparative Cranial Description***

MSD-VP-1/27 is an excellently preserved cranium with an associated edentulous mandibular fragment (Plate 1). Based on its overall size and the presence of large zygomatic knobs, it is identified as a male. The left zygomatic knob is partly broken although the right zygomatic knob is well-preserved and intact. The basicranium is also well-preserved, except for the left occipital condyle. The cranial vault, the frontal, and nasals are generally in a good state of preservation although there are some cracks running along the skull's longitudinal axis. Few transverse cracks are also apparent, smaller ones on the cranial vault and larger ones on the frontal and nasals. The tip of the nasal (rhinarium) part is also missing. 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 on its infero-lateral portion. The posterior half of the frontal and parietal are also well preserved. Likewise, the dentition, particularly the cheek teeth, is intact with only a slight damage to the left upper third molar. The incisors and canines are missing although the alveoli are undamaged. The cranium also has an associated edentulous mandibular fragment extending from the fourth premolar to the third molar.

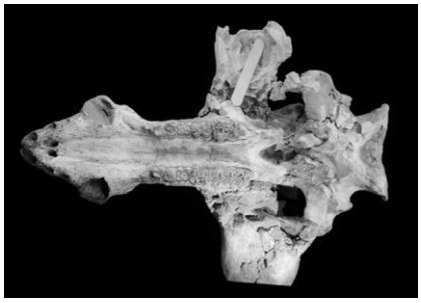
The nasal region in MSD-VP-1/27 is transversely convex towards the anterior half and flattened at midline towards its posterior half. This area is virtually flat in other *Ny. jaegeri* specimens such as KNM-KP 264 as well as in KNM-ER 3183 and up-curved in *Not. euilus* specimens such as A.L. 107-13. The nasals in KNM-ER 3540 and 3541 are convex posteriorly but bisected by medial depressions in front of the canine alveoli. The Hadar *Notochoerus euilus* skulls exhibit straight and parallel sided nasals. The MSD-VP-1/27 nasal is broader at the level of the supra-canine flange which is also seen in both A.L. 137-4 and KNM-ER 3183 and gradually tapering towards the anterior. This region in KNM-ER 3540 and 3541 are elongate and gently slope anteriorly. 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 is ossified. The specimen has also a slightly broad supracanine flange with weakly ornamented dorsal ridge. This ornamentation is also present in the Koobi Fora specimens

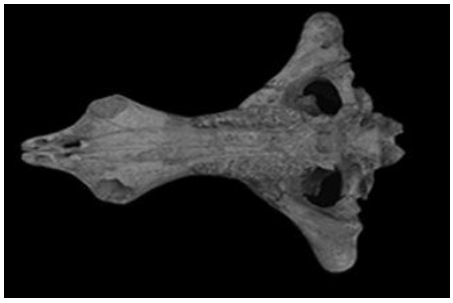
KNM-ER 3540 and KNM-ER 3541. The canine flange of MSD-VP-1/27 continues backward behind the canine alveolus almost to the level of the second and third premolars and its supracanine gutter is relatively broad as in KNM-ER 3540 and KNM-ER 3541 (Fig.5.1).

Position of the orbits in MSD-VP-1/27 is low on the skull compared to KNM-ER 3541 and A.L. 172-1. The shape of its orbit is also different in being oval unlike in KNM-ER 3540, KNM-ER 3541, and A.L. 172-1, which is circular. The orbital rim of the Woranso-Mille specimen is relatively thick. Its posterior portion of the orbit is marked by large postorbital processes. The MSD-VP-1/27 frontal bone between the orbits is strongly concave whereas it is domed in KNM-ER 3541. In A.L. 172-1 it is marked by two depressions on either side of the medially elevated part. The zygomatic knob is more massive than *Not. euilus* specimens such as A.L. 172-1 and hence MSD-VP-1/27 is definitely a male.. Its zygomatic protuberance diverges from the sagittal axis at right angles like KNM-KP 264, A.L. 107-13, as well as other Hadar *Not. euilus* specimens. There is also a similarity in the origin of the root of the zygoma between MSD-VP-1/27, KNM-KP 264 and A.L. 172-1 where in all cases it starts behind the infraorbital foramina (Fig.5.1).

Maximum width of the cranial vault in MSD-VP-1/27, A.L. 137-4, A.L.172-1, and A.L.108-3 is between the postorbital processes and narrows towards the nuchal crest. The vault of the Woranso-Mille specimen is strongly concave at midline. It is also smoothly concave between the temporal lines in KNM-KP 264. Likewise, a slight depression of this bone is seen in KNM-KP 239 and A.L. 137-4.This depression, when initially observed in the Hadar *Ny. kanamensis* specimens, was considered as an artifact of preservations although it was later proved to be a real cranial feature of the genus *Nyanzachoerus*. In sharp contrast, the top of the cranium in KNM-ER 3541 and A.L. 172-1 as well as A.L. 108-3 is flat. The Naso-frontoparietal angulation is very high in MSD-VP-1/27, KNM-KP 239, KNM-KP 30186 and the edentulous partial cranium KNM-ER 3183. Even though the angulation seems more pronounced in the males as it is noted in MSD-VP-1/27 and KNM-KP 30186, the A.L. 137-4 which is presumed female *Ny.kanamensis* has still slightly higher angulation than in KNM-ER 3541 and A.L. 172-1.

Position of the temporal lines coincides with the lateral edges of the cranial vault both in MSD-VP-1/27 and KNM-ER 3541. However, there is a strong difference in the temporal fossae where the former reveals deeply excavated fossae like A.L. 137-4 while the later and other *Not. euilus* materials such as A.L. 172-1 and A.L. 108-3 have generally very shallow fossae. The temporal fossae are over-hanged by edges of the cranial vault in almost all specimens regardless of the genus. The parietal constriction is narrow in *Not. euilus*



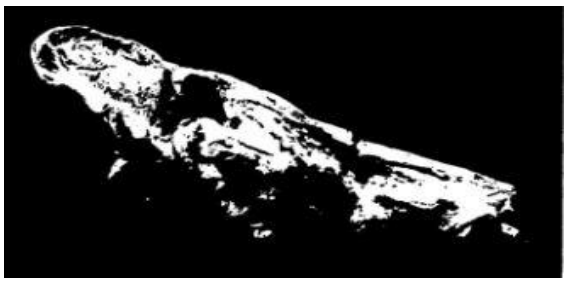


Ny.jaegeri (MSD-VP-1/27) *Not.euilus* (A.L. 172-1)

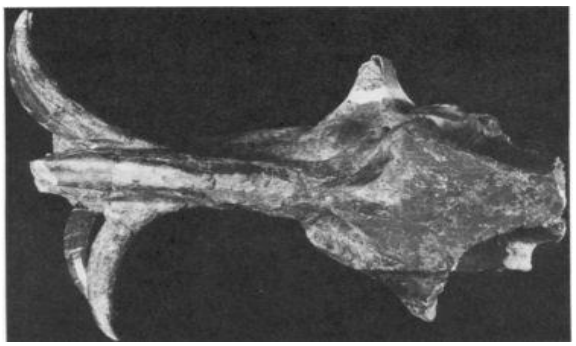
A.Ventral Views

Ny.jaegeri (MSD-VP-1/27) *Not.euilus* (A.L. 172-1)

B. Lateral views



Ny.kanamensis (A.L. 137-4)



Ny.jaegeri (MSD-VP-1/27) *Not.euilus* (KNM-ER 3541)

C. Dorsal views

Figure 5.1: Cranial morphology of *Ny.jaegeri*,*Ny.kanamensis* and *Not.euilus:* A.Ventral; B.Lateral; C. Dorsla views.

specimens such as KNM-ER 3541, A.L. 172-1, and A.L. 108-3. Contrary to this, the constriction is broader in MSD-VP-1/27 and A.L. 137-4. On the parietal bone 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. The supraoccipital is laterally expanded below the nuchal crest and tapers towards the foramen magnum as noted from MSD-VP-1/27, *Ny. knamensis* and *Not. euilus* materials. The occipital condyles of the individual are relatively small. They are positioned midway between plane of orbit and palatal plane as in KNM-ER 3541 and KNM-KP 239. There is a sharp angle between the parietal and supraoccipital region both in A.L. 107-13 and MSD-VP-1/27. The angle is about 45^0 in A.L. 137-4 (Fig.5.1).

The palate is relatively elongated in the Woaranso-Mille specimen compared to the *Ny. kanamensis*. Its palate is expanded at the canine alveoli and narrows behind and in front of it as in KNM-KP 239 and KNM-KP 264. The shape of the palatonarial border is almost V-shaped in MSD-VP-1/27. The notch is also much narrower in KNM-KP 239. However, A.L. 137-4 has slightly broader notch but it is much broader in A.L 172-1. The position of this palatonarial border is far behind the level of the third molar talon in MSD-VP-1/27, A.L. 137-4, KNM-ER 3541, and A.L. 172-1. 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 third molar in this specimen. The incisive foramina are also very large. The palate of the specimen is generally shallow.

As it is noted earlier the cranial features of *Ny.jaegeri* were less known and new morphological data generated from the Woranso-Mille cranium have been compiled under Table 8.

Cranial measurements of MSD-VP-1/27 and the comparative specimens of *Ny. kanamensis* and *Not. euilus* are presented in Tables 10 and 11. The vertex length of MSD-VP-1/27 (646 mm) is longer than in both the *Ny. kanamensis* (534mm) and *Not. euilus* (565 mm) specimens. Similarly, the bizygomatic width (526 mm) of the specimen is larger than the average values of *Ny. kanamensis* (345 mm) and *Not. euilus* (325 mm). The ratio of vertex length to bizygomatic breadth of MSD-VP-1/27 (1.23) is lower than the average values of both *Ny. kanamensis* (1.55) and *Not. euilus* (1.74). Regarding the width across postorbital processes, MSD-VP-1/27 has an intermediate value (177 mm) between *Ny. kanamensis* (151 mm) and *Not. euilus* (191 mm). On the contrary, the specimen is the widest at the parietal constriction (87 mm), which is closer to *Ny. kanamensis* (82 mm) while *Not. euilus* has an

average value of about 58 mm. The maximum breadth of the nasals is slightly broader in MSD-VP-1/27 (70 mm) by about 5 mm than the two comparative species. The breadth of the muzzle at the infraorbital foramen is exactly the same with the average values for *Not. euilus* (71 mm) whereas it is narrow in the *Ny. kanamensis* (56 mm). The palatal length in MSD-VP-1/27 (372 mm) is higher than the values in *Ny. kanamensis* (327 mm) and *Not. euilus* (261 mm). Another feature which is of interest is that MSD-VP-1/27 has tooth rows that are parallel particularly from the third premolar to the third molar. The breadth of the palate at the third molars and third premolars is equal (41 mm). On the other hand, *Not. euilus* tooth rows converge posteriorly. The breadth at the third premolars is 64 mm and 51 mm at the third molars.

Bivariate scatter plot of premolar series length versus molar series length indicates that *Ny.jaegeri* forms a cluster with *Ny. kanamensis* than with *Notochoerus euilus* (Fig.5.2). The ratio of molar to premolar length shows MSD-VP-1/27 as an intermediate but closer to *Ny. kanamensis* (Fig.5. 3).

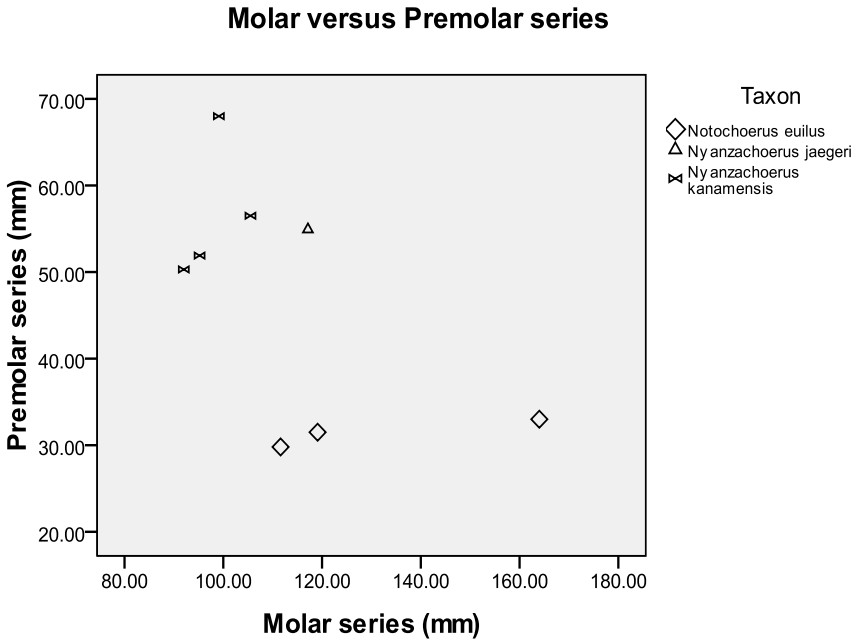


Figure 5.2: A bivariate plot showing molar and premolar series length of *Nyanzachoerus jaegeri* (as represented by MSD-VP-1/27), *Nyanzachoerus kanamensis* and *Notochoerus euilus*.

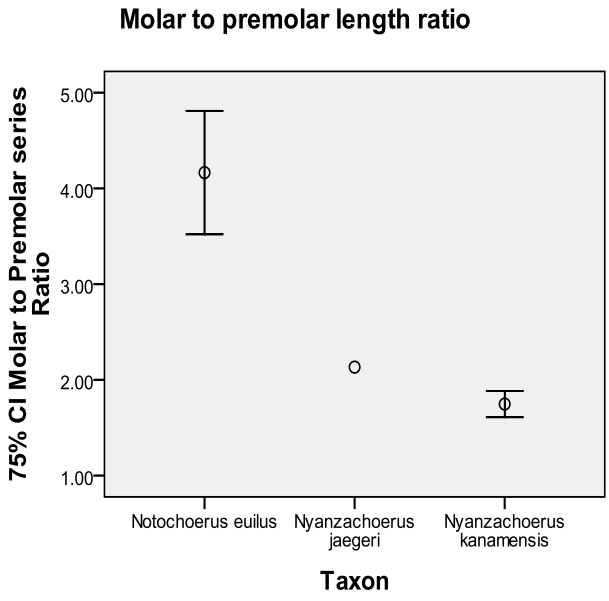


Figure 5.3: A univariate plot of the molar to premolar series ratio of *Nyanzachoerus jaegeri* (as represented by MSD-VP-1/27), *Nyanzachoerus kanamensis* and *Notochoerus euilus.*

*5.1.1.2 **Comparative Description of Upper dentition***

Description of each tooth is presented below. Metric comparisons of the Woranso-Mille materials with *Ny. jaegeri* and *Not. euilus* specimens from other localities were also conducted. The results are presented in multiple bivariate plots. The measurement values of the Woranso-Mille *Ny.jaegeri* upper dentition are presented in Table 12 and figured in Plate 1-4.

Upper incisors

Identification of isolated incisors to the species level is very difficult. The description and/or observations presented here in relation to upper incisors is based on MSD-VP-1/27. There are three pairs of incisors as it is judged from the alveoli of MSD-VP-1/27. The same number of incisors is also noted from the incisor sockets in KNM-KP 264. However, only a single pair of upper incisors is present in KNM-ER 3540 and 3541 and the Hadar *Notochoerus euilus* specimens. The size of the incisors of the specimen is also determined from each alveolus. Therefore, the central incisor is larger than the second incisor. The central incisors are separated from each other by a small diastema. Relatively larger diastema are also present between the first and second, as well as second and third incisors. The gap becomes very large between the third incisors and the canines (canine alveolus). The incisors are generally arranged in an almost occlusally V-shaped appearance in the premaxillae.

Upper canines

Canines of MSD-VP-1/27 were not recovered. However, the alveoli indicate that they were large in all of their dimensions. The root sockets and orientation of the alveolar margins indicate that the canines emerge horizontally and slightly forward. Similar orientation of the upper canines is observed in specimens such as KNM-KP 264 and A.L. 137-4. The Hadar *Not. euilus* specimens similarly show the canine to emerge near the palatal plane. The shape of the canine is triangular at least at the base of the alveolus of MSD-VP-1/27. The upper canine cross section in KNM-KP 239 and KNM-KP 264 is oval in shape and slightly pointing anteriorly. However, KNM-ER 3541 has a triangular transverse cross section. The shape of the canine is triangular at least at the base of the alveolus in the Woranso-Mille specimen while other *Ny.jaegeri* specimens have oval cross section (Harris and White, 1979).

Upper second premolars

MSD-VP-1/27 has no trace of upper first premolar. There are only three pairs of upper premolars (P2-P4) like KNM-KP 239 and KNM-KP 264. On the other hand, the Hadar *Not. euilus* crania also lack the upper second premolars. Description of the upper second premolar presented here is based on MSD-VP-1/27. The tooth is very similar to the specimens described from Kanapoi (Cooke and Ewer, 1972). It is highly reduced relative to the upper third and fourth premolars. It has been described to possess a centrally placed main cusp. Both anterior and posterior cingula are present; the former is rudimentary while the later is more prominent. The lingual part of the posterior cingulum tends to develop into an incipient cusp. Similarly, the Kanapoi specimens show a secondary cusp posterior to the main cusp (Cooke and Ewer, 1972). The anterior and posterior cingula are connected via a sagittal ridge. When viewed occlusally, the tooth has an overall bucco-lingually compressed oval shape. Relative to the cranial axis, the tooth is oriented from mesiobuccal to the distolingual corner.

Upper third premolars

The upper third premolar is substantially larger than in *Not.euilus*. However, the overall size is smaller than the fourth premolar of the same individual. The shape is almost rectangular in occlusal view with mesiodistally elongated dimension unlike the oval shape in other *Ny.jaegeri* third premolars. There are two major crown elements - large paracone covering most of the occlusal crown area and a smaller protocone. Anterior and posterior

cingula are present and the posterior is slightly larger. Nevertheless, internal and external cingula are absent. Enamel is smooth.

Metric values of MSD-VP-1/27 upper third premolar show that its basal length is lower than the Kanapoi specimens while the breadth is within the range of the specimens included in the analysis (Fig. 5.4).

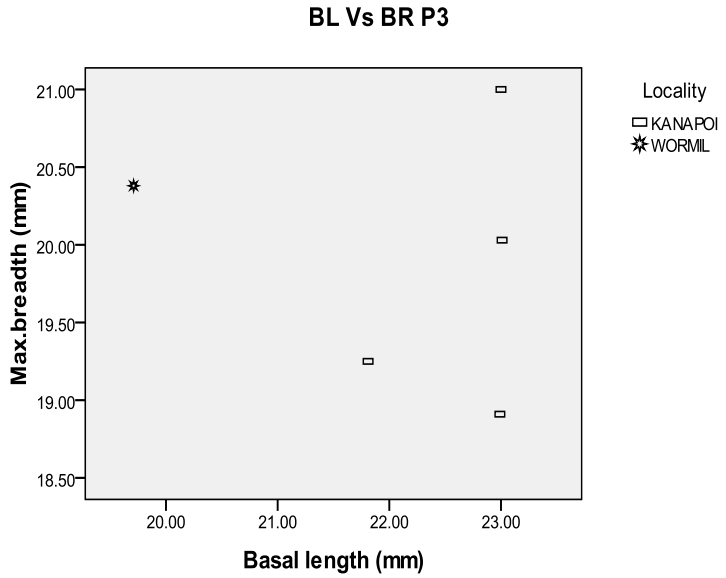


Figure 5.4: A bivariate plot of the basal length and breadth of *Nyanzachoerus jaegeri* upper third premolars. *WORMIL=Woranso-Mille

Upper fourth premolars

The MSD-VP-1/27 P4 is relatively larger than in *Not.euilus* but similar to other Woranso-Mille *Ny. jaegeri* specimens such as ARI-VP-1/98 and ARI-VP-1/311. In MSD-VP-1/27, this tooth is square-shaped like the Kanapoi specimens (Cooke and Ewer, 1972). There are two transversely oriented main cusps; the larger (paracone) is labially positioned relative to the smaller protocone. However, the Kanapoi fourth premolars have a pair of buccal cusps (paracone and metacone) and lingually positioned protocone (Cooke and Ewer, 1972). The paracone in one of the Woranso-Mille specimens (ARI-VP-1/311) is also apically bifurcated. Another specimen, ARI-VP-1/98, has a small additional cusplet positioned posteriorly on the distal part of the paracone. Anterior and posterior cingula are present in all of the fourth premolars from Woranso-Mille and the posterior cingulum is more prominent as in the Kanapoi specimens (Cooke and Ewer, 1972). Both cingula have small mammilations. In ARI-VP-1/311 an isolated cingular cusplet emerges in the middle of the anterior cingulum. The

cingula are not extended labially and lingually to the width of the crown, similar to *Ny.kanamensis* and *Not.euilus*. As seen in ARI-VP-1/98, there are three roots placed antero-labially, postero-labially and lingually. Enamel texture is variably displayed ranging from smooth to slightly rough. In AMA-VP-2/38 it is slightly rough. The texture is, however, smooth in MSD-VP-1/27. Several grooves are also observed on the crown surface in ARI-VP-1/311.

In terms of the basal length and breadth, the Woranso-Mille specimens fall within the range documented for the Kanapoi specimens (Fig. 5.5). However, the majority of the Kanapoi specimens are relatively short mesiodistally. The Woranso-Mille specimens show strong variation in their breadth.

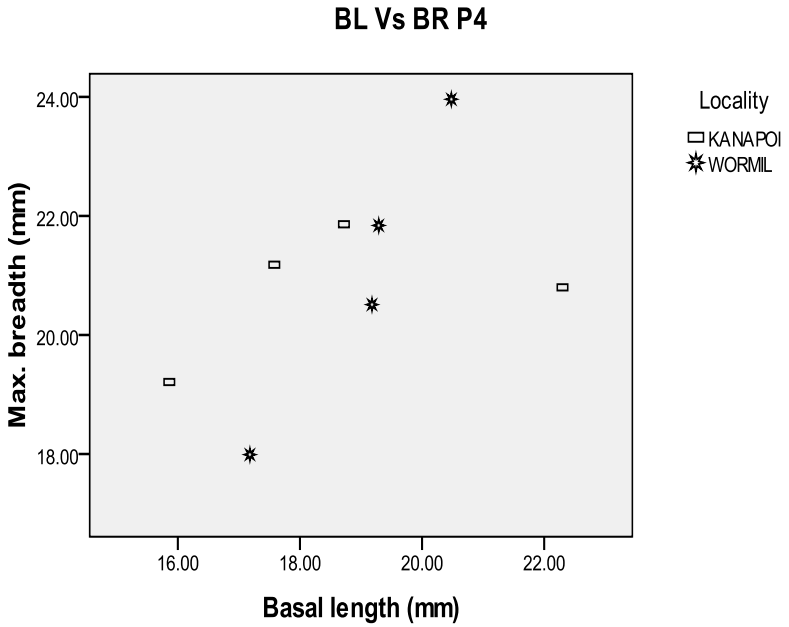


Figure 5.5: A bivariate plot showing basal length and breadth of upper fourth premolars of *Ny. jaegeri*.

*Upper first molar*s

Length and breadth of the first molar is comparable to the fourth premolar. However, most of the specimens are too worn to describe occlusal morphology. However, occlusal morphology of the upper first molars is usually similar to the upper second molars except for their smaller size. The two lateral pillar pairs are separated by single median pillar. Lingual lateral pillars are more flattened than the labial ones. The labial pillars positioned slightly mesially than their lingual counterparts. The tooth is not strongly bilobed. Both anterior and

posterior cingula are present. The posterior one is larger than the anterior and it slightly bulges posteriorly. As seen in MSD-VP-2/59, the tooth possesses both endo- and ectostyles. The same specimen also shows the presence of four roots. Comparative bivariate plot for this tooth is not presented here because *Ny. jaegeri* upper first molar metric data is not reported from other localities.

*Upper second molar*s

Upper second molars are relatively larger and more robust than the first molars. The larger lateral pillar pairs are separated by a single median pillar. The inner and outer pillars are a bit bulged as in the Chiwondo Beds specimens of *Ny. jaegeri* (Kullmer, 2008). On the buccal surface the pillars are separated by deep valley, particularly in MSD-VP-5/5. Additional smaller cusps also present between the anterior cingulum and first pillar pair as well as the posterior cingulum and the second lateral pillar pair. The ectostyle is slightly larger than the endostyle. Anterior and posterior cingula are moderate in size but the posterior cingulum slightly bulges posteriorly. When worn, the enamel forms an irregular outline tending to form a five armed enamel island as in the Laetoli (Bishop, 2011) as well as the Kanapoi (Cooke and Ewer, 1972) specimens. The Galili and Chiwondo Beds specimens are different in this regard and show strong mesial and distal vertical folds instead (Kullmer, 2008; Kullmer et al., 2008). The tooth is generally smooth and lacks cement cover.

A bivariate plot of the length and breadth of the second molars shows that the Woranso-Mille and Kanapoi specimens have comparable length although the former are broader than the latter (Fig.5.6).

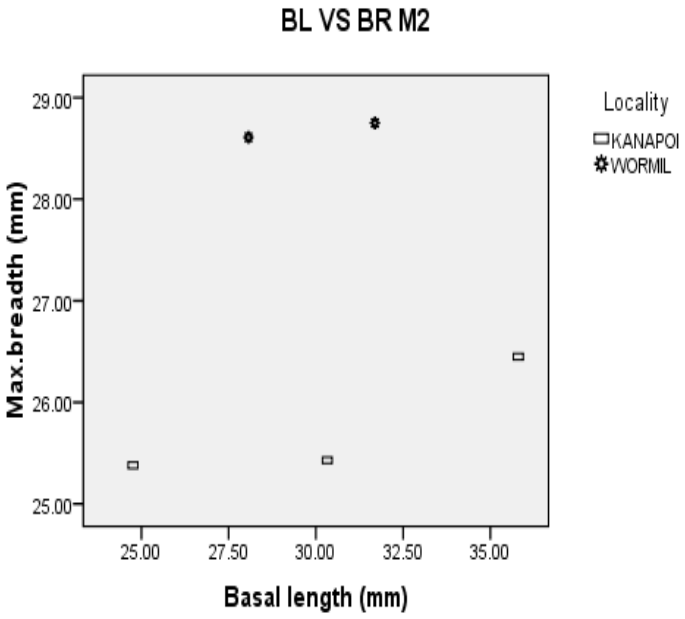


Figure 5.6: A bivariate plot of basal length to breadth of upper second molar of *Ny.jaegeri*

Upper third molars

First lateral pillar pairs of the upper third molar 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 third molars have both endostyle and ectostyle at the trigon/talon junction, a feature also seen in the Kanapoi specimens (Cooke and Ewer, 1972). However, some Woranso-Mille *Ny. jaegeri* third molars such as AMA-VP-2/56 and ARI-VP-1/430 lack the ectostyle. In AMA-VP-2/56 the endostyles are present at the base of the valleys separating the lateral pillars, while in the second it is only found at the trigon/talon junction. 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 upper third molars recovered from the Woranso-Mille show a single median pillar separating the trigon from the talon as opposed to the *Not.euilus* upper third molars usually contains double median pillars. The talon comprises a large single lingual pillar, a terminal pillar and smaller labial cusps with variable numbers. *Ny.jaegeri* upper third molars 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*. Some specimens such as MSD-VP-1/27 and AMA-VP-2/56 tend to show an incipient third pillar pair whereas the third pair is well developed in the Kanapoi specimens (Cooke and

Ewer, 1972). The Woranso-Mille specimens indicate a slight lateral bulging in their lateral pillars like the Chiwondo Beds *Ny.jaegeri* (Kullmer, 2008) while *Not.euilus* has flatter lateral pillars. The lateral pillars of the Woranso-Mille materials coalesce at their bases and diverge toward the occlusal surface while *Not.euilus* pillars are divergent all the way from the base. More particularly, the pillars join almost to the peak in MSD-VP-1/27.The lateral pillars in AMA-VP-2/56 are mound shaped. Unlike *Not.euilus* the pillar pairs described to be *Ny.jaegeri* from the study site lack an anterior curvature. Median pillars are oval in shape. They can also be columnar as it is observed from AMA-VP-2/56. Both the major lateral and terminal pillars are very large and robust in MSD-VP-1/27, have moderate crown height, and less hypsodont than *Not.euilus*. The enamel of the upper third molar is generally rough in texture but slightly smooth in MSD-VP-1/27. In addition, there are longitudinal grooves in each of the lateral pillars in AMA-VP-2/56. Occlusally, the enamel surface of MSD-VP-1/27 and ARI-VP-1/430 are convoluted and has a general irregular outline as in the *Ny.jaegeri* specimens from other sites (Harris and White, 1979). This is different from the strong mesial and distal vertical folds reported for the Chiwondo Beds (Kullmer, 2008) and Galili (Kullmer et al., 2008) specimens.

A bivariate plot of the upper third molar basal length and breadth is shown in Fig. 5.7. The values of the Woranso-Mille specimens are within the range of variation documented for the Kanapoi specimens. However, *Ny. jaegeri* specimens from Galili and majority of the Kanapoi specimens have elongated basal length compared to the Woranso-Mille specimens although their breadth is comparable.

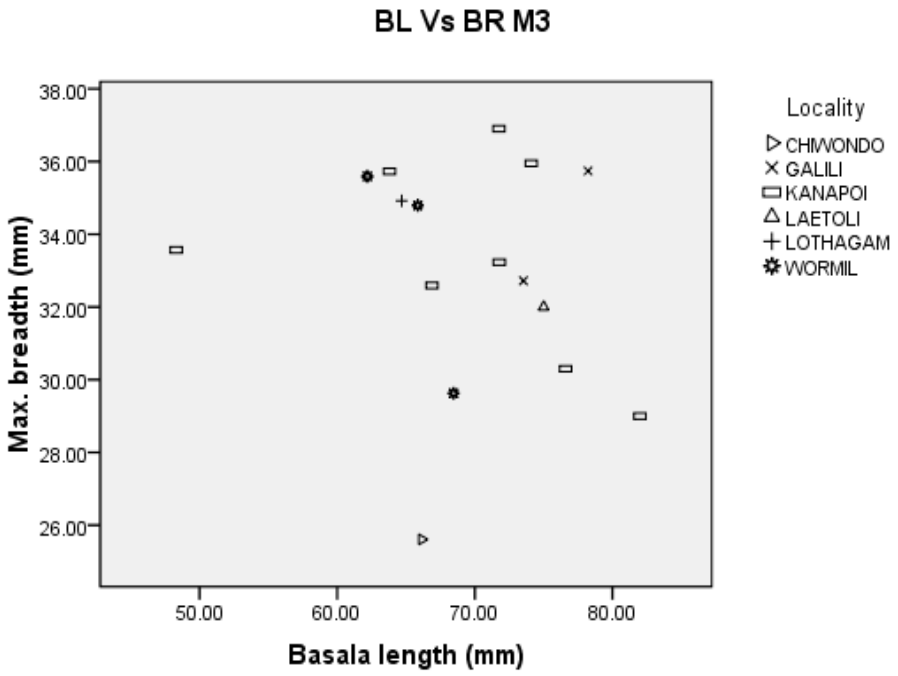


Figure 5.7: A bivariate plot showing the basal length and breadth of upper third molars of *Ny. jaegeri* from various localities.

5.1.1.3 Comparative Description of Lower dentition

Lower dentitions are also described and compared in the same manner as the upper dentitions. Dental measurements of Woranso-Mille specimens identified here as belonging to this species are presented in Table 13. Figures are shown in Plate 5 and Plate 6.

Lower third premolars

Lower third premolars of *Ny. jaegeri* from the Woranso-Mille are relatively large and medio-laterally compressed like other known lower third premolars of the species. The tooth possesses a single posteriorly inclined main cusp. The anterior crest which runs from the main cusp tip to the anterior cingulum is steep. Both anterior and posterior cingula are present. The posterior cingulum is more prominent than the anterior, which is rudimentary and manifested as an incipient cusp at the base of the anterior crest. The third premolars from Kanapoi also show a prominent posterior cingulum than the anterior one (Cooke and Ewer, 1972). The upper third premolar morphology of the Woranso-Mille specimens is generally similar with *Not.euilus* although slightly larger in size.

Basal length and breadth of the lower third premolars from Woranso-Mille is generally comparable with the Kanapoi materials (Fig. 5.8). The shortest third premolar is documented from Galili and the longest ones from Kanapoi and Lothagam.

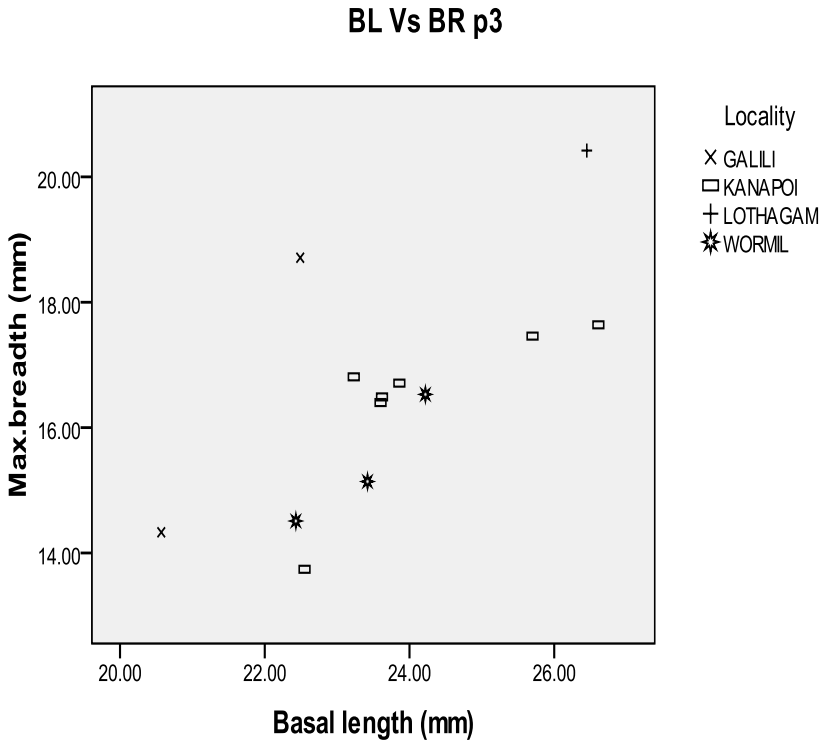


Figure 5.8: A bivariate plot showing basal length and breadth of the lower third premolars of *Ny.jaegeri*.

Lower fourth premolars

The fourth premolar is generally shorter and wider than the third premolar. MSD-VP-2/187 is relatively large compared to other specimens of the species. The overall size of this tooth is generally larger than in *Not.euilus* although there is substantial overlap in morphology. Both anterior and posterior cingula are present. The posterior cingulum is larger than the anterior. On the other hand, the anterior cingulum is represented by a small isolated cusp. With wear, however, the posterior cingulum reduces its size and becomes shorter than the anterior one as seen in MSD-VP-2/187. The posterior cingulum is also taller than the posterior cingulum of the lower third premolar. Additional smaller cusplets are present between the anterior cingulum and the main cusp as well as the posterior cingulum and the main cusp. In slight wear, the main cusp is fused with the posterior cingulum and forms a single enamel island as seen in MSD-VP-2/187.

Majority of the lower fourth premolars recovered from the Woranso-Mille are narrower than the specimens from Kanapoi, Galili and Lothagam. However, the Woranso-Mille specimens show extreme variation in their basal length documenting the minimum and maximum values recorded for the species. On average, the basal length is comparable with the Kanapoi specimens (Fig. 5.9).

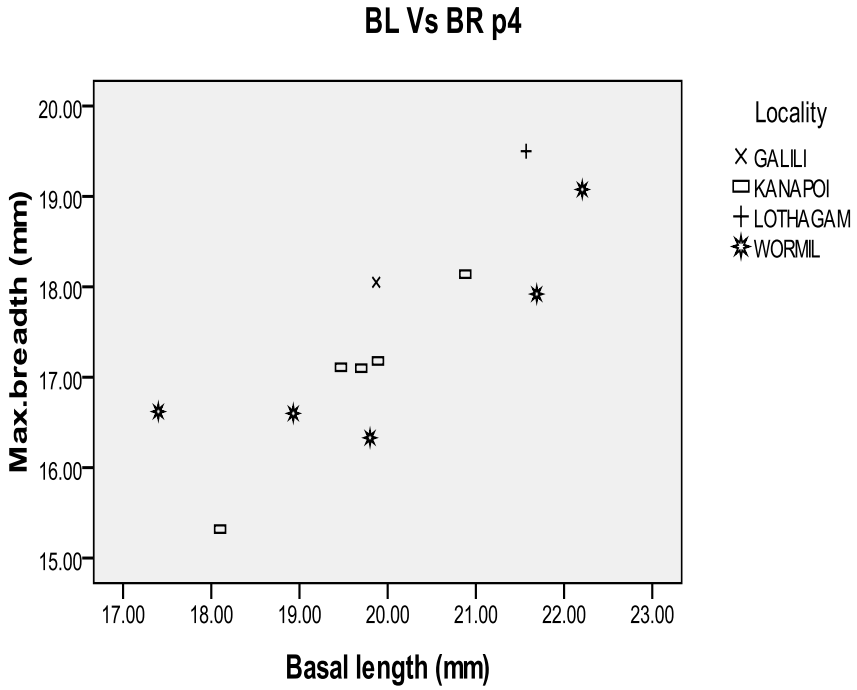


Figure 5.9: A bivariate plot showing basal length and breadth of lower fourth premolars of *Ny. jaegeri.*

Lower first molars

Most of the lower first molars are heavily worn and hence some are excluded from the following description. ARI-VP-1/477 shows a strongly bilobed morphology. There are two major pillar pairs that are separated by single median pillar. Anterior and posterior cingula are present. The posterior cingulum is more prominent and slightly expanded distally although not as much as in *Not.euilus*. The posterior cingulum in the latter species is flanked by smaller cusps on either side and strongly bowed posteriorly (Harris and White, 1979). Endostylids are present between the pillar pairs although some specimens such as ARI-VP-1/477 also have ectostylid.

Figure 5.10. shows a bivariate plot of the basal length and breadth of the lower first molars. The Woranso-Mille specimens are broader but generally comparable with the Kanapoi specimens in their basal length.

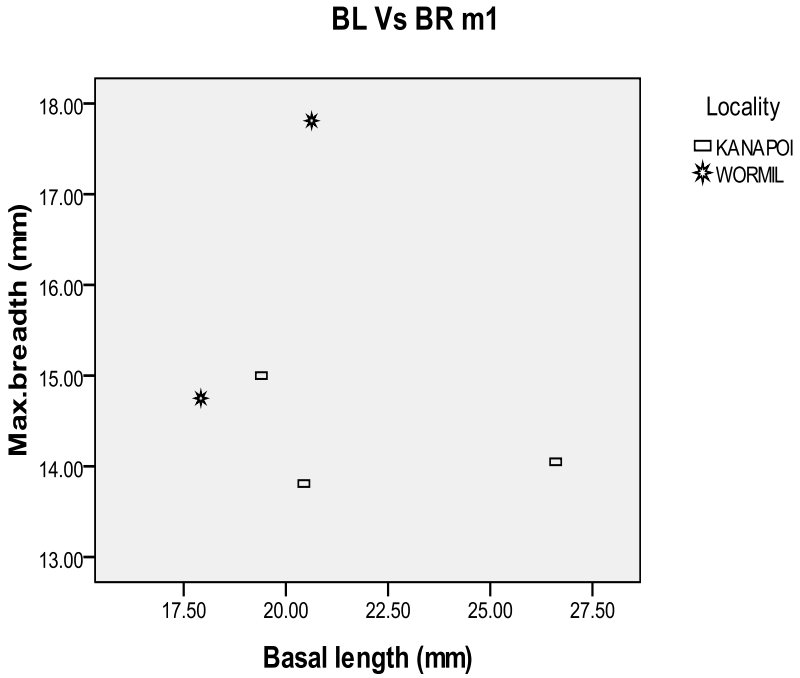


Figure 5.10: A bivariate plot showing basal length and breadth of the lower first molars of *Ny. jaegeri***.**

Lower second molars

The lower second molar is described only based on MKM-VP-1/261 and it is relatively larger and elongated than the upper first molar. The two lateral pillar pairs are separated by a single median pillar. The median pillar is rounded. Enamel shows strong mesial and distal vertical folding as the *Ny.jaegri* materials from Galili and Chiwondo Beds (Kullmer et al., 2008; Kullmer, 2008). Anterior and posterior cingula are present. Posterior cingulum is larger than the anterior one and forms slight shelf like structure posteriorly as the Kanapoi *Ny.jaegeri* (Cooke and Ewer, 1972). Enamel is relatively smooth.

Metric analysis shows that the Woranso-Mille specimen is less elongated and lies at the lower margin of the Kanapoi materials .Unlikely, its breadth is within the variation of the Kanapoi *Ny.jaegeri* samples (Fig. 5.11).

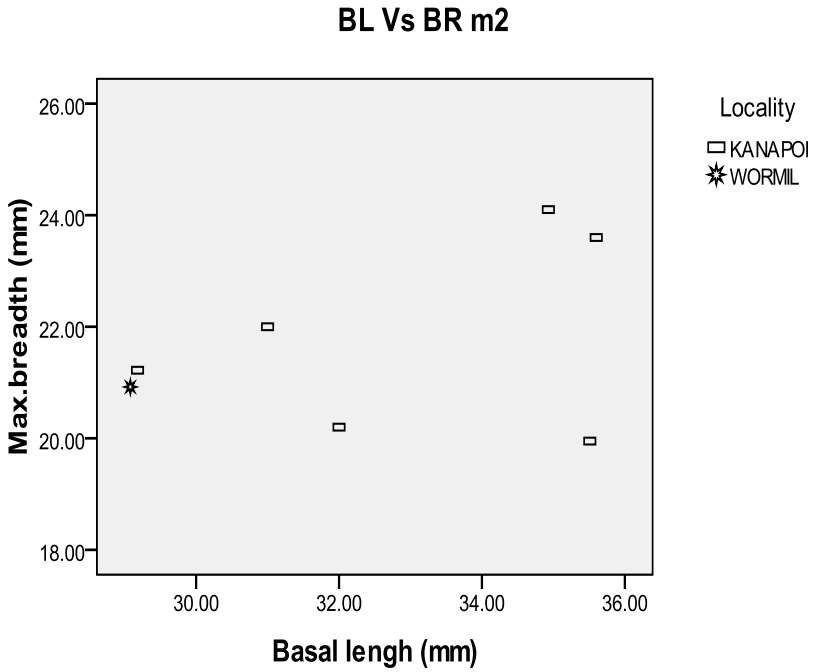


Figure 5.11: A bivariate plot of the basal length and breadth of the lower second molars of *Ny.jaegeri*

5.1.2 ***Notochoerus euilus***

Class MAMMALIA

Order ARTIODACTYLA Owen, 1848

Family SUIDAE Gray, 1821

Subfamily TETRACONODONTINAE Lydekker, 1876

Genus NOTOCHOERUS Broom, 1925

Species *Notochoerus euilus* (Hopwood), 1926

Referred Specimens*:* AMA-VP-2/10, left lower first molar; AMA-VP-2/44, left lower third molar; ARI-VP-1/440, left upper third premolar; ARI-VP-1/367, left lower first molar; ARI-VP-1/46, right upper fourth premolar and associated broken molar; ARI-VP-1/299, right upper third molar; ARI-VP-1/53, right upper fourth premolar and left upper third premolar; ARI-VP-1/454, right and left maxillary fragment (M1-M2); MKM-VP-1/53, left upper third premolar and right and left upper fourth premolars associated with dental fragments; MKM-VP-1/271, right maxillary fragment (P3-M1); MKM-VP-1/55, right maxillary fragment (P4-M3), left maxillary fragment (M2-M3) and left upper fourth

premolar; MKM-VP-1/185, right lower third molar including lower premolar fragments and broken lower incisors; MSD-VP-5/6, left upper third premolar and upper molars and canine fragments; MSD-VP-5/24, right upper third premolar and upper molar fragment; MSD-VP-3/9, left upper third premolar; MSD-VP-2/67, right upper first molar; MSD-VP-2/16, right upper fourth premolar; MSD-VP-2/144, left upper fourth premolar; MSD-VP-1/58, left upper first molar; MSD-VP-1/10, right maxillary fragment (M2-M3); MSD-VP-3/9, left lower fourth and second premolars, left lower second molar and molar fragments; MSD-VP-3/8, left lower third premolar; MSD-VP-2/103, right mandibular fragment (dp4-m1); MSD-VP-2/225, right mandibular fragment (p4); MSD-VP-2/70, left lower third premolar and right lower fourth premolar; MSD-VP-2/177, right mandibular fragment (m3) and right lower third premolar; MSD-VP-5/27, left lower third molar; MSD-VP-1/7, left mandibular fragment (m2-m3).

Localities and Age*:* Specimens from Am-Ado (AMA), Aralee Issie (ARI), Mesgid Dora (MSD) and Makah Mera (MKM) were recovered from sediments radiometrically dated to between 3.82±0.18Ma and 3.57±0.014Ma.

5.1.2.1 ***Comparative Description of Upper dentition***

Description and metric evaluation of *Not. euilus* follows the methods used above in the description of *Ny. jaegeri*. Metric measurements of the upper dentition are given in Table 14. Figures of the upper dentition of the Woranso-Mille *Not. euilus* are illustrated in Plates 7-10.

Upper third premolars

Upper third premolars of *Not. euilus* are relatively smaller in size compared to *Ny.jaegeri*. When viewed occlusally, they are triangular in shape with the apex of the paracone positioned anteriorly. The centrally placed paracone occupies majority of the crown area and the protocone is positioned on the posterolingual corner of the crown. A deep longitudinal groove is present on the mesiolingual side of the paracone (e.g., MKM-VP-1/271). Smaller grooves are also present on the lingual side of the paracone in other specimens. A very small accessory cusp separates the main cusp from the posterior cingulum. However, this smaller cusp is described as a larger metacone in other *Not.euilus* specimens (Harris and White, 1979). An anterior ridge connects the paracone with the anterior cingulum. Internal and external cingula are absent. Anterior and posterior cingula are present and

generally smaller, characteristic of *Not.euilus*. The posterior cingulum is larger in size than the anterior cingulum. Enamel is rough and strongly grooved lingually.

Majority of the Woranso-Mille upper third premolar basal length values are greater than several Hadar and Koobi Fora specimens. However, the Hadar samples are slightly broader than specimens from the Woranso-Mille (Fig. 5.12).

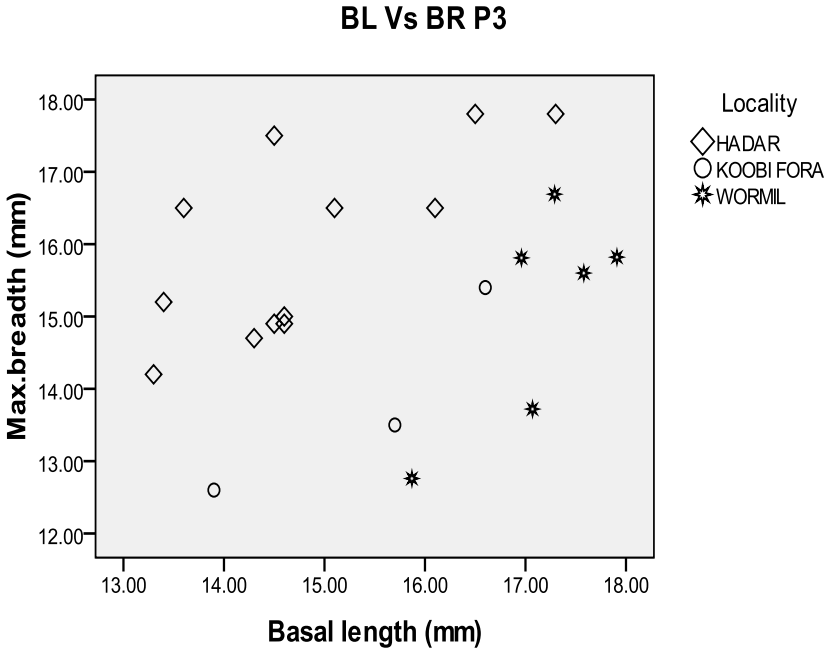


Figure 5.12: A bivariate plot displaying the basal length and breadth of upper third premolars of *Notochoerus euilus*

Upper fourth premolars

The upper fourth premolar is bunodont as well as relatively smaller and shorter in height compared to the third premolar. The tooth has shown a *Not.euilus* morphological features and it is smaller in size than the *Ny.jaegeri* upper fourth premolar. The two major cusps are transversely oriented. On the paracone, there is strong mesial and distal enamel folding in MKM-VP-1/271. The two main cusps are separated by a transverse groove. Additional cusp is present between paracone and posterior cingulum which is considered as an incipient metacone in other *Not.euilus* specimens (Harris and White, 1979). Anterior and posterior cingula are present where the latter is prominent. Both cingula extend less labially. Posterior cingulum is with smaller subsidiary cusps in MKM-VP-1/55. The anterior cingulum is serrated in ARI-VP-1/53. Enamel is rough. Furthermore, it is folded in ARI-VP-1/53.

By comparison the Woranso-Mille specimens are elongated than most of the Hadar and Koobi Fora materials. However, the breadth is generally within the Hadar intra-specific variation although the narrowest specimen is also recorded from the Woranso-Mille (Fig. 5.13).

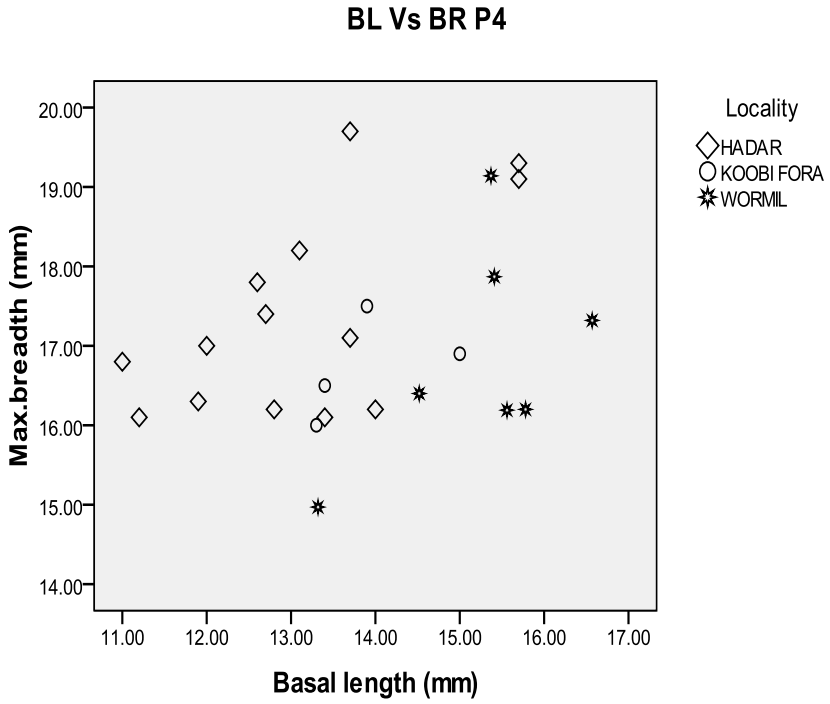


Figure 5.13: A bivariate graphical plot showing the basal length and breadth of upper fourth premolars of *Notochoerus euilus*

Upper first molars

This tooth is usually the most heavily worn in the dental row. The occlusal features mentioned here are documented from those that are less worn. MSD-VP-2/67 is bilobed with two well-developed pillar pairs, also seen in the Hadar and other *Not.euilus* first molars (Cooke, 1978b; Harris and White, 1979). The first molar is smaller than the second molar but with similar occlusal morphology. A small single median pillar separates the lateral pillar pairs. Anterior and posterior cingula are present and the anterior cingulum is broader and shorter. Like the Hadar specimens, the posterior cingulum is modest and slightly bulging. In the Woranso-Mille specimens, endostyle and ectostyle are present. ARI-VP-1/454 only has a small ectostyle. However, both endo-and ecostyle are present in MSD-VP-1/58. The presence both styles in upper M1 is not reported from other *Not.euilus* specimens. MSD-VP-1/58 also

shows that the tooth had four separate roots. Enamel is slightly rough based on observation of the same specimen.

Upper first molars of the Woranso-Mille are elongated than the Hadar specimens while breadth is comparable at both localities (Fig. 5.14).

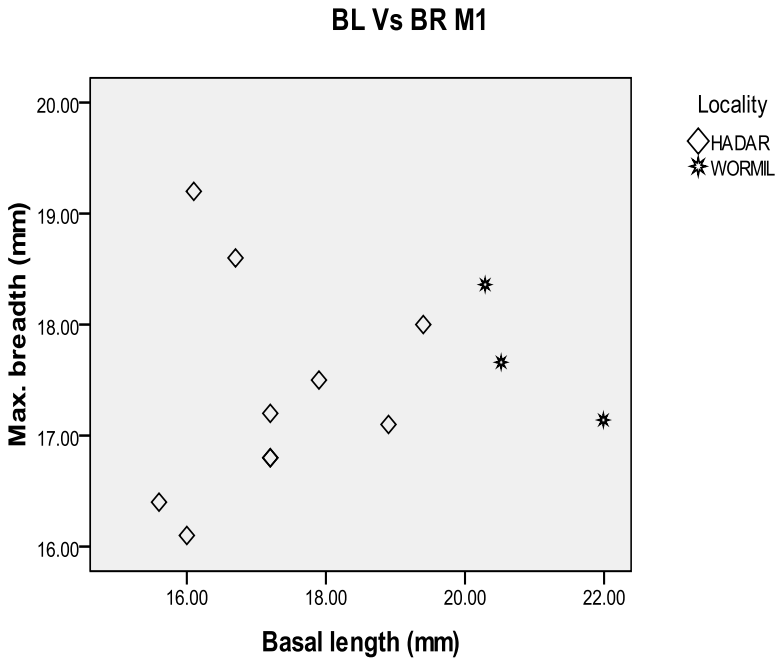


Figure 5.14: A bivariate plot displaying the basal length and breadth of upper first molars of *Notochoerus euilus*.

Upper second molars

The two pairs of lateral pillars are well separated by a deep valley with a single median pillar between them. Additional smaller cusps are also present between the second lateral pillar pair and the posterior cingulum as well as between the first pillar pair and anterior cingulum. This is similar to the condition seen in *Not.euilus* (Harris and White, 1979). Major lateral pillar pairs are slightly flat. Anterior and posterior cingula are present. Both of which are slightly expanded as in the Hadar specimens (Cooke, 1978b). Anterior cingulum is broader than the posterior one. Posterior cingulum has little mammilations and bulged from base-up. Endo- and ectostyles are present in a similar way as in *Not.euilus* specimens (Harris and White, 1979). The enamel is rough. There are strong mesial and distal enamel folds especially on the buccal pillars (forming dumb bell-shaped pattern). Lingual pillars have more irregular outline (e.g., MKM-VP-1/55).

Metric values of both basal length and breadth of the Woranso-Mille samples are within the range of the Hadar and Koobi Fora materials (Fig. 5.15). However, the Woranso-Mille specimens have relatively elongated basal length than the majority of the Hadar specimens.

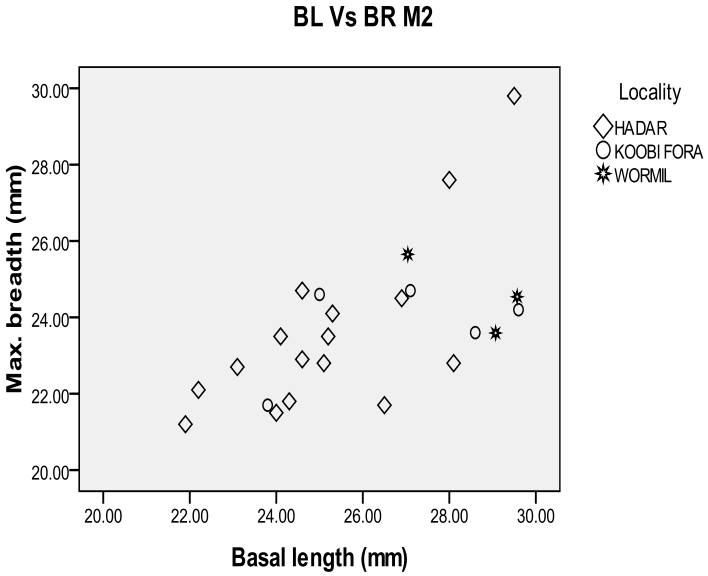


Figure 5.15: A bivariate scatter plot showing the basal length and breadth of upper second molars of *Notochoerus euilus* from various localities.

Upper third molars

Upper third molars of *Not. euilus* from Woranso-Mille are generally similar with the Hadar (Cooke, 1978b) and Galili (Kullmer et al., 2008) third molars in possessing four pillar pairs with the fourth usually less developed as seen in the specimens recovered from MKM. However, some specimens of the Woranso-Mille such as from ARI, MSD and even some specimens from MKM has three pillar pairs and a posterior complex. The Woranso-Mille materials are also comparable in their anterior complex as they retain a rugose anterior cingulum with subsidiary cusps. The talon noted from the Woranso-Mille samples consists of single pillar pair and complex smaller cusps or two pillar pairs and a single terminal pillar. Furthermore, an example of bilateral asymmetry is also observed in the talon of MKM-VP-1/55 right and left sides. The right upper third molar of MKM-VP-1/55 forming single pillar pair while the left counterpart has double pillar pair with a terminal pillar. However, the Koobi Fora specimens bear a talon with two or three pillar pairs (Harris, 1983). The trigon is separated from the talon by single and sometimes double median pillars in the Woranso-Mille, Hadar (Cooke, 1978b) and Koobi Fora (Harris, 1983) specimens. In addition,

specimens from the study area indicate single/double large lingual pillars separating the trigon from the terminal pillar. The first lingual pillar of the talon usually forms a pair. However, the Koobi Fora specimens show two or three lingual pillars in the talon (Harris, 1983). The trigon lateral pillars are slightly flattened whereas the talon pillars are a bit bulged like in the Koobi Fora (Harris, 1983) and Hadar (Cooke, 1978b) specimens. There is a well-built similarity in the lateral separation of the major pillars in the Wornaso-Mille, Hadar and Galili (Kullmer et al., 2008) materials. The Woranso-Mille upper third molars have corrugated enamel and strongly folded on the mesial and distal vertical faces to form an initial H-shaped pattern. However, the Hadar materials bear relatively good H-shaped enamel band in late stages of wear (Cooke, 1978b). On the other hand, materials from the Koobi Fora display variable degree of enamel folding (Harris, 1983). Smaller endo- and ectostyles are uniquely present in the Woranso-Mille materials. The materials have also shown thin cement cover whereas the *Not.euilus* from the Chiwondo Beds has thick cementum (Kullmer, 2008). Of course, the examination of cement thickness is dependent on the personal evaluation.

Metric values of upper third molar *Not. euilus* from various sites are graphically compared (Fig. 5.16). The Woranso-Mille measurement values of this tooth indicate a distribution within the range of the Hadar intra-specific variations. Their basal length values are also within the range of the Koobi Fora measurement values though the Woranso-Mille specimens are broader.

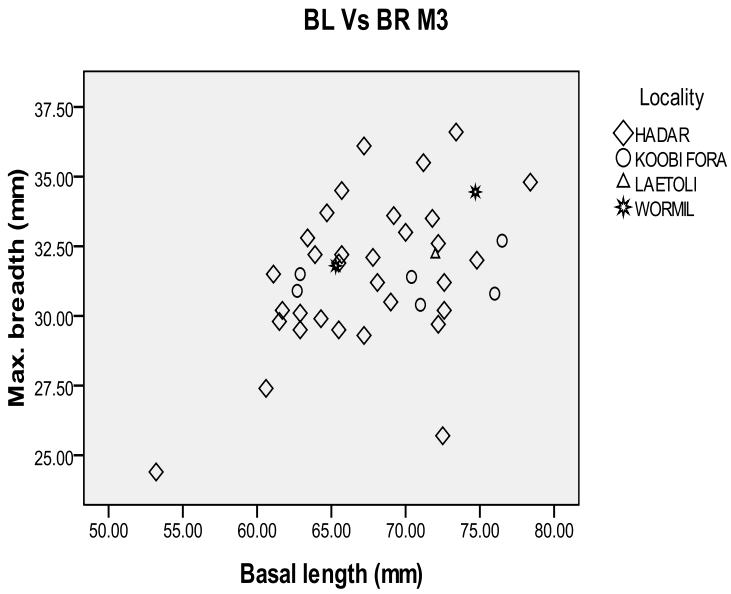


Figure 5.16: A bivariate plot indicating the basal length and breadth of upper third molars of *Notochoerus euilus* from various localities.

*5.1.2.2 **Comparative Description of Lower dentition***

Description and metric comparison of lower dentition follows similar style like the uppers. The metric values of the Woranso-Mille *Not.euilus* lower dentition is presented in Table 15 and Plates 11 to 13 also include figures of these dentitions.

Lower third premolar

The features of this tooth described below fits the characters of the *Not.euilus*. The lower third premolar is relatively smaller. But it is taller than in the fourth premolar. The overall size is smaller than the *Ny.jaegeri* materials. It contains simple conical and medio-laterally compressed crown. It has single backwardly raked main cusp. The anterior border is steep and straight. Anterior cingulum is rudimentary whereas the posterior one is prominent.

A bivariate scatter plot analysis shows that the basal length and breadth of the lower third premolars recovered from the Woranso-Mille are greater than Hadar, Koobi Fora, and Lothagam materials (Fig. 5.17).

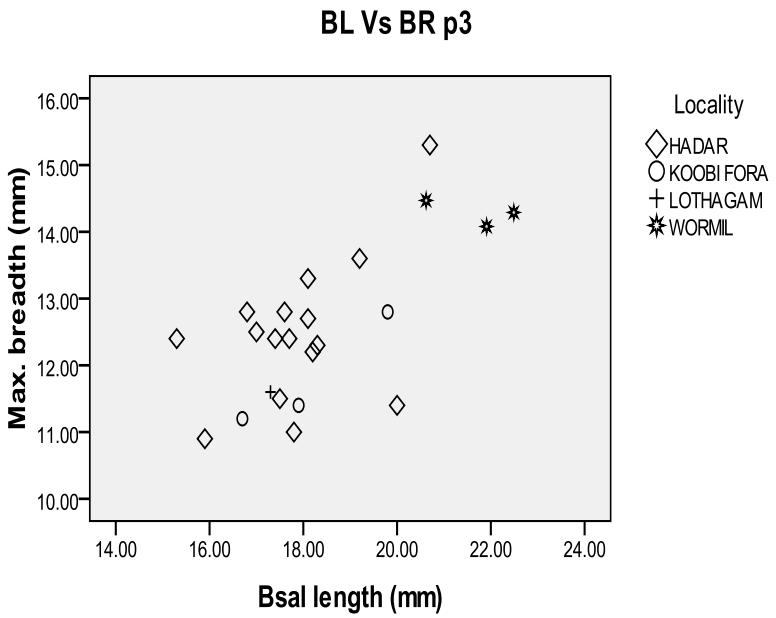


Figure 5.17: A bivariate plot showing the basal length and breadth of the lower third premolar of *Notochoerus euilus* from various localities.

Lower fourth premolar

The tooth is relatively smaller in size compared to *Ny.jaegeri*. The main cusp is centrally placed. In addition, subsidiary cusps are also present on the midline in front the posterior cingulum and smaller one on the anterior sagittal ridge. Anterior and posterior cingula are present with larger posterior cingulum. A strong ridge connects the main cusp with anterior cingulum.

Comparison of metric values of the lower fourth premolar indicates similar result as the lower third premolar. Accordingly, the Woranso-Mille specimens have greater basal length and breadth than several of Hadar and all Koobi Fora and Lothagam materials (Fig.5.18). Specimens from Kanapoi have also shown very wide range of values where the Woranso-Mille materials lie between these range both in length and breadth.

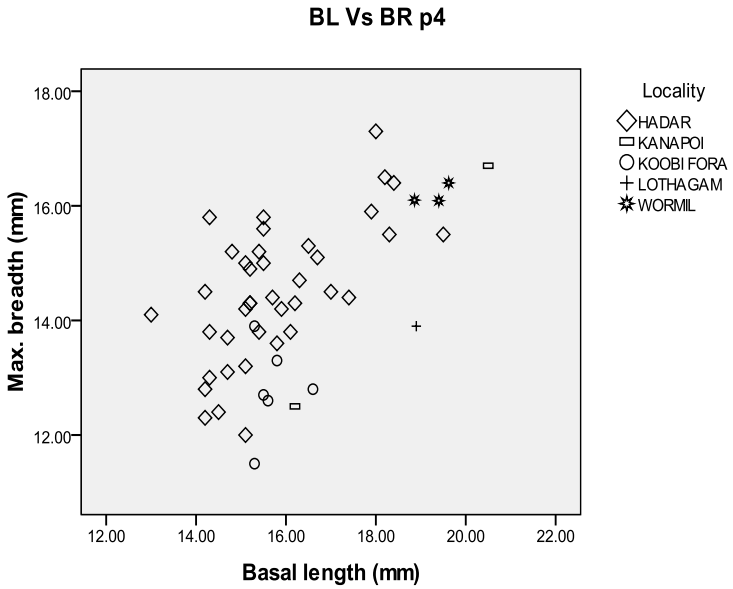


Figure 5.18: A bivariate graphical comparison of the basal length and breadth of the lower fourth premolar of *Notochoerus euilus* from various localities.

Lower first molar

In several specimens the tooth is heavily worn. Some materials indicate that it is composed of two major pillar pairs. It is smaller than the second molar but with similar morphology. Single median pillar is separating the lateral pillar pairs. There is an additional cusp between anterior cingulum and the first pillar pair as in MSD-VP-2/103. Anterior and posterior cingula are present where the posterior one is prominent and forms a slight bowing but not as much in the second molar of the *Not.euilus*. The posterior cingulum is also not well developed as in other *Not.euilus* first molars which bear two terminal cusps and flanked by another two smaller cusps (Harris and White, 1979). However, it is slightly expanded than the *Ny.jaegeri* specimens. The anterior cingulum is represented by smaller subsidiary cusps. It is generally very rudimentary. This cingulum is separated from the first lateral pillar pair by subsidiary cusp which is situated more towards the protoconid. The tooth is generally narrower as in the *Not.euilus* first molars (Cooke, 1978b).

Results of the metric value comparison showed below pointed out that the Woranso-Mille materials have extreme variation for both basal length and breadth (Fig.5.19). But generally, the Koobi Fora materials are larger than the Woranso-Mille specimens.

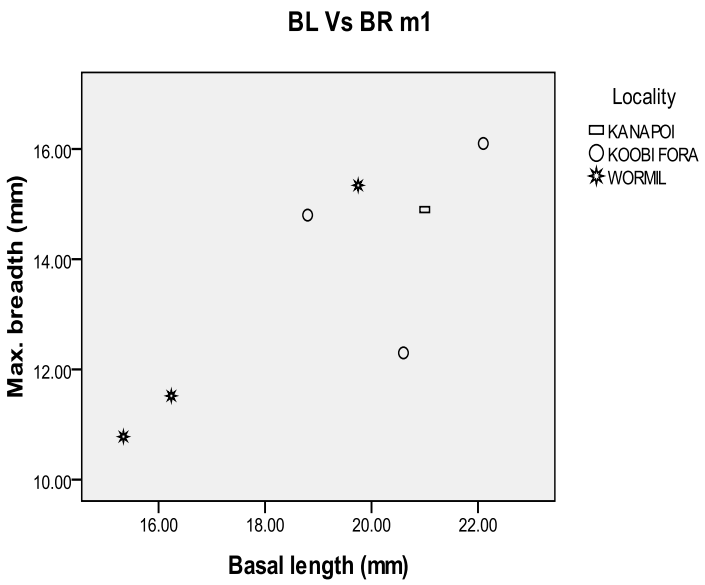


Figure 5.19: A bivariate plot which indicates the basal length and breadth of the lower first molar of *Notochoerus euilus* from various localities.

Lower second molar

Two pillar pairs separated by a single median pillar. Lateral pillar pairs are well separated to the base for instance in MSD-VP-3/9. Additional smaller cusps are present between the second lateral pillar pair and the posterior cingulum and between the first pillar pair and anterior cingulum. Anterior and posterior cingula are present; the posterior cingulum is larger and expanded above the base. However, the posterior cingulum is not as developed as the Hadar materials where they form an incipient third pair of laterals (Cooke, 1978b).Lateral pillar pairs are relatively flattened. There is strong mesial and distal enamel folding as the *Not. euilus* from Galili (Kullmer et al., 2008) and Chiwondo Beds (Kullmer, 2008). But the Woranso-Mille materials generally exhibited an initial H-shaped pattern. Enamel is slightly rough. Median pillar is rounded based on observation from MSD-VP-1/7 which is similar as the Chiwondo Beds and Galili specimens (Kullmer, 2008; Kullmer et al., 2008).

The Woranso-Mille materials are broader than the Koobi Fora and Lothagam specimens. Furthermore, they are also larger than the Kanapoi samples. The breadth is scattered within the Laetoli metric variations but the Woranso-Mille are less elongated than the former materials (Fig.5.20).

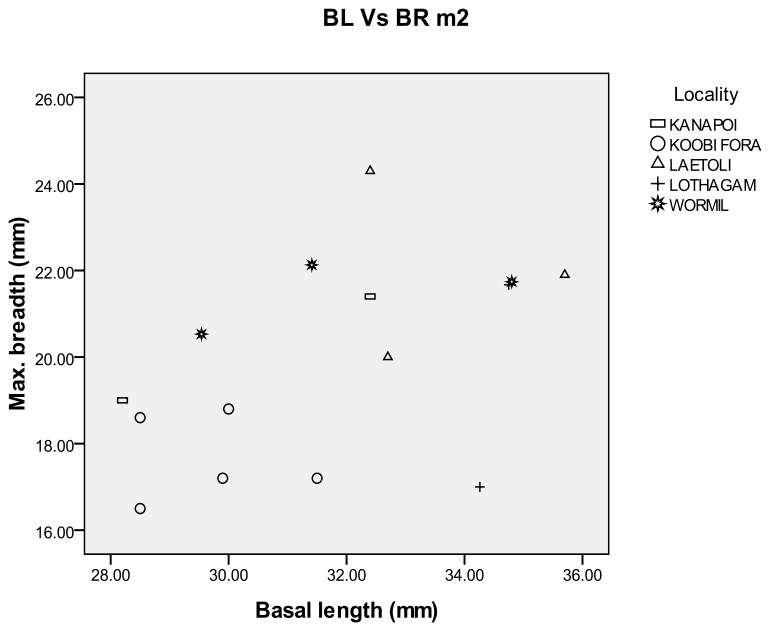


Figure 5.20: A bivariate scatter plot of basal length and breadth of the lower second molar of *Notochoerus euilus* from various localities.

Lower third molar

Lower third molars of the Woranso-Mille have four pillar pairs. However, the Hadar materials possess four well developed pillar pairs and posterior complex of pillars which usually form an incipient fifth pair (Cooke, 1978b). In some specimens the fifth pair is as large as the pillars anterior to it. The Koobi Fora materials, on the other hand, provide four to six pillar pairs (Harris, 1983). Harris and White (1979) briefly expressed *Not.euilus* lower third molars have four to six pillar pairs while earlier forms have fewer ones. The lateral pillar pairs are separated to the base in the lower third molars of the Woranso-Mille, Koobi Fora and Hadar samples. Materials from the study area have shown variable lateral inflations where some are a bit flattened while others show a slight inflation. The major lateral pillars are separated by single or sometimes double median pillars in specimens of the Woranso-Mille and Koobi Fora. For instance, double median pillars separate the major lateral pillars in MSD-VP-2/177. However, composite features appear in MSD-VP-1/7 where the first median pillars are two smaller ones and the second is single and large. The median pillars are with typical *Not.euilus* characters which are rounded to oval in shape. Furthermore the samples exhibit an initial H-shaped enamel wear pattern in the Woranso-Mille and variably occur in the Koobi Fora materials ranging from highly convolute to simpler one. However, the Hadar specimens demonstrate a stellate island in early wear but later become a good H-shaped

pattern. One specimen from the Woranso-Mille, MKM-VP-1/185, has a strong serration on the posterior edges of the trigonid pillars. Cement covering is present in specimens from the three localities. The Woranso-Mille lower third molars have shown marked symmetry as the *Not.euilus*. Smaller endo-and ectostylid are also present on the talonid and at the trigonid/talonid junctions.

A bivariate plot for basal length and breadth of the tooth is given in Figure 5.21. The values are analyzed in that the basal length and breadth of the lower third molar from Woranso-Mille are within the range of the Hadar materials. However, the breadth is higher than several Hadar as well as the Lothagam and Koobi Fora specimens. On the other hand, majority of the Koobi Fora specimens are elongated than the Woranso-Mille samples. The Chiwondo materials show strong variation

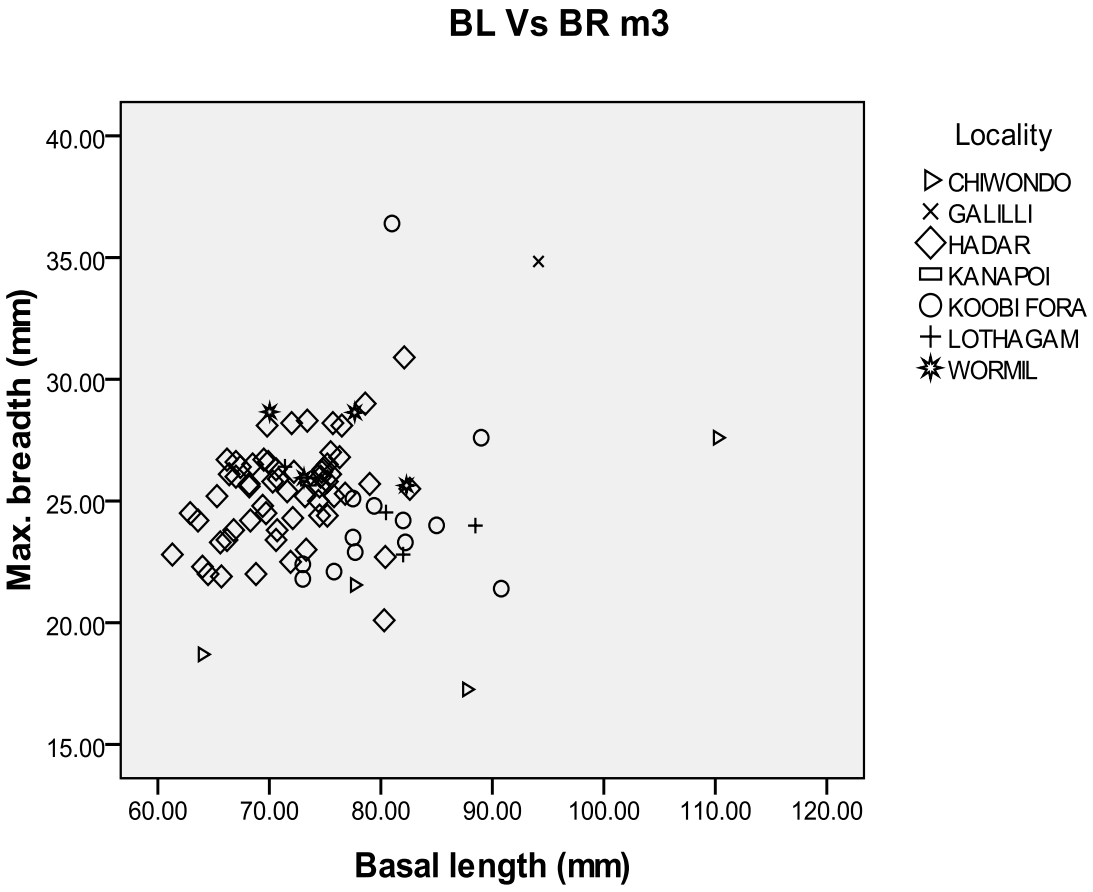
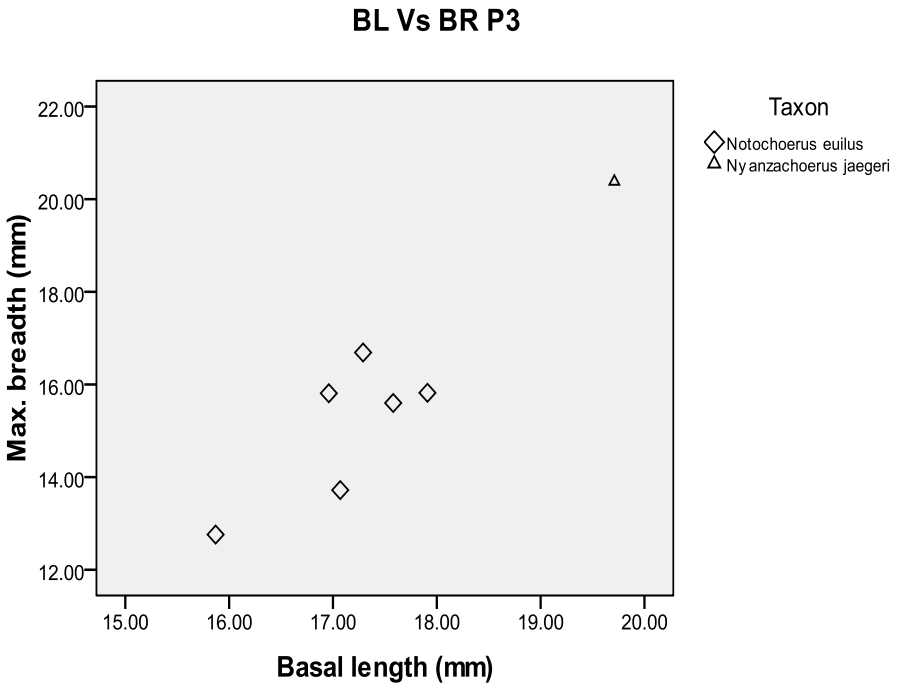


Figure 5.21: A bivariate plot displaying the basal length and breadth of the lower third molar of *Notochoerus euilus* from various localities.

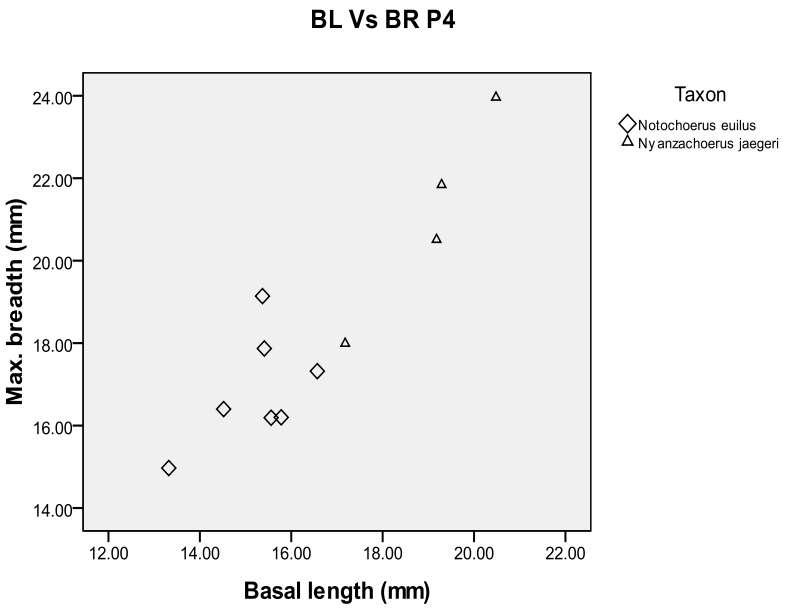
for both basal length and breadth of the tooth and an elongated lower third molar of the species has come from this site. However, a material with maximum width is reported from the Koobi Fora locality.

5.2 Discussion

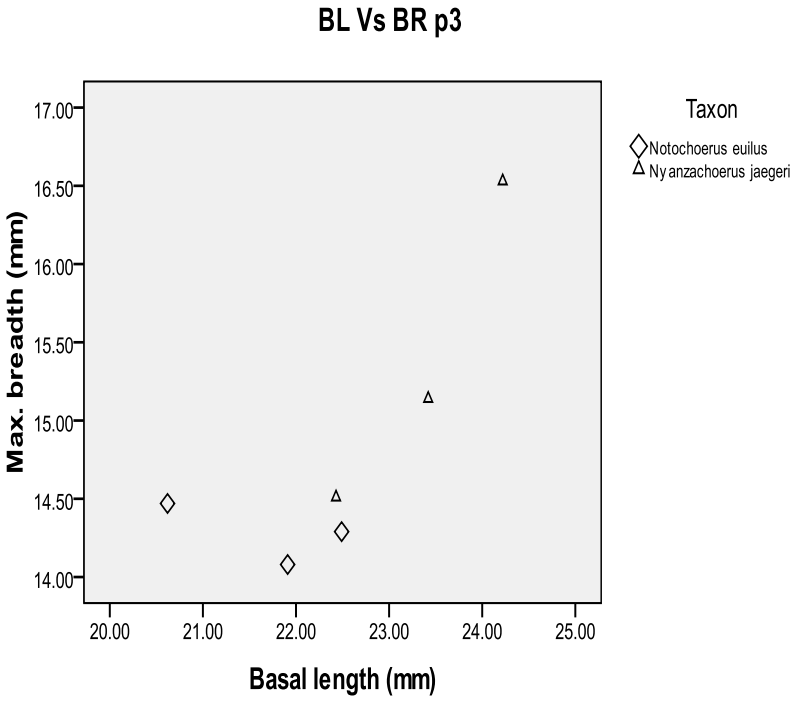
Intra-comparative morphological description of the Woranso-Mille tetraconodonts indicates that the premolars of the *Ny.jaegeri* are relatively larger than *Not.euilus* specimens. The third molars of *Not.euilus* have shown more complex talon and hence elongated than *Ny.jaegeri*. Furthermore, the third molar pillars are also slightly taller in *Not.euilus*. Generally, the dentitions of the two species have shown morphological overlaps. However, the combination of both morphological and metric data separate specimens to respective taxa. Therefore, *Not. euilus* has smaller premolars than *Ny.jaegeri* (Fig. 5.22 A-D).



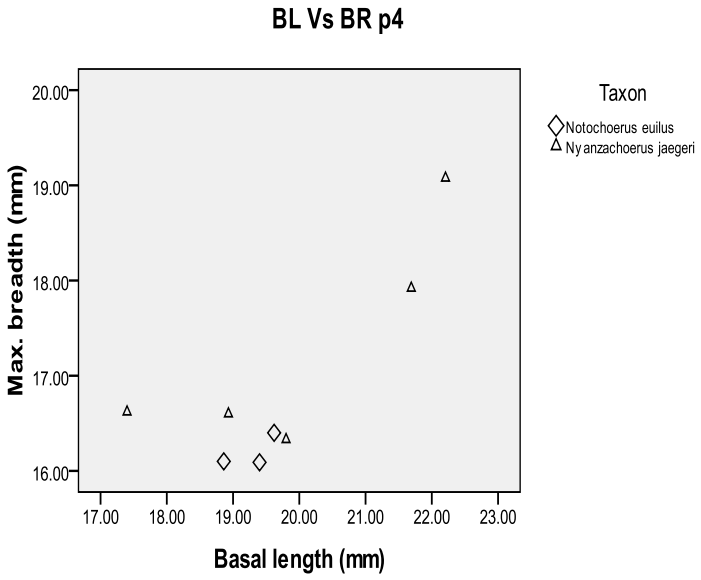
A.


BL Vs BR P4
Max. breadth (mm)
24.00
22.00
20.00
18.00
16.00
14.00
12.00
14.00
16.00
18.00
20.00
22.00
Basal length (mm)
Taxon
Notochoerus euilus
Nyanzachoerus jaegeri

B.


BL Vs BR p3
Max. breadth (mm)
17.00
16.50
16.00
15.50
15.00
14.50
14.00
20.00
21.00
22.00
23.00
24.00
25.00
Basal length (mm)
Taxon
Notochoerus euilus
Nyanzachoerus jaegeri

C.



D.

Figure 5.22: A bivariate plot of basal length and breadth of upper and lower premolars of the Woranso-Mille *Ny.jaegeri* and *Not. euilus*. A) Upper third premolar; B) Upper fourth premolar; C) Lower third premolar; D) Lower fourth premolar

On the other hand, the third molar is an elongated and relatively less broad than *Ny.jaegeri* though there is an overlap in some specimens' metric values (Fig.5.23).

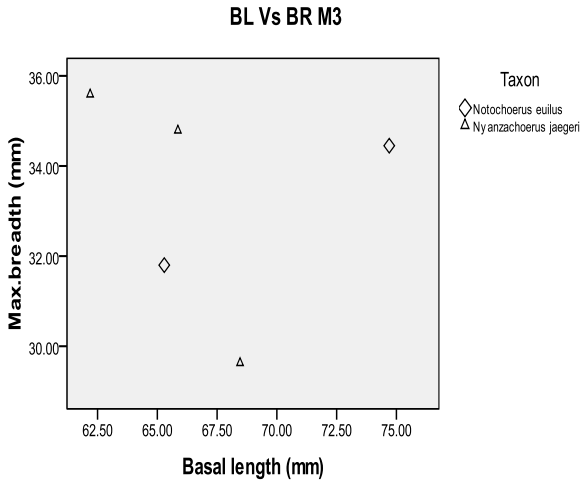
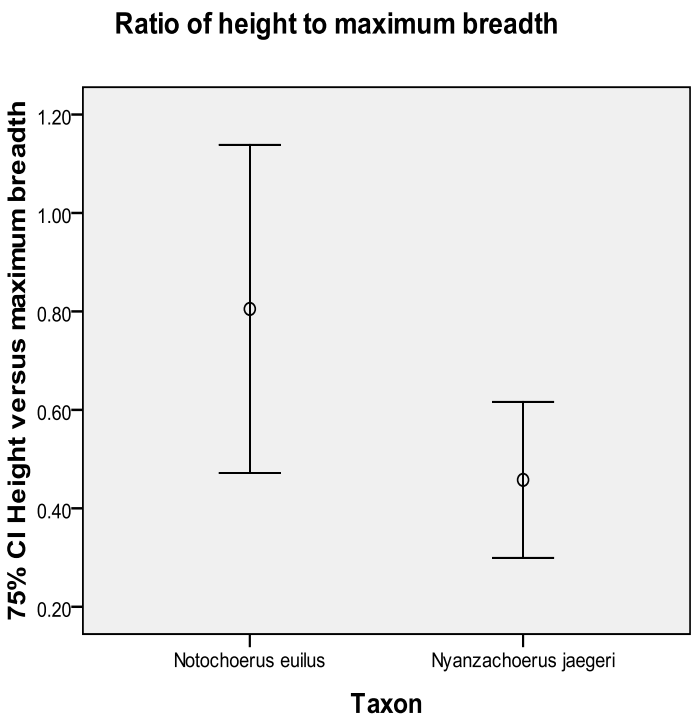
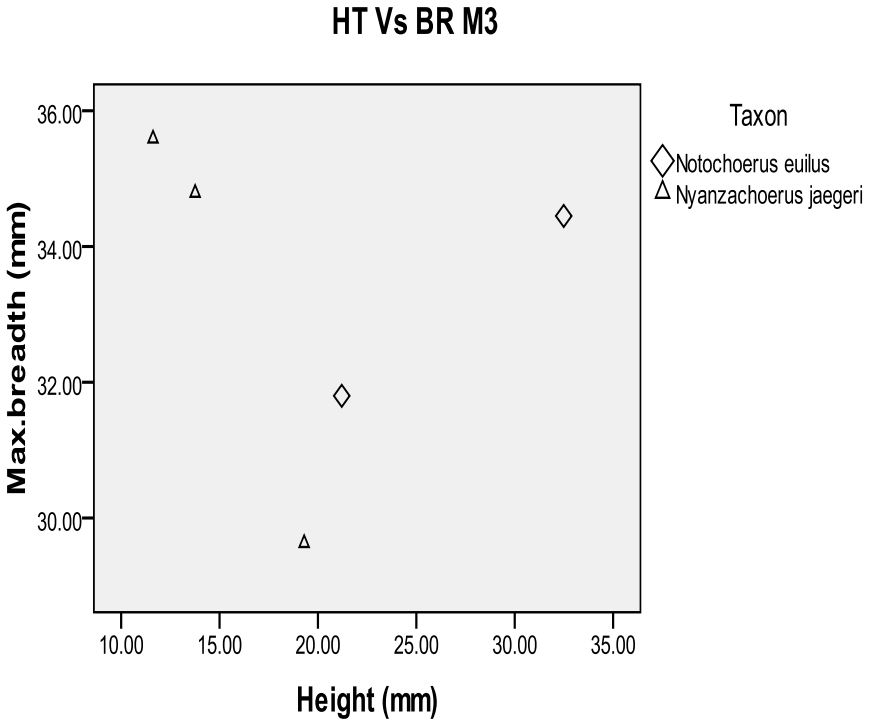


Figure 5.23: A bivariate plot of basal length and breadth of the upper third molar of the Woranso-Mille *Ny.jaegeri* and *Not.euilus*.

Similarly, the crown height as well as the ratio of height to breadth of the third molar for *Ny.jaegeri* is lower than *Not.euilus* (Fig. 5.24 A-B).



A.



B.

Figure 5.24: A) univariate plot showing the ratio of height to breadth of upper third molar of the Woranso-Mille *Ny.jaegeri* and *Not. euilus*; B) bivariate plot showing height and breadth of the upper third molar of the Woranso-Mille *Ny.jaegeri* and *Not.euilus*.

Chapter 6: Taxonomy and Phylogenetic Relationships of *Nyanzachoerus jaegeri and Notochoerus euilus*

The taxonomy and phylogenetic relationships of *Not. euilus* have been discussed by different workers for decades although the results in each case were highly variable. However, there is a consensus that *Not.euilus* is a descendant of *Ny.jaegeri* despite the lack of agreement on the mode of the transition. Harris and White (1979), White and Harris (1977) and Van der Made (1999) have suggested that *Not. euilus* emerged as a lineal continuation of its presumed ancestor *Ny. jaegeri*. Cooke (1978a), on the other hand, proposed cladistic emergence of the species where it branches off from the ancestral *Ny.jaegeri* stock. Furthermore, there is also little agreement on the time of origin and extinction of the species *Not.euilus*. White (1995) has recognized the First Appearance Datum (FAD) of the taxon at ca. 3.75 Ma while Behrensmeyer et al. (1997) pushed the datum further back to ca. 4.35 Ma. Bishop (1994, 2010) argued that the oldest *Not. euilus* is from Koobi Fora Formation and dated to 3.89 Ma. Specimens of the species from the Lower Lomekwi and Kataboi are also considered as old as 4.1-3.36 Ma (Harris et al., 1988). The fossil evidence from the Woranso-Mille paleontological site has enormous contribution in answering questions related to the origins and tempo and mode of evolution of the taxon. This is due to the fact that at Woranso-Mille, the earliest *Not. euilus* from ca. 3.76 – 3.72 Ma overlaps with its putative ancestor *Ny. jaegeri* and because the specimens derive from a temporally well-calibrated horizon.

Eastern African fossil specimens currently recognized as *Ny. jaegeri* were initially assigned to *Ny. plicatus* while *Ny. jaegeri* referred to specimens recovered from north African sites (Cooke and Ewer, 1972). Harris and White (1979) later recognized the two species as synonyms and the name *Ny. jaegeri* was retained because of priority. However, very recently, the species was moved to the genus *Notochoerus* by some workers and renamed *Notochoerus jaegeri* (Harris and Leakey, 2003; Fesseha, 1999; Kullmer, 2008; Bishop, 2010, 2011). The renaming was based on morphological description of new complete mandibular material from Kanapoi. The complete cranium from the Woranso-Mille generates new cranial morphological data significant to test the generic reassignment of *Ny. jaegeri* by allowing a detailed comparison of *Ny.jaegeri*, *Ny.kanamensis*, and *Not. euilus* crania.

6.1 The Woranso-Mille *Notochoerus euilus*

The Woranso-Mille *Not. euilus* material mostly derives from sediments above a tuff dated to 3.72 Ma. Isolated teeth from lower horizons are difficult to definitively identify as *Not. euilus* due to their similarity with derived *Ny. jaegeri*. However, the overall tetraconodont hypodigm suggests that *Not. euilus* might have appeared at Woranso-Mille as early as 3.76 Ma (based on a radiometrically dated tuff below the recovered fossils). The apparent morphological overlap and the transitional nature of some craniodental characters and metric values clearly support the ancestral-descendant relationship of the two species. While the apparent coexistence of *Ny. jaegeri* and *Not. euilus* for about 40,000 yrs (3.76-3.72 Ma) in the Woranso-Mille area lends support to this relationship, it questions the mode of evolution in this lineage. *Not.euilus* was argued to have evolved from *Ny. jaegeri* through a linearly progressive anagenetic mode of evolution. Indeed, *Ny. jaegeri* at Woranso-Mille appears to be absent in sediments younger than 3.72 Ma although three isolated teeth (two lower fourth premolars and a second molar) from sediments below a tuff dated to 3.57 Ma appear to belong to the species. However, this requires recovery of more complete specimens. Alternatively, the three isolated teeth could very well belong to an early *Not. euilus*. This is a clear indication that some isolated teeth from the 3.6 – 3.8 Ma time frame could be extremely difficult to assign to either species. Clearly *Not. euilus* specimens are relatively abundant in the deposits younger than 3.72 Ma. Overall, the mode of evolution of *Not. euilus* is more likely as a side branch of the main *Ny.jaegeri* population.

When the dentition of the Woranso-Mille *Not. euilus* is compared with material of the same taxon from Hadar, Koobi Fora, Lothagam, Laetoli, Galili and Chiwondo Beds, one can see that the upper third molars of the Woranso-Mille are similar with the Hadar and Galili samples in possessing four pillar pairs. They are also similar to the comparative sample in their anterior third molar complex in retaining an anterior cingulum with subsidiary cusps. The Woranso-Mille upper third molars show less talon complexity than the Koobi Fora specimens. Enamel wear pattern recorded from the Woranso-Mille materials are an initial H-shaped while the Hadar samples exhibit good H-shaped pattern in late stages of wear.

Furthermore, there is a pronounced difference in the lower third molar between Woranso-Mille, Hadar and Koobi Fora materials. The Woranso-Mille specimens have fewer pillar pairs, mostly four, while the Hadar lower third molars have five lateral pillar pairs but the fifth is usually incipient in some and fully developed in others. In the Koobi Fora

specimens, it ranges from four to six. Like the upper third molar, the enamel exhibits an initial H-shaped wear pattern in the Woranso-Mille samples and variably occurs in the Koobi Fora materials ranging from highly convoluted to simpler one. However, the Hadar specimens demonstrate a stellate island in early wear but later form a relatively perfect H-shaped pattern. In other features, every specimens of the taxon looks similar.

Dental morphological characters of the Woranso-Mille *Not.euilus* specimens suggest that they belong to an earlier form of the species. Variation in the number of pillar pairs described from the Woranso-Mille, Hadar, and Koobi Fora samples accords with the temporal distribution of these materials. The Woranso-Mille specimens are constrained to between 3.82± 0.18 Ma to 3.57± 0.014 Ma, whereas the Hadar and Koobi Fora are dated to 3.4-2.92Ma (Walter and Aronson, 1993; Walter, 1994) and 4.1-3.32 Ma (McDougall, 1985), respectively. This clearly indicates an increase in pillar pairs through time. The metric data also supports that the Wornaso-Mille *Not.euilus* represents an early form of the species. Overall, the upper and lower premolars recovered from the study site are relatively larger. The metric values indicate slightly bulging molars.

6.2 Taxonomic re-evaluation of *Nyanzachoerus jaegeri*

Harris and Leakey (2003) reclassified *Ny. jaegeri* into the genus *Notochoerus* by arguing that the mandibular corpus of the Kanaopi *Nyanzachoerus jaegeri* specimens (KNM-KP 30178 and KNM-KP 30452) are longer and less robustly constructed than *Ny.kanamensis* and *Ny.syrticus*. Moreover, the breadth and flatness of the mandibular symphysis, the horizontal arrangement of the lower incisors, and the lower canine orientation resemble 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, the complete cranium from the Woranso-Mille, sheds some light on testing the validity of the generic reassignment of *Ny. jaegeri* by allowing a detailed comparison of *Ny.jaegeri*, *Ny.kanamensis*, and *Not. euilus* crania.

Comparison of the available crania of the three species provides evidence for the 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. 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.kanamensis*. On the other hand, *Not.euilus* generally possesses very weak temporal fossae. Relative breadth of the parietal constriction also indicates the proximity of *Ny.jaegeri* to *Ny.kanamensis* rather than to *Not.euilus*. *Ny.jaegeri* frontal bone between the orbits differs in shape from the *Not.euilus*. Likewise, the zygomatic knob is vey massive in *Ny.jaegeri* than in *Not.euilus*.

In addition to the above mentioned cranial morphological features, dental characters also indicate resemblances between *Ny.jaegeri* and *Ny.kanamensis*. The presence of three upper incisors and three upper premolars in both species is worth mentioning. *Notochoerus euilus* is known to have a single pair of upper incisors and two pairs of upper premolars. Furthermore, bivariate and univariate scatter plots of molar to premolar series and ratio of molar to premolar length confirm close affinity between *Ny.jaegeri* and *Ny.kanamensis*.

Generally, the craniodental morphological attributes and metric data clearly suggest that *Ny.jaegeri* is best kept in the genus *Nyanzachoerus*. There is no clear cranial morphological evidence to transfer it to *Notochoerus* except for some subtle features related to the mandibular symhyseal shape, which appear to be variable even within *Ny. jaegeri*. Therefore, the complete mandibles described from Kanapoi by Harris and Leakey (2003) might show substantial variation across taxa and may not be taxonomically significant.

6.3 Phylogenetic relationships

In the study of African suid evolution, the third molars have been usually considered as significant in taxonomy and phylogenetic relationships. However, White (1995) has cautioned not to entirely rely on this element in order to determine the taxonomy and phylogeny of suids. One of the reasons for this reliance of the third molars is the lack of complete crania and mandibles across taxa. The complete cranium of *Ny. jaegeri* from the Woranso-Mille (MSD-VP-1/27) is a very important addition to the Pliocene fossil suid hypodigm and adds to the evidence derived from the third molars in terms of determining phylogenetic relationships, particularly between *Ny.jaegeri* and *Not.euilus*. Although there are enough morphological variations between *Ny.jaegeri* and *Not.euilus* to warrant separate generic rank, their ancestral-

descendant relationship is also clearly demonstrated by numerous cranial and dental characters.

The nasal region is transversely convex in both species even though the Hadar *Not. euilus* specimens have straight sided nasals. Ornamentation of the dorsal ridge of the supracanine flange, presence of broad supracanine gutter, the right angle divergence of the zygomatic knob, and position of the root of the zygomatic arch are features shared by the two species in addition to further traits of the cranial vault. The maximum width of the vault is at the postorbital processes and the cranium tapers towards the nuchal crest. The temporal lines of the cranial vault coincide with the lateral edges of the vault. Farther back on the cranium, the supraoccipital laterally expands and narrows towards the foramen magnum. Occipital condyles of both species are placed between planes of the orbit and palate.

Dental morphological and metric data also support the relationships between the two taxa. There is a strong morphological similarity in the premolars and molars except for the overall enlarged premolar size in *Ny.jaegeri* and greater talon complexity in *Not.euilus* upper third molars. As a result of such strong morphological similarities between early *Not. euilus* and derived *Ny. jaegeri*, there has always been difficulty in identifying isolated dental materials to either species. In general, the tendency has been reduction of premolar size and increase in the third molar length and height in the *Not.euilus* lineage. The fossil evidence from the Woranso-Mille supports previously suggested inferences that the dentition of *Not.euilus* is a progressive form of advanced *Ny.jaegeri*. The appearance of *Not.euilus* with relatively long and hypsodont third molars might be related to the exploitation of abrasive diet in a possibly open habitat. However, a detailed paleoenvironmental study of the Woranso-Mille study area is imperative to test the correlation between the increase in third molar length and hypsodonty in *Not. euilus* with environmental changes at the beginning of the middle Pliocene.

CHAPTER 7: CONCLUSION

African Pliocene tetraconodonts have been a subject of numerous studies in the past, largely due to their abundance in the Pliocene African fossil record, but also due to their significance in biochronology. However, some of their phylogenetic relationships and taxonomy remains unresolved. The main purposes of this work were to address issues related to the tempo and mode of evolution of *Not. euilus* and address the phylogenetic relationships between *Ny. jaegeri* and *Not. euilus* using newly discovered fossils from the Woranso-Mille paleontological study area located in the central Afar region of Ethiopia. In order to accomplish this, three broad objectives were laid out. The first was to conduct a complete description and taxonomic assignment of the new fossil materials from the Woranso-Mille radiometrically dated to between 3.6 and 3.8 Ma. Secondly, to analyze the taxonomic assignment of the new material in relation to the origin (first appearance in the fossil record) and evolutionary trends of *Not. euilus*. Finally, the newly acquired data was used to assess the relationships between *Not.euilus* and *Ny.jaegeri*. This further re-evaluates the generic reassignment of *Ny.jaegeri*,the presumed ancestor of *Not.euilus*. Comparative morphological descriptions and metric evaluations were conducted to investigate both cranial and dental features. The new complete cranium of *Ny.jaegeri* recovered from the Woranso-Mille was compared with crania of *Ny.kanamensis* and *Not.euilus*. Cranial and dental metric measurements were analyzed using bivariate and univariate analyses. While morphological observations were made, and metric data collected, on the original Woranso-Mille materials, the comparative material included both original (*Not. euilus* specimens from Hadar) and published materials from contemporaneous sites in eastern Africa such as Kanapoi, Koobi Fora, Galili, and the Chiwondo Beds of Malawi.

The description of MSD-VP-1/27, the first complete cranium of the species *Ny. jaegeri* from the Woranso-Mille is one of the best achievements of this work. The cranial morphology of this species was unknown previously largely due to the lack of complete specimens. This research further shows that *Not.euilus* probably appeared as early as 3.76 Ma, earlier than previously thought and *Ny.jaegeri* persisted until about 3.72 Ma, much later than previously thought (3.75 Ma; Harris and White, 1979; White, 1995). Furthermore, detailed examination of the Woranso-Mille *Ny. jaegeri* and *Not. euilus* dental remains further confirm that there was a continuous increase in the third molar length and height accompanied by reduction in size of the premolars towards the *Not.euilus* lineage. Moreover, since the Woranso-Mille material represents the earliest record of *Not. euilus*, it is clear that the trend mentioned above

continued even within *Not. euilus* itself. The relatively younger *Not. euilus* specimens from Hadar and Koobi Fora show more elongated third molars and further reduced premolars compared to those from the Woranso-Mille. Analyses of the Woranso-Mille *Not.euilus* specimens indicate fewer third molar pillar pairs and slightly larger premolars compared to those from Hadar and Koobi Fora. At the same time, both *Ny. jaegeri* and *Not. euilus* share some cranial and dental features confirming their ancestor-descendant relationship. However, the overall cranial morphology of the Woranso-Mille complete cranium, compared with skulls of *Ny. kanamensis* and *Not. euilus*, clearly shows strong affinity with the *Ny.kanamensis* crania suggesting that *Ny. jaegeri* is better retained in the genus *Nyanzachoerus* contrary to recent suggestions of its reassignment into the genus *Notochoerus* (Harris and Leakey, 2003)

In terms of the tempo and mode of evolution of *Not. euilus*, the results from this work suggest that *Not.euilus* most probably emerged as a branch from the ancestral *Ny.jaegeri* stock at around 3.76 Ma or earlier and specimens of this species recovered from the Woranso-Mille represent an earlier form of the taxon. Morphological description and metric analysis of the cranio-dental materials from the study area confirm ancestral-descendant relationships between the two taxa (White and Harris, 1977; Harris and White, 1979). However, this relationship may not have been anagenetic as previously suggested. The presumed anagenetic relationship, added to the description of complete suid mandibles from Kanapoi, prompted some researchers to rename *Ny. jaegeri* as *Not.jaegeri* (Harris and Leakey, 2003). On the contrary, fossil evidence from the Woranso-Mille suggests cranial morphological homogeneity within the genus *Nyanzachoerus*. The closer affinity in the cranial characters of the Woranso-Mille complete cranium to *Ny.kanamensis* than to *Not.euilus* further supports this homogeneity. The mandibular features listed by Harris and Leakey (2003) and used to transfer *Ny.jaegeri* to the genus *Notochoerus*, may represent variations in the mandibular morphology of *Ny. jaegeri* as seen in some mandibular remains of the latter species from other sites such as the Middle Awash.

To sum up, the research work has provided important results which contribute to our understanding of the *Ny. jaegeri-Not. euilus* lineage and also yielded significant insights into the cranial morphology of *Ny. jaegeri*, which was previously unknown. The results suggest a cladistic emergence of *Not.euilus* from an ancestral *Ny.jaegeri* stock at ca.3.76 Ma or earlier and that both species co-existed for at least 40,000 years. However, these results do not falsify earlier conclusions on the ancestral-descendant relationship between the two taxa. Furthermore, the Woranso-Mille *Not. euilus* specimens represent the primitive form of the species. Finally, this research work, based on the currently available fossil evidence, does not

support the reassignment of *Ny.jaegeri* to the genus *Notchoerus* but rather presents sufficient cranial morphological evidence to retain the taxanomic status quo. Finding more tetracondont fossils from sites such as Woranso-Mille and Kanapoi will further test the conclusions reached from this work.

Table1. The Wornaso-Mille materials of *Ny. jaegeri* and *Not.euilus*

Skull and Upper dentitions

Specimen no.	Locality	Element	Side	WS	Taxon
AMA-VP-2/38	Am-Ado	P4	L		*Ny. jaegeri*
AMA-VP-2/56	Am-Ado	M3	L		*Ny. jaegeri*
		Molar frags.			
ARI-VP-1/430	Aralee Issie	M3	L	4	*Ny. jaegeri*
ARI-VP-1/98	Aralee Issie	P4	R		*Ny. jaegeri*
ARI-VP-1/311	Aralee Issie	P4	R		*Ny. jaegeri*
MSD-VP-1/27	Mesgid Dora	Skull (P2-M3)	R+L	4	*Ny. jaegeri*
MSD-VP-5/5	Mesgid Dora	M2	R		*Ny. jaegeri*
MSD-VP-2/59	Mesgid Dora	M1	R		*Ny. jaegeri*
		dP4	R		
ARI-VP-1/440	Aralee Issie	P3	L		*Not. euilus*
ARI-VP-1/46	Aralee Issie	P4	R		*Not. euilus*
		Associated with broken M2	R		
ARI-VP-1/299	Aralee Issie	M3	R	4	*Not. euilus*
ARI-VP-1/53	Aralee Issie	P4	R		*Not. euilus*
		P3	L		
ARI-VP-1/454	Aralee Issie	Max. fragment (M1-M2)	R+L		*Not. euilus*
MKM-VP-1/53	Makah Mera	P3	L		*Not. euilus*
		P4	R+L		
		Associated with dental frags.			
MKM-VP-1/271	Makah Mera	Max. fragment (P3-M1)	R		*Not. euilus*
MKM-VP-1/55	Makah Mera	Max. fragment (P4-M3)	R	4	*Not. euilus*
		Max. fragment (M2-M3)	L		
		P4	L		
MSD-VP-5/6	Mesgid Dora	P3	L		*Not. euilus*
		Upper molars and canine frags.			
MSD-VP-5/24	Mesgid Dora	P3	R		*Not. euilus*
		Upper molars frag.			
MSD-VP-3/9	Mesgid Dora	P3	L		*Not. euilus*
MSD-VP-2/67	Mesgid Dora	M1	R		*Not. euilus*
MSD-VP-2/16	Mesgid Dora	P4	R		*Not. euilus*
MSD-VP-2/144	Mesgid Dora	P4	L		*Not. euilus*
MSD-VP-1/58	Mesgid Dora	M1	L		*Not. euilus*
MSD-VP-1/10	Mesgid Dora	Max. fragment (M2-M3)	R	4	*Not. euilus*

Lower dentitions

Specimen no.	Locality	Element	Side	WS	Taxon
ARI-VP-3/222	Aralee Issie	p3	R		*Ny. jaegeri*
ARI-VP-1/477	Aralee Issie	m1	L		*Ny. jaegeri*
MKM-VP-1/261	Makah Mera	p4	R+L		*Ny. jaegeri*
		m2	L		*Ny. jaegeri*
		Mand. and lower molar frags.			
MKM-VP-1/146	Makah Mera	p4	L		*Ny. jaegeri*
MSD-VP-5/26	Mesgid Dora	p3	R		*Ny. jaegeri*
		p4	L		*Ny. jaegeri*
MSD-VP-2/188	Mesgid Dora	p3	R		*Ny. jaegeri*
MSD-VP-2/187	Mesgid Dora	p4	L		*Ny. jaegeri*
AMA-VP-2/10	Am-Ado	m1	L		*Not.euilus*
AMA-VP-2/44	Am-Ado	m3	L	1	*Not.euilus*
ARI-VP-1/367	Aralee Issie	m1	L		*Not.euilus*
MKM-VP-1/185	Makah Mera	m3	R	2	*Not.euilus*
		Lower premolar frags.			
		broken lower incisor			
MSD-VP-3/9	Mesgid Dora	p4	L		*Not.euilus*
		p2	L		*Not.euilus*
		m2	L		*Not.euilus*
		Molar frags.			
MSD-VP-3/8	Mesgid Dora	p3	L		*Not.euilus*
MSD-VP-2/103	Mesgid Dora	Mand. fragment (dp4-m1)	R		*Not.euilus*
MSD-VP-2/225	Mesgid Dora	Mand. fragment (p4)	R		*Not.euilus*
MSD-VP-2/70	Mesgid Dora	p3	L		*Not.euilus*
		p4	R		*Not.euilus*
MSD-VP-2/177	Mesgid Dora	Mand. fragment (m3)	R	4	*Not.euilus*
		p3	R		*Not.euilus*
MSD-VP-5/27	Mesgid Dora	m3	L	5	*Not.euilus*
MSD-VP-1/7	Mesgid Dora	Mand. fragment (m2-m3)	L	4	*Not.euilus*

Lower case stands for lower dentition

Upper case stands for upper dentitions

R=Right

L=Left

Ws=Wear Stage

Table 2: Suid cranial character states described by Harris and White (1979)

Element	Characters
Rhinarium	Relative width
	Degree of tapering
	Ossification
Supracanine flange	Relative width
	Presence/absence of dorsal ridge
	Ornamentation of dorsal ridge
	Continuity of ridge
	Relative width of supra canine gutter
Nasal region	Convexity
	Relative width
	Medial sagittal depression
	Extension of nasal wall overhanging the maxilla
	Nasal-premaxillar ossification
Orbital region	Shape of orbit
	Position of orbit
	Orbital rim thickness
	Posterior portion of orbit
	Frontal bone between orbits
Zygoma	Divergence from sagittal axis
	Relative size and shape of boss
	Position of zygomatic knob
	Relative size of zygomatic knob
	Root of zygoma
Cranial vault	Maximum width
	Bone thickness
	Shape
	Angle of nasal-frontoparietal region
	Position of temporal lines
	Temporal fossa
Occipital region	Supraoccitpital lateral expansion
	Position of occipital condyles
Palate	Relative length
	Relative width
	Shape of palatonarial border
	Position of palatonarial border
	Position of posterior palatine foramina

Table 3. Dental and mandibular character states described by Harris and White (1979) and Fesseha (1999).

Element	Characters
Symphysis	Relative length
	Anterior portion
	Inferior surface slope
	Posteroventral projection
	Postcanine constriction
	Relatively widest point
	Superior surface
Mand.Corpus	Thickness and length
	Lateral inflation
	Extramolar shelf presence/absence
	Level of inferior surface
	Min.depth of corpus
Mand. Ramus	Thickness of superior portion
	Degree of eversion
	Condyle position
P^3	Relative size
	Shape
	Enamel texture
	Major crown elements
	Presence/absence of internal and external cingulum
	Presence of anterior/posterior cingula
P^4	Relative size
	Number of major cusps
	Position of subsidiary cusps
	Enamel texture
	Anterior and posterior cingula extension
	Fusion with wear
M^1	Lobe formation
	Shape and size
	Anterior cingulum
	Posterior cingulum
M^2	Presence/absence of endo/ectostyles
	Cingulum composition
	Wear pattern
	Anterior composition
	Lateral flaring

M^3	Anterior complex
	Presence/absence of endo/ectostyle
	Median pillars separating talon from trigon
	Talon composition
	Lateral inflation of pillars
	Pillar separation
	Waisting at Trigon/talon junction
	Cement cover
	Enamel texture
	Enamel folding
	Major pillar curvature
Lower Incisors	Number of incisors
	Alignment across symphyseal border
	Relative size of incisors
Lower Canines	Cross section
	Orientation/emergence
	Presence/absence of enamel
	Position of wear facet
	Curvature
P_1	Presence/absence
P_2	Shape
	Anterior and posterior cingula
	Internal and external cingula
	Position of main cusp
	Position of subsidiary cusp
P_3	Relative size
	Number of main cusps
	Anterior border
	Anterior cingulum
	Posterior cingulum
P_4	Size and thickness
	Posterior cingulum size
	Anterior cingulum size
	location of additional cusps
M_1	Relative size
	Presence/absence of stylid
M_2	Shape
	Relative size
	Antero-posterior expansion

	Presence/absence of endo/ectostylid
M_3	Enamel folding
	Number of pillar pairs
	Trigonid pillar height
	Tooth symmetry
	Presence/absence of endo/ectoylid
	Cement cover
	Talonid complex
	Wear pattern
	Serration of major pillars
	Shape of median pillars

Table 4. Suid cranial dimensions as complied by Van der Made (1996) and Driesch (1976)

Vertex length	Diastema between I3-P2, C-P2,C-P3, I1-P2,I1-P3
Basilar length	Length of molar and premolar series
Bizygomatic breadth	Length of P2-M3,P3-M3,P3-P4
Width at post orbital processes	Dental length
Parietal constrictions	Condylobasal length
Maximum width of occiput	Premolar-prosthion length
Greatest breadth across nasals	Short skull length
Muzzle breadth between infraorbital foramen	Maximum palatal breadth
Canine flange breadth	Estimated bicondylar width
Palatal length	Minimum width of orbits
Breadth of palate at M3-M3,P3-P3 and P2-P2	
Premaxilla breadth at I3-I3	

Table 5. Suid dental dimensions as complied by Harris and White (1979), Fesseha (1999), and Cooke (2007).

Premolar and molar length
Premolar and molar breadth
Area of premolars and molars
Trigon/id length of third molar
Crown height
Length to breadth ratio of premolars and molars
Crown height to breadth ratio

Table 6. Cranio-dental character states of *Notochoerus euilus* complied from Harris and White, 1979; Cooke, 1978; Harris, 1983; Fesseha, 1999.

Element	Character state	Expression
Rhinarium	Relative width	Narrow
	Degree of tapering	Taper gently in front of canines
	Ossification	Nasal cartilage ossified in one specimen
Supracanine flange	Relative width	Broad
	Presence/absence of dorsal ridge	Present
	Ornamentation of dorsal ridge	low carinate dorso-laterally
	Continuity of ridge	continues forward in front of canine alveolus
	Relative width of supra canine gutter	Broad
Nasal region	Convexity	transversely convex
	Relative width	wide towards the canine alveoli
	Medial sagittal depression	Present, bisecting the nasal region
	Extension of nasal wall overhanging the maxilla	Infraorbital region-anterior edge of orbit
	Nasal-premaxillar ossification	present laterally
Orbital region	Shape of orbit	circular
	Position of orbit	high on skull behind preorbital fossae
	posterior portion of orbit	marked by strong postorbital processes
	Frontal bone between orbits	slightly domed as well as concave
Zygoma	Divergence from sagittal axis	at right angle
	Relative size and shape of boss	shape similar to *Ny.jaegeri* but smaller
	Position of zygomatic knob	at ventrolateral edge
	Root of zygoma	begins behind infraorbital foramen
Cranial vault	Maximum width	at orbit and narrows toward nuchal crest
	Bone thickness	robust
	Shape	variable; flat, concave and convex
	Angle of nasal-frontoparietal region	slight angulation
	Position of temporal lines	coincide on lateral edges of cranial vault
	Temporal fossa	deeply excavated from Koobi Fora specimens
	parietal constriction	narrow
Occipital region	Supraoccitpital lateral expansion	expanded below nuchal crest, gradually tapered towards foramen magnum
	Position of occipital condyles	mid way between plane of orbit and palate
Palate	Relative length	longer than in *Ny.jaegeri*

	Relative width	narrow
	Shape of palatonarial border	nr
	Position of palatonarial border	farther behind than in *Ny.jaegeri*
	Position of posterior palatine foramina	level with talon of M^3
Symphysis	Relative length	elongated reaching P_3
	Anterior portion	broad and straight
	Inferior surface slope	gently sloping
	Posteroventral projection	same as in *Ny.jaegeri*
	Postcanine constriction	less marked than *Ny.jaegeri*
	Relatively widest point	at canine alveoli
	Superior surface	less deeply excavated
Mand.Corpus	Thickness and length	long and narrow
	Lateral inflation	variable
	Extramolar shelf presence/absence	mid line of corpus extend lateral to the axis of cheek teeth
	Level of inferior surface	same as *Ny.jaegeri*
	Min.depth of corpus	located below M1
Mand. Ramus	Thickness of superior portion	relatively thickened
	Degree of eversion	not everted
	Condyle position	medially sited relative to rest of ramus
Upper incisros	Number of pairs	single pair (in adult)
	Shape	hook-shaped
	Wear facet position	posterolaterally situated
	Relative length	tall
Upper canines	Cross section	triangular
	Orientation/emergence	horizontally only small rise at the tip
	Location and depth of groove	Anteroventrally strong groove and dorsally broad shallow one
	Presence/absence of enamel	present on all surfaces except on median longitudinal groove
	Presence/absence of cement	nr
	Position of wear facet	proximal anteroventral surface
	Curvature	strong (1/3 of a circle)
P^1	Presence/absence	absent
P^2	Presence/absence	absent
P^3	Relative size	Substantially smaller than in *Ny.jaegeri*

	Shape	triangular (apex anteriorly)
	Enamel texture	smooth
	Major crown elements	paracone(buccally), metacone (buccally), and protocone (lingually)
	Presence/absence of internal and external cingulum	absent
	Presence of anterior/posterior cingula	present but small
P^4	Relative size	Smaller than in *Ny.jaegeri*
	Number of major cusps	two transversely oriented (large paracone, small protocone)
	Position of subsidiary cusps	between paracone and anterior and posterior cingula
	Enamel texture	enamel is folded
	Anterior and posterior cingula extension	extend less labially and lingually
	Fusion with wear	main cusps fuse in extreme wear
M^1	Lobe formation	heavily bilobed
	Shape and size	similar to M^2 but smaller
	Anterior cingulum	weak
	Posterior cingulum	modest
M^2	Presence/absence of endo/ectostyles	endo-and ectostyles may be present
	Cingulum composition	posterior cingulum bulge substantially
	Wear pattern	more enamel foldings in worn
	Anterior composition	single median between first pair and anterior cingulum
	Lateral flaring	same as *Ny.jaegeri*
M^3	Anterior complex	more complex, anterior cingulum rugose with subsidiary cusps
	Presence/absence of endo/ectostyle	endo/ectostyle may be present
	Median pillars separating talon from trigon	single large/ sometimes double
	Talon composition	two/three strong lingual pillars, terminal pillar, and smaller labial cusps
	Lateral inflation of pillars	bulging lateral pillars (primitive form)
	Pillar separation	well separated to the base
	Waisting at Trigon/talon junction	more prominent
	Cement cover	thin cover
	Enamel texture	corrugated
	Enamel folding	same as *Ny.jaegeri*
	Major pillar curvature	curve anteriorly

Lower Incisors	Number of incisors	three pairs (third may be lost)
	Alignment across symphyseal border	straight
	Relative size of incisors	small (peg like)
Lower Canines	Cross section	heart-shaped to U-shaped
	Orientation/emergence	horizontal, parallel to uppers
	Presence/absence of enamel	present on three faces, absent onventral groove and proximal posterior portion
	Position of wear facet	along superior edge of posterior face and anterior margin
	Curvature	strong curvature
P_1	Presence/absence	Absent
P_2	Shape	Generally absent
	Anterior and posterior cingula	
	Internal and external cingula	
	Position of main cusp	
	Position of subsidiary cusp	
P_3	Relative size	simple conical,mediolaterally compressed
	Number of main cusps	single
	Anterior border	steep and straight
	Anterior cingulum	reduced to incipient cusp
	Posterior cingulum	prominent
P_4	Size and thickness	shorter and broader than P_3
	Posterior cingulum size	prominent than anterior cingulum
	Anterior cingulum size	stronger than in P_3
	location of additional cusps	between main cusp and posterior cingulum
M_1	Relative size	larger as compared to premolar size
	Presence/absence of stylid	structure like M_2
M_2	Shape	same as M_1
	Relative size	larger than M_1
	Antero-posterior expansion	much expanded above the base
	Presence/absence of endo/ectostylid	present behind second external pillar
M_3	Enamel folding	strongly folded (sometimes variable convolute-simple)
	Number of pillar pairs	four/five
	Trigonid pillar height	relatively tall
	Tooth symmetry	marked symmetry
	Presence/absence of endo/ectoylid	thick cover
	Cement cover	thick cement

Talonid complex	number varies from two to four (fewer in early forms) with terminal pillar
Wear pattern	H- shaped
Serration of major pillars	anterior and posterior edges serrated
Shape of median pillars	Rounded

Table 7. Cranio-dental character states of *Nyanzachoerus jaegeri* as compiled by Harris and White, 1979; Cooke and Ewer, 1972; Harris and Leakey, 2003.

Element	Character state	Expression
Rhinarium	Relative width	nr
	Degree of tapering	nr
	Ossification	nr
Supracanine flange	Relative width	relatively broad
	Presence/absence of dorsal ridge	slight dorsal ridge present
	Ornamentation of dorsal ridge	weakly carinated
	Continuity of ridge	continues backward behind canine alveolus
	Relative width of supra canine gutter	relatively broad
Nasal region	Convexity	laterally convex (in males)
	Relative width	narrower than in *Ny.tulotos* or *kanamensis*. Maximum expansion level with supra canine flange
	Medial sagittal depression	flattened towards the midline
	Extension of nasal wall overhanging the maxilla	zygoma-canine alveolus
	Nasal-premaxillar ossification	laterally ossified
Orbital region	Shape of orbit	oval
	Position of orbit	low on the skull
	Orbital rim thickness	relatively thick
	Posterior portion of orbit	marked by large post orbital processes
	Frontal bone between orbits	strongly concave
Zygoma	Divergence from sagittal axis	at 90^0
	Relative size and shape of boss	shape similar to *Not. euilus* but larger
	Position of zygomatic knob	at ventrolateral edge
	Root of zygoma	starts behind the infraorbital foramen
Cranial vault	Maximum width	at postorbital process narrow toward nuchal crest
	Bone thickness	very thick
	Shape	strongly concave on the midline
	Angle of nasal-frontoparietal region	strong angulation
	Position of temporal lines	coincides with lateral edges of cranial vault
	Temporal fossa	deeply excavated
	parietal constriction	broad

Occipital region	Supraoccitpital lateral expansion	expand below nuchal crest and taper towards the foramen magnum
	Position of occipital condyles	midway between palatal and orbital plane
Palate	Relative length	relatively long
	Relative width	wide at the canine alveoli
	Shape of palatonarial border	gothic arched/ about V-shaped
	Position of palatonarial border	well behind level of M^3
	Position of posterior palatine foramina	between firs pillars of third molars
Symphysis	Relative length	elongated reaching P_{3-4}
	Anterior portion	broad and straight
	Inferior surface slope	gently sloping
	Posteroventral projection	below level of corpus
	Postcanine constriction	more marked than in *Not.euilus*
	Relatively widest point	at canine alveoli
	Superior surface	less deeply excavated
Mand.Corpus	Thickness and length	thick and elongate
	Lateral inflation	small
	Extramolar shelf presence/absence	absent except lateral to M_3
	Level of inferior surface	above the posterior edges of symphysis and angle of ramus
	Min.depth of corpus	nr
Mand. Ramus	Thickness of superior portion	nr
	Degree of eversion	nr
	Condyle position	nr
Upper incisros	Number of pairs	three pairs
	Shape	nr
	Wear facet position	nr
	Relative length	nr
Upper canines	Cross section	bilobate oval
	Orientation/emergence	emerge horizontally and forwards
	Location and depth of groove	shallow grooves ventrally and dorsally
	Presence/absence of enamel	devoid of enamel
	5Presence/absence of cement	not preserved
	Position of wear facet	broad wear facet on anterior lower face
	Curvature	nr
P^1	Presence/absence	absent

P^2	Presence/absence	very small tooth with central cone, and anterior and posterior ridges
P^3	Relative size	large and hypsodont
	Shape	oval
	Enamel texture	smooth
	Major crown elements	single main cusp with strongly expressed hypocone
	Presence/absence of internal and external cingulum	external absent, internal rudimentary
	Presence of anterior/posterior cingula	anterior, moderately strong; posterior, narrow and high
P^4	Relative size	large and hypsodont
	Number of major cusps	two transversly oriented (large paracone, small protocone)
	Position of subsidiary cusps	between anterior cingulum and major cusps,and lateral and posterior cingulum
	Enamel texture	smooth
	Anterior and posterior cingula extension	extend less labially and lingually
	Fusion with wear	single dentine island with irregular outline
M^1	Lobe formation	nr
	Shape and size	similar to M^2 but smaller
	Anterior cingulum	weak
	Posterior cingulum	larger than anterior one
M^2	Presence/absence of endo/ectostyles	endo-and ectostyles present
	Cingulum composition	posterior cingulum with mammilations
	Wear pattern	stellate at early stage, bell-shaped in advanced wear
	Anterior composition	broad symmetrical anterior cingulum
	Lateral flaring	marked from the cervix to the crown
M^3	Anterior complex	less complex than in *Not.euilu*
	Presence/absence of endo/ectostyle	strong endostyle on trigon, endo-and ectostyle at trigon/talon junction
	Median pillars separating talon from trigon	single median pillar
	Talon composition	single lingual pillar, terminal pillar plus smaller labial cusps (variable number)
	Lateral inflation of pillars	lateral pillars bulge
	Pillar separation	coalescing at the base, well separated at the upper part
	Waisting at Trigon/talon junction	nr

	Cement cover	nr
	Enamel texture	tendency for folding
	Enamel folding	strong mesial and distal vertical folds
	Major pillar curvature	nr
Lower Incisors	Number of incisors	three pairs
	Alignment across symphyseal border	straight
	Relative size of incisors	small
Lower Canines	Cross section	flattened verrucose
	Orientation/emergence	horizontal
	Presence/absence of enamel	absent from posterior surface and ventral groove
	Position of wear facet	on superior portion of posterior surface
	Curvature	curved posteriorly at distal portion
P_1	Presence/absence	absent
P_2	Shape	triangular
	Anterior and posterior cingula	well developed
	Internal and external cingula	both rudimentary
	Position of main cusp	centrally placed
	Position of subsidiary cusp	towards lingual and labial edges of posterior cingulum
P_3	Relative size	short and narrow
	Number of main cusps	single backwardly raked
	Anterior border	steep and straight
	Anterior cingulum	present only as isolate cusp
	Posterior cingulum	prominent
P_4	Size and thickness	shorter and wider than P_3
	Posterior cingulum size	taller than in P_3
	Anterior cingulum size	nr
	location of additional cusps	midline in front of posterior cingulum, on anterior sagittal ridge
M_1	Relative size	larger as compared to premolar size
	Presence/absence of stylid	strong ectostylid between first and second pillar pairs
M_2	Shape	same as M_1
	Relative size	larger than M_1
	Antero-posterior expansion	elongate, having strong shelf like posterior cingulum
	Presence/absence of endo/ectostylid	strong ectostylid, lacks endostylid

M_3	Enamel folding	more folded
	Number of pillar pairs	four
	Trigonid pillar height	relatively tall
	Tooth symmetry	symmetrical, sometimes terminate with asymmetric cusps
	Presence/absence of endo/ectoylid	no endostylid, ectostylid present only at trigonid/talonid junction
	Cement cover	thick cement
	Talonid complex	variable mostly two symmetrical pairs with terminal pillar
	Wear pattern	initial stage of *Nothochoerine* type (tendency of strong mesial and distal folds)
	Serration of major pillars	apically serrated
	Shape of median pillars	irregular in outline

Table 8. New cranial characters of *Ny. jaegeri* based on the new complete cranium (MSD-VP-1/27) from the Woranso-Mile.

Element	Characters	Expression
Supracanine flange	Relative width	relatively broad
	Ornamentation of dorsal ridge	weakly carinated
	Continuity of ridge	continues backward behind canine alveolus
	Relative width of supra canine gutter	relatively broad
Nasal region	Nasal-premaxillar ossification	laterally ossified
Orbital region	Shape of orbit	oval
	Position of orbit	low on the skull
	Orbital rim thickness	relatively thick
	Posterior portion of orbit	marked by large post orbital processes
	Frontal bone between orbits	strongly concave
Zygoma	Divergence from sagittal axis	at 90^0
Cranial vault	Maximum width	at postorbital process narrow toward nuchal crest
	Bone thickness	very thick
	Shape	strongly concave on the midline
	Angle of nasal-frontoparietal region	strong angulation
	Position of temporal lines	coincides with lateral edges of cranial vault
	Temporal fossa	deeply excavated
	parietal constriction	broad
Occipital region	Supraoccitpital lateral expansion	expand below nuchal crest and taper towards the foramen magnum
	Position of occipital condyles	midway between palatal and orbital plane
Palate	Relative length	relatively long
	Relative width	wide at the canine alveoli
	Shape of palatonarial border	gothic arched/ about V-shaped
	Position of posterior palatine foramina	between firs pillars of third molars
Upper incisors	Number of pairs	three

Table 9. Cranial character states of *Ny. kanamensis* as compiled by Harris and White, 1979; Cooke, 1978; Cooke and Ewer, 1972.

Element	Character state	Expression
Rhinarium	Relative width	nr
	Degree of tapering	nr
	Ossification	nr
Supracanine flange	Relative width	males have less developed flange
	Presence/absence of dorsal ridge	nr
	Ornamentation of dorsal ridge	nr
	Continuity of ridge	nr
	Relative width of supra canine gutter	nr
Nasal region	Convexity	virtually flat
	Relative width	wider than in *Ny.tulotos*, generally narrow
	Medial sagittal depression	nr
	Extension of nasal wall overhanging the maxilla	nr
	Nasal-premaxillar ossification	ossified with slight thickening
Orbital region	Shape of orbit	nr
	Position of orbit	nr
	Orbital rim thickness	nr
	Posterior portion of orbit	nr
	Frontal bone between orbits	nr
Zygoma	Divergence from sagittal axis	less sharply than in *Ny.tulotos*
	Relative size and shape of boss	nr
	Position of zygomatic knob	on anterior external part
	Root of zygoma	starts behind the infra orbital foramina
Cranial vault	Maximum width	at the orbits
	Bone thickness	nr
	Shape	flattened, mainly concave
	Angle of nasal-frontoparietal region	nr
	Position of temporal lines	nr
	Temporal fossa	nr
	parietal constriction	broad
Occipital region	Supraoccitpital lateral expansion	nr
	Position of occipital condyles	higher above the occlusal plane

Palate	Relative length	nr
	Relative width	wider at the canines, slightly wider than in *Ny.tulotos*
	Shape of palatonarial border	U-shaped, gothic arch and broadly rounded
	Position of palatonarial border	well behind the level of the upper third molar
	Position of posterior palatine foramina	nr

Table 10. Metric measurements of MSD-VP-1/27 (*Ny. jaegeri)* compared to *Not. euilus*

(all measurements are in mm)

		Not. euilus							
Characters	MSD-VP-1/27	KNM-ER 3540	KNM-ER 3541	AL 172-1	AL 171-1	AL 342-9	AL 108-3	AL 167-15	Mean*
Vertex length (Max. Length)	646.67			580	610	620	395	620	565
Basilar length	501.66	555	578	496	510	530	320	340	475.57
Bizygomatic breadth	526.67	331	197	392		380			325
Width postorbital processes	177.67			187	175	200	166	230	191.6
Parietal constrictions	87			50		59	49	74	58
Crest breadth/Max. width of occiput	183						135	178	156.5
Greatest breadth across nasals	70			57	77	62			65.33
Muzzle breadth between infraorbital foramen	71.33			65	70	80			71.67
Canine flange breadth	169.33	134	157	163.5					151.5
Palatal length	372.33			369		320	152	205	261.5
Breadth of Palate at M3-M3	41.19			46.7	51.5	59	46.7	53.7	51.52
Breadth of Palate at P3-P3	41.96			53.1	58	79		67.3	64.35
Diastema I1-P3	177.17			175					175
Diastema C-P3	61.3			74					74
Premolar series	54.92			29.8	31.5			33	31.43
Molar series	117.14			111.6	119.1		129	131.7	122.85
Length of P3-M3	160.67			141.4	150			164	151.8
Dental length	358.5								
Condylobasal length	525								
Premolar-Prosthion	185.83								
Short skull length	329.66								
Max.Palatal breadth	121.16								
Estimated Bicondylar width	82.66								
Palatal breadth at P2-P2	66.32								
Premaxilla breadth at I3-I3	81.84								
Diastema I1-P2	161.67								
Diastema C-P2	49.35								
Length of P3-P4	41.45								
Length of P2-M3	175								
Diastema I3-P2	110.2								
Minimum width of orbits	47.33								

***:** Mean values are for *Not. euilus*

Table 11. Metric measurements of MSD-VP-1/27 (*Ny. jaegeri)* compared to *Ny. kanamensis*

(all measurements are in mm)

		Ny. kanamensis					
Characters	MSD-VP-1/27	KNM-KP 264	KNM-KP 30186 M	KNM-KP 239	AL 107-13	AL 137-4	Mean*
Vertex length (Max. Length)	646.67	620		480	457	580	534.25
Basilar length	501.66	500		425	440	490	463.75
Bizygomatic breadth	526.67	480	400	270	308	270	345.6
Width postorbital processes	177.67		140		147	166	151
Parietal constrictions	87	76			72.5	98	82.17
Crest breadth/Max.width of occiput	183		136		108	155	133
Greatest breadth across nasals	70	71	70	53		62	64
Muzzle breadth between infraorbital foramen	71.33	66		48		56	56.67
Canine flange breadth	169.33		136				136
Palatal length	372.33	352		301	305	353	327.75
Breadth of Palate at M3-M3	41.19	40		33	35	43	37.75
Breadth of Palate P2-P2	66.32	73		52.5	40.2	71.5	59.3
Premaxilla breadth at I3-I3	81.84	95		69		76	80
Diastema I3-P2	110.2	101		72			86.5
Diastema C-P2	49.35	35		39.5		49	41.17
Length of premolar series	54.92	68		51.9	50.3	56.5	56.68
Length of molar series	117.14	99.1		95.2	92	105.5	97.95
Length of P2-M3	175	161		147	142	162	153
Dental length	358.5						
Condylobasal length	525						
Premolar-Prosthion	185.83						
Short skull length	329.66						
Max.Palatal breadth	121.16						
Estimated Bicondylar width	82.66						
Breadth of Palate at P3-P3	41.96						
Diastema I1-P2	161.67						
Diastema I1-P3	177.17						
Diastema C-P3	61.3						
Length of P3-M3	160.67						
Length of P3-P4	41.45						
Mim.width of orbits	47.33						

***:** Mean values are for *Ny. Kanamensis*

Table12. Metric values of the Woranso-Mille *Nyanzachoerus jaegeri* upper dentition
(All measurements in mm)

Upper Third Premolars

Specimen no.	BL	BR	BL/BR	BL*BR
MSD-VP-1/27	19.71	20.38	0.97	401.69

Upper Fourth Premolars

Specimen no.	BL	BR	BL/BR	BL*BR
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

Specimen no.	BL	BR	BL/BR	BL*BR
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

Specimen no.	BL	BR	BL/BR	BL*BR
MSD-VP-5/5	31.69	28.75	1.1	911.09
MSD-VP-1/27	28.07	28.61	0.98	803.08

Upper Third Molars

Specimen no.	BL	BR	BL/BR	BL*BR	HT	TRIG	HT/BR
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

*:BL=Basal length
:BR=Maximum breadth
:HT=Height
:TRIG=Trigon/id length

Table13. Metric values of the Woranso-Mille *Ny. jaegeri* lower dentition
(All measurements are in mm)

Lower Third Premolars

Specimen no.	BL	BR	BL/BR	BL*BR
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

Specimen no.	BL	BR	BL/BR	BL*BR
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

Specimen no.	BL	BR	BL/BR	BL*BR
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

Specimen no.	BL	BR	BL/BR	BL*BR
MKM-VP-1/261	29.08	20.92	1.39	608.35

Lower Third Molars

Specimen no.	BL	BR	BL/BR	BL*BR	TRIG	HT (mm)
MSD-VP-2/38						20.3
MSD-VP-2/177						16.64

Table 14. Metric measurements of the Woranso-Mille *Not. euilus* upper dentition

(all measurements are in mm)

Upper Third Premolars

Specimen no.	BL	BR	BL/BR	BL*BR
ARI-VP-1/440	17.58	15.6	1.13	274.25
MKM-VP-1/271	17.29	16.69	1.04	288.57
MKM-VP-1/53	16.96	15.81	1.07	268.14
MSD-VP-3/9	17.91	15.82	1.13	283.34
MSD-VP-5/6	15.87	12.76	1.24	202.5
MSD-VP-5/24	17.07	13.72	1.24	234.2

Upper Fourth Premolars

Specimen no.	BL	BR	BL/BR	BL*BR
ARI-VP-1/53	16.57	17.32	0.96	286.99
ARI-VP-1/46	14.52	16.4	0.89	238.13
MKM-VP-1/271	15.37	19.14	0.8	294.18
MKM-VP-1/53	15.56	16.19	0.96	251.92
MKM-VP-1/55	15.41	17.87	0.86	275.38
MSD-VP-2/16	15.78	16.2	0.97	255.64
MSD-VP-2/144	13.32	14.97	0.89	199.4

Upper First Molars

Specimen no.	BL	BR	BL/BR	BL*BR
ARI-VP-1/454	20.29	18.36	1.11	372.52
ARI-VP-3/267	20.95			
MSD-VP-2/67	21.99	17.14	1.28	376.91
MSD-VP-1/58	20.52	17.66	1.16	362.38

Upper Second Molars

Specimen no.	BL	BR	BL/BR	BL*BR
ARI-VP-1/454	29.57	24.54	1.2	725.65
ARI-VP-1/46	27.5			
MKM-VP-1/55	27.04	25.65	1.05	693.58
MSD-VP-1/10	29.07	23.59	1.23	685.76

Upper Third Molars

Specimen no.	BL	BR	BL/BR	BL*BR	HT	TRIG	HT/BR
ARI-VP-1/299	74.7	34.45	2.17	2573.42	32.49	38.69	0.94
ARI-VP-3/268					23.76		
MKM-VP-1/13					27.21		
MKM-VP-1/55	65.29	31.8	2.05	2076.22	21.21	35.82	0.67
MKM-VP-1/51		33.77					
MSD-VP-1/10	68.46	29.63	2.31	2028.47	19.3	34.94	0.65
MSD-VP-3/7					20.02		
MSD-VP-5/54	72.86				31.51	37.41	

Table15. Metric measurements of the Woranso-Mille *Not. euilus* lower dentition

(All measurements are in mm)

Lower Third Premolars

Specimen no.	BL	BR	BL/BR	BL*BR
MKM-VP-1/132	20.59			
MSD-VP-2/10	21.91	14.08	1.56	308.49
MSD-VP-2/70	22.49	14.29	1.57	321.38
MSD-VP-3/8	20.62	14.47	1.43	298.37

Lower Fourth Premolars

Specimen no.	BL	BR	BL/BR	BL*BR
MSD-VP-2/70	19.62	16.4	1.2	321.77
MSD-VP-3/9	18.86	16.1	1.17	303.65
MSD-VP-2/225	19.4	16.09	1.21	312.15

Lower First Molars

Specimen no.	BL	BR	BL/BR	BL*BR
AMA-VP-2/10	15.34	10.78	1.42	165.37
ARI-VP-1/367	19.75	15.34	1.29	302.97
MSD-VP-2/103	16.24	11.52	1.41	187.08

Lower second molars

Specimen no.	BL	BR	BL/BR	BL*BR
MKM-VP-1/291	31.41	22.13	1.42	695.1
MSD-VP-2/54	34.8	21.74	1.6	756.55
MSD-VP-1/7	29.54	20.53	1.44	606.46
MSD-VP-2/55		21.28		
MSD-VP-3/9		20.1		

Lower Third Molars

Specimen no.	BL	BR	BL/BR	BL*BR	HT	TRIG	HT/BR
AMA-VP-2/44	82.3	25.64	3.21	2110.17	33.03	37.72	1.29
MKM-VP-1/179		25.71					
MKM-VP-1/185	70.03	28.66	2.44	2007.06	27.38	36.78	0.96
MSD-VP-1/7	73.11	25.95	2.82	1897.2	24.79	35.73	0.96
MSD-VP-5/27	77.66	28.64	2.71	2224.18	13.11	40.96	0.46

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Plate 1. *Nyanzachoerus jaegeri*. Ventral, right lateral and dorsal views: A) MSD-VP-1/ 27, male cranium

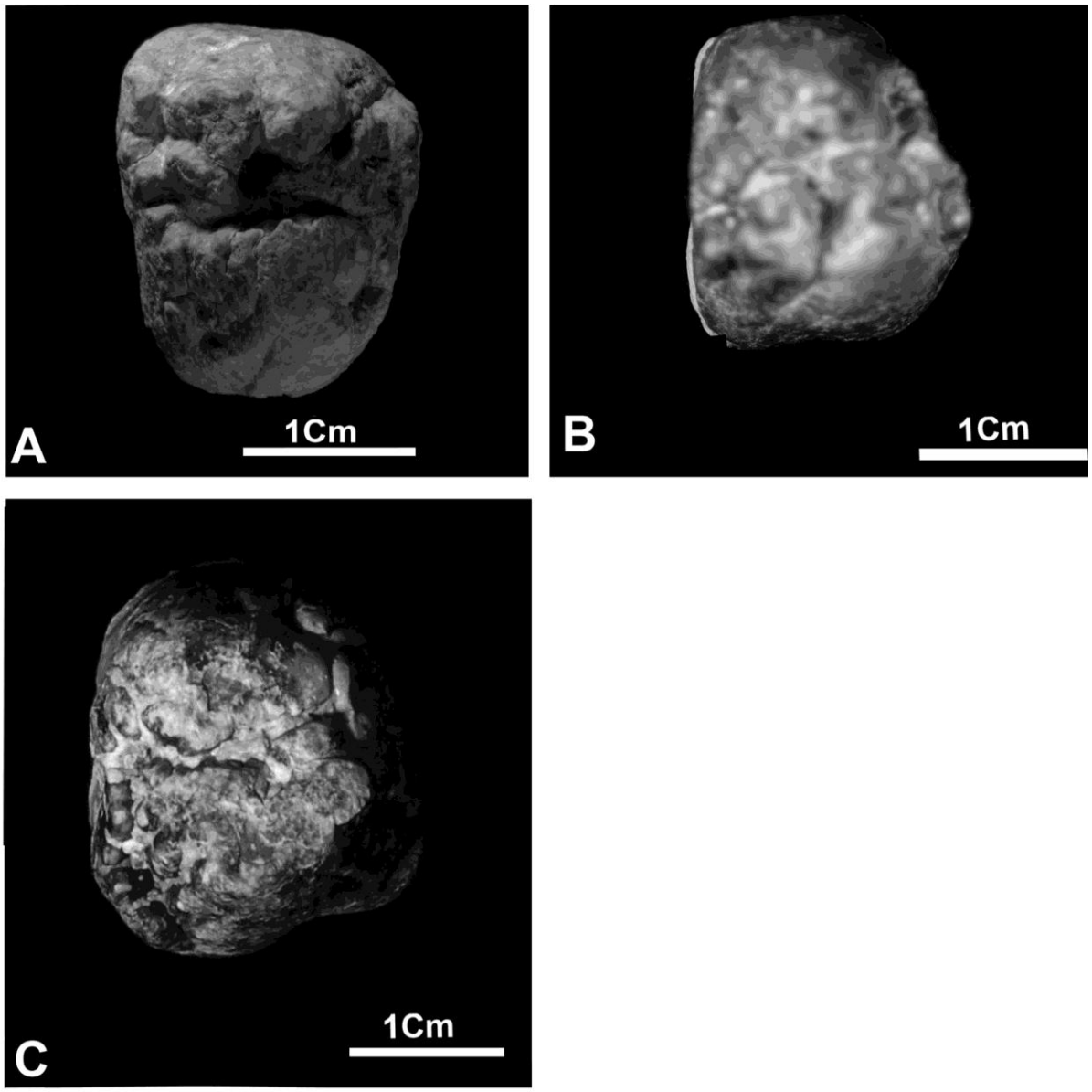

Plate 2. *Nyanzachoerus jaegeri*. Occlusal views: A) AMA-VP-2/38, left upper fourth premolar; B) ARI-VP-1/311, right upper fourth premolar; C) ARI-VP-1/98, right upper fourth premolar

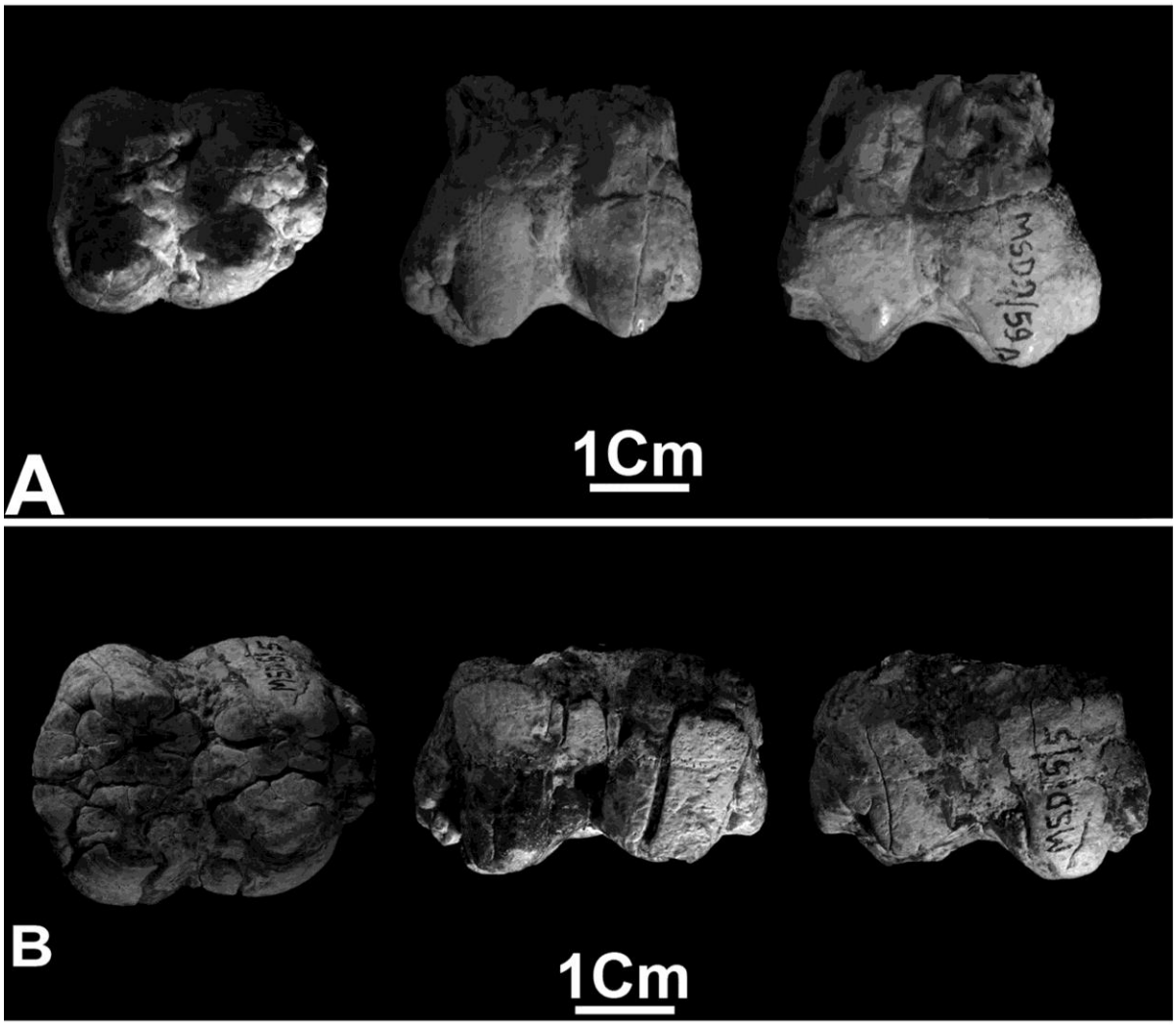

Plate 3. *Nyanzachoerus jaegeri*. Occlusal,buccal and lingual views: A) MSD-VP-2/59,right upper first molar; B) MSD-VP-5/5,right upper second molar

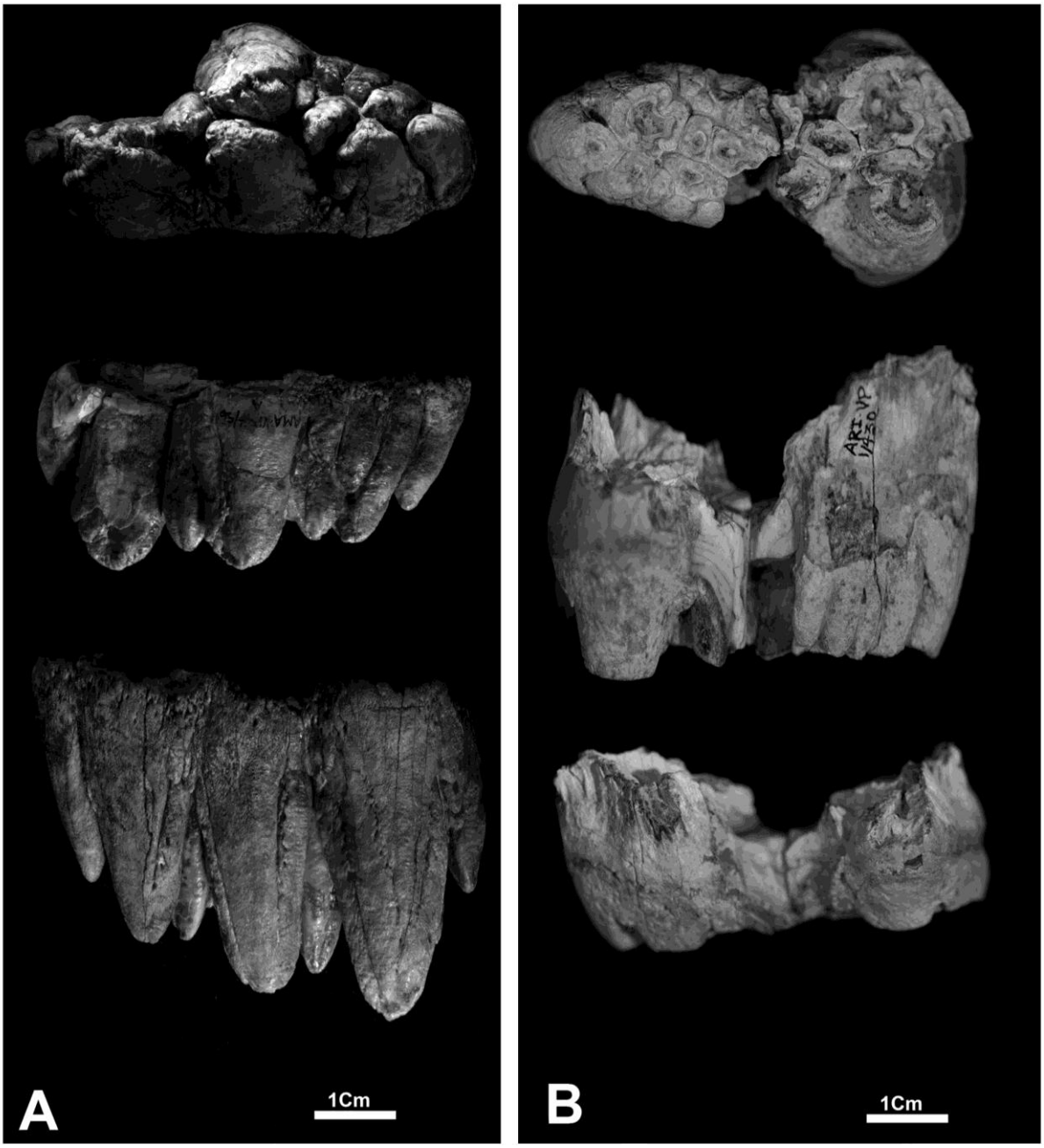

Plate 4. *Nyanzachoerus jaegeri*. Occlusal,buccal and lingual views: A) AMA-VP-2/56,left upper third molar, B) ARI-VP-1/430,left upper third molar

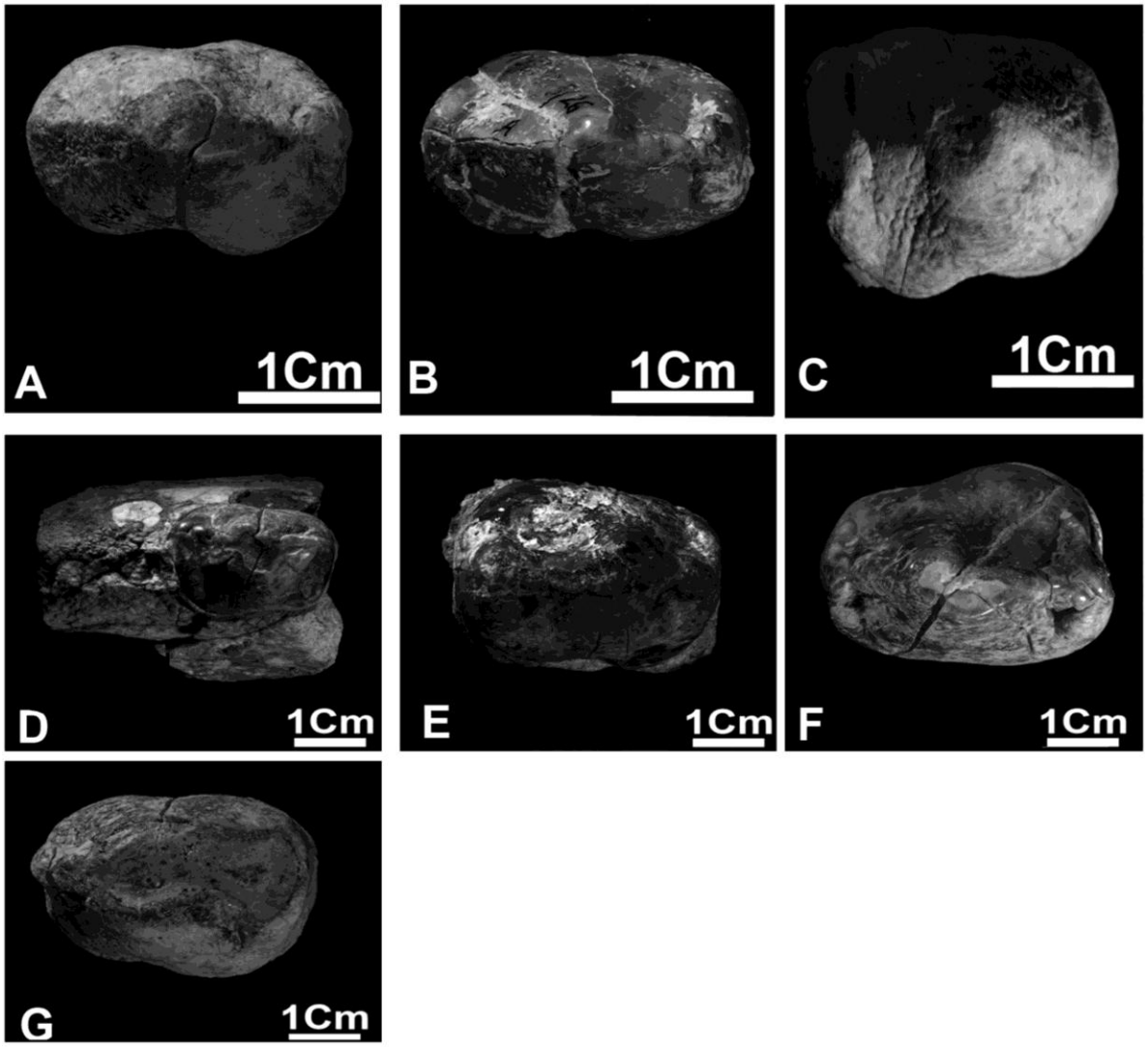

Plate 5. *Nyanzachoerus jaegeri*. Occlusal views: A) MSD-VP-2/188,right lower third premolar; B) MSD-VP-5/26,right lower third premolar; C) ARI-VP-3/222,right lower third premolar; D) MKM-VP-1/261,right mandibular fragment (p4); E) MSD-VP-5/26,left lower fourth premolar; F) MKM-VP-1/146,left lower fourth premolar; G) MSD-VP-2/187,left lower fourth premolar

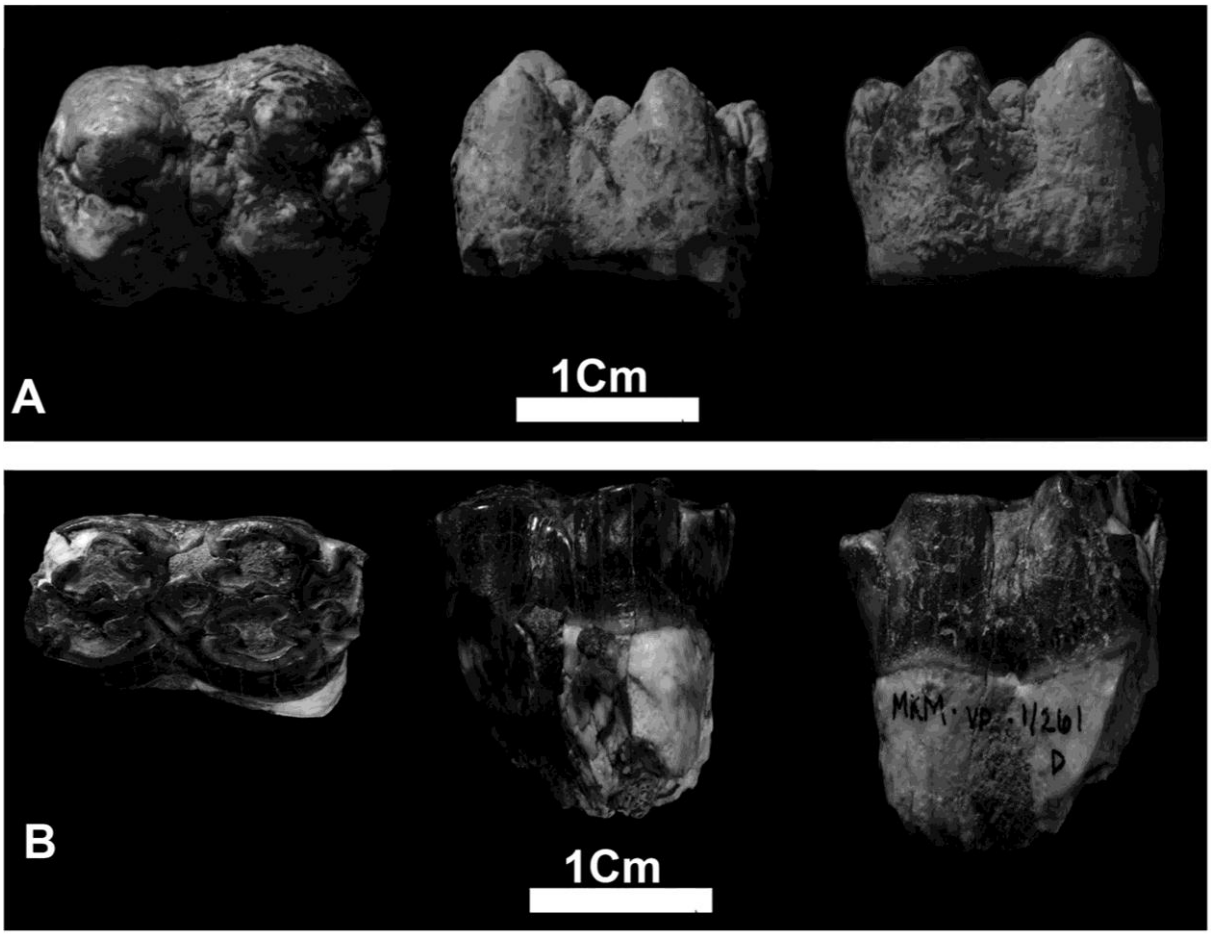

Plate 6. *Nyanzachoerus jaegeri*. Occlusal, buccal and lingual views: A) ARI-VP-1/477, left lower first molar; B) MKM-VP-1/261, left lower second molar

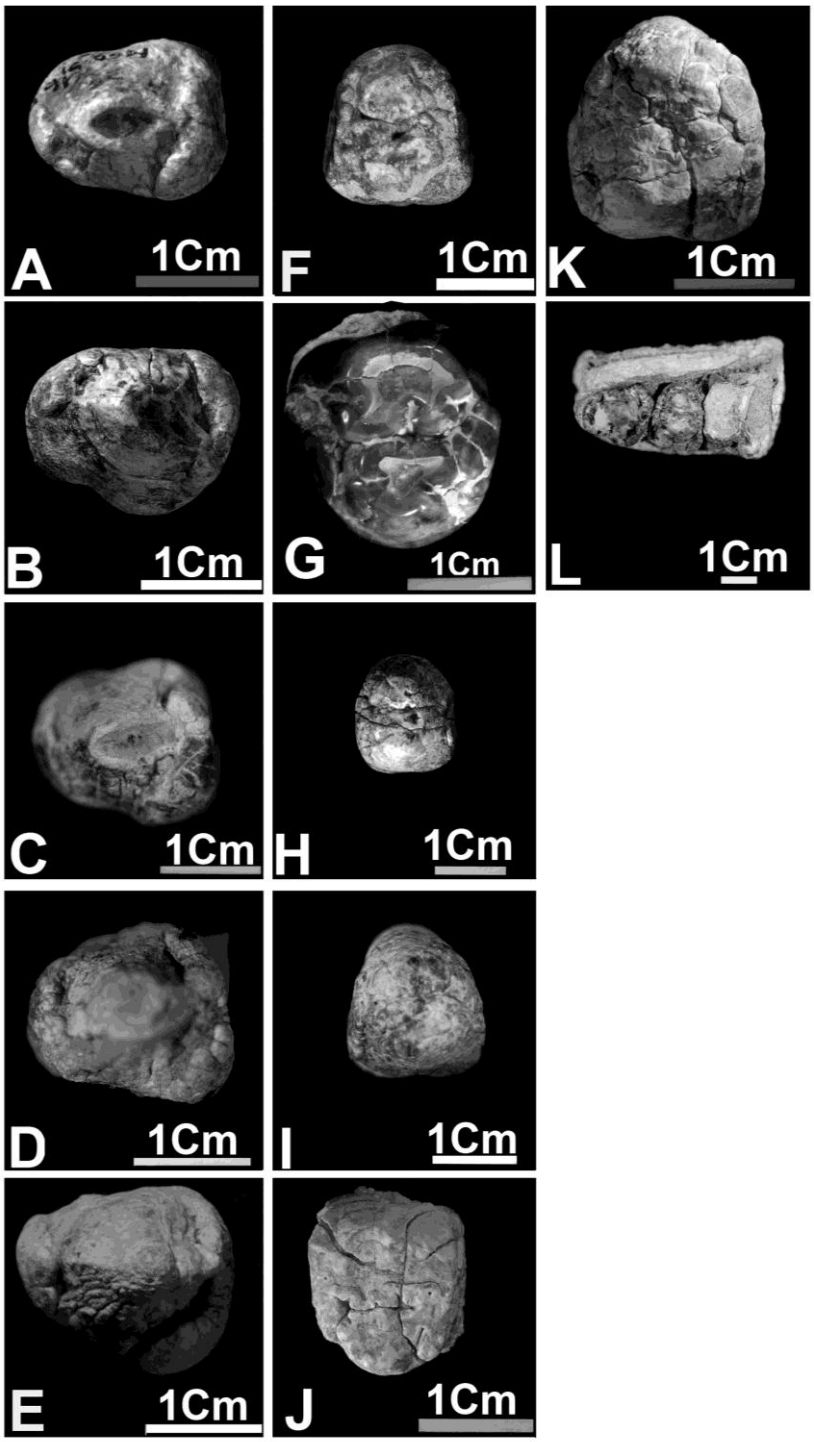

Plate 7. *Notochoerus euilus*. Occlusal views: A) MSD-VP-5/6, left upper third premolar; B) MSD-VP-5/24,right upper third premolar; C) MSD-VP-3/9,left upper third premolar; D) MKM-VP-1/53,left upper third premolar; E) ARI-VP-1/440,left upper third premolar; F) MKM-VP-1/53, right upper fourth premolar; G) MKM-VP-1/55,left upper fourth premolar; H) ARI-VP-1/46,right upper fourth premolar; I) ARI-VP-1/53,right upper fourth premolar; J) MSD-VP-2/144,left upper fourth premolar; K) MSD-VP-2/16,right upper fourth premolar; L) MKM-VP-1/271,right maxillary fragment (P3-M1)

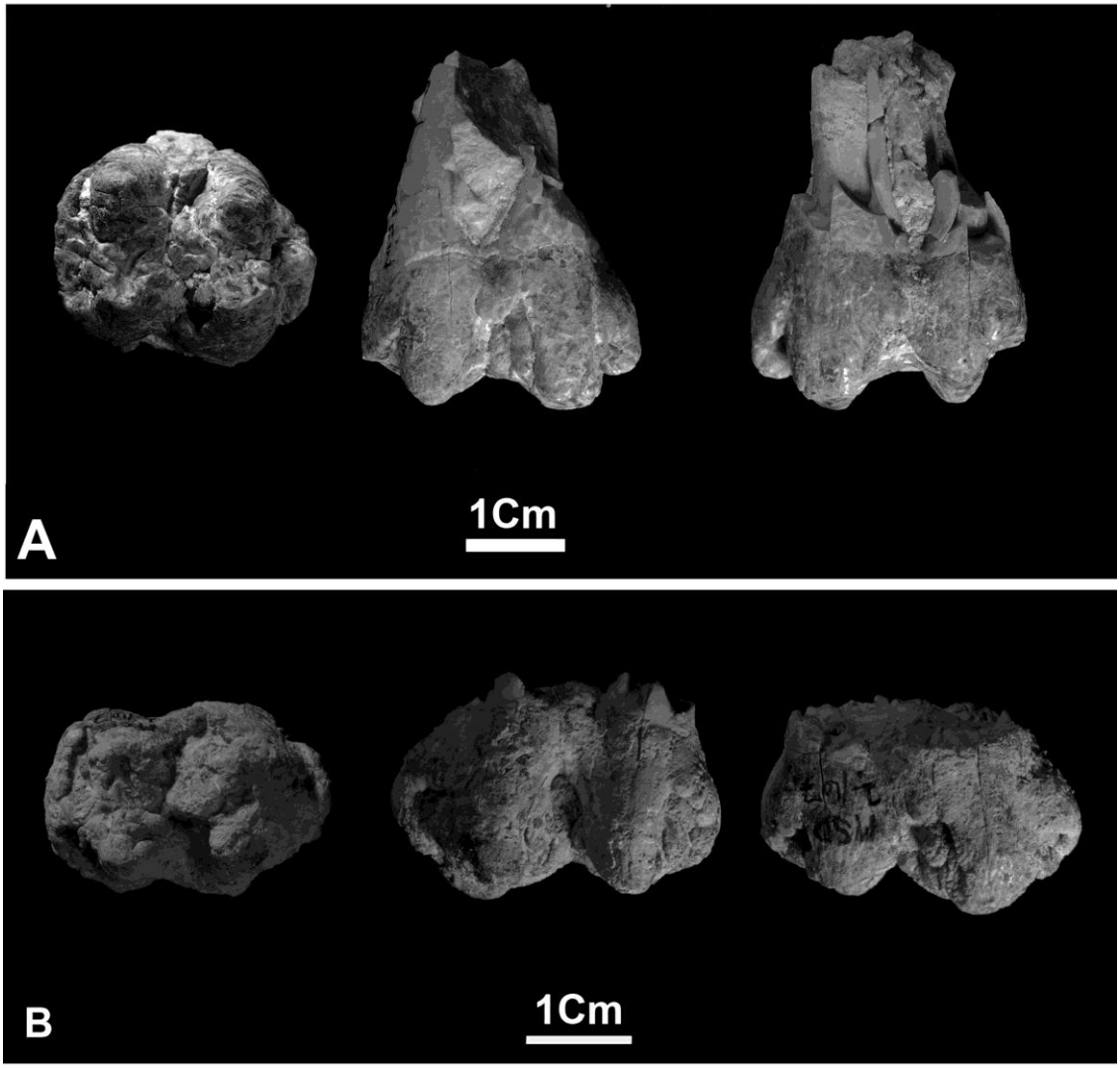

Plate 8. *Notochoerus euilsu*. Occlusal, buccal and lingual views: A) MSD-VP-1/58,left upper first molar; B) MSD-VP-2/67,right upper first molar

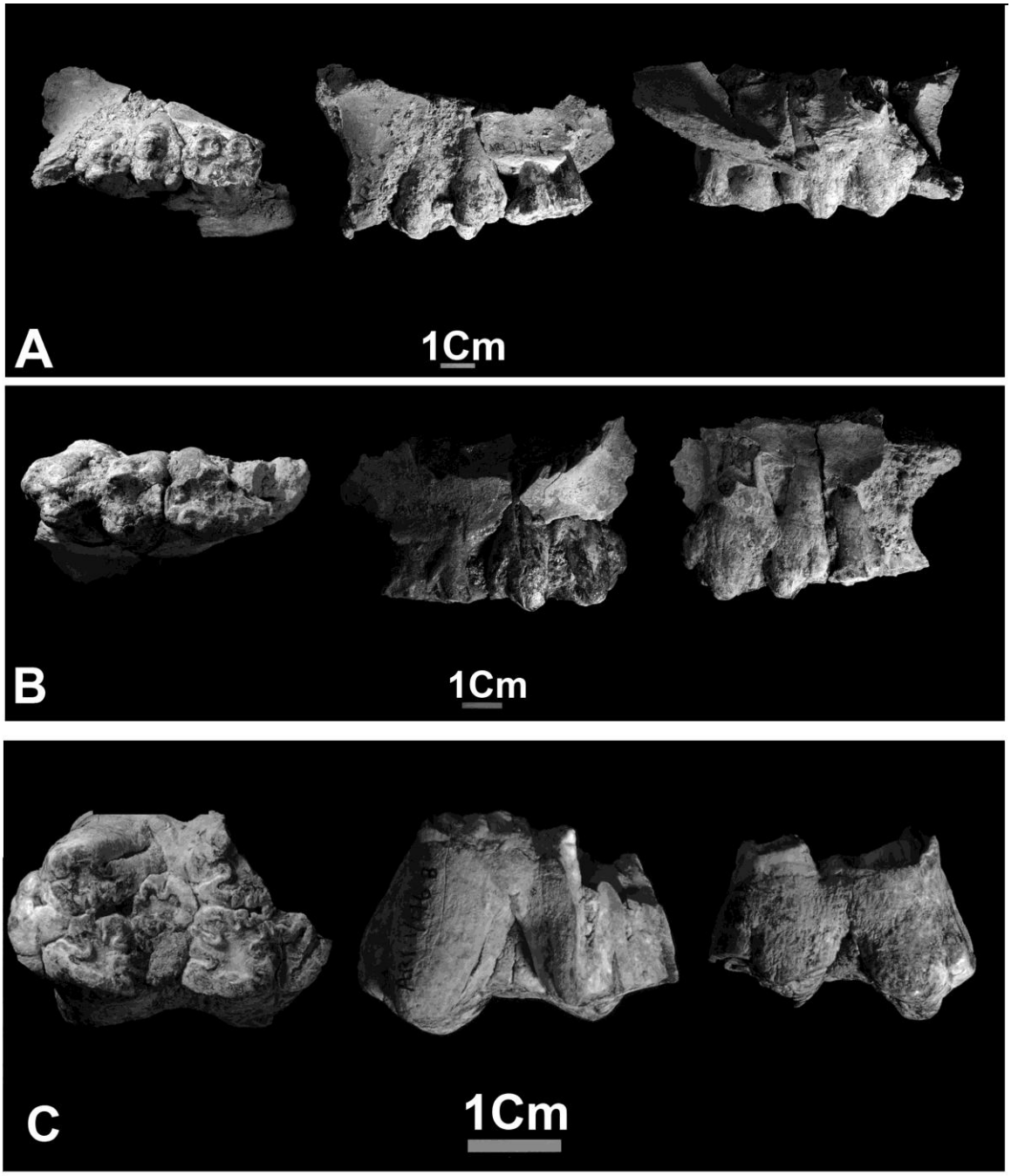

Plate 9. *Notochoerus euilus*. Occlusal, buccal and lingual views: A) ARI-VP-1/454,right maxillary fragment (M1-M2); B) ARI-VP-1/454,left maxillary fragment (M1-M2); C) ARI-VP-1/46,right upper second molar

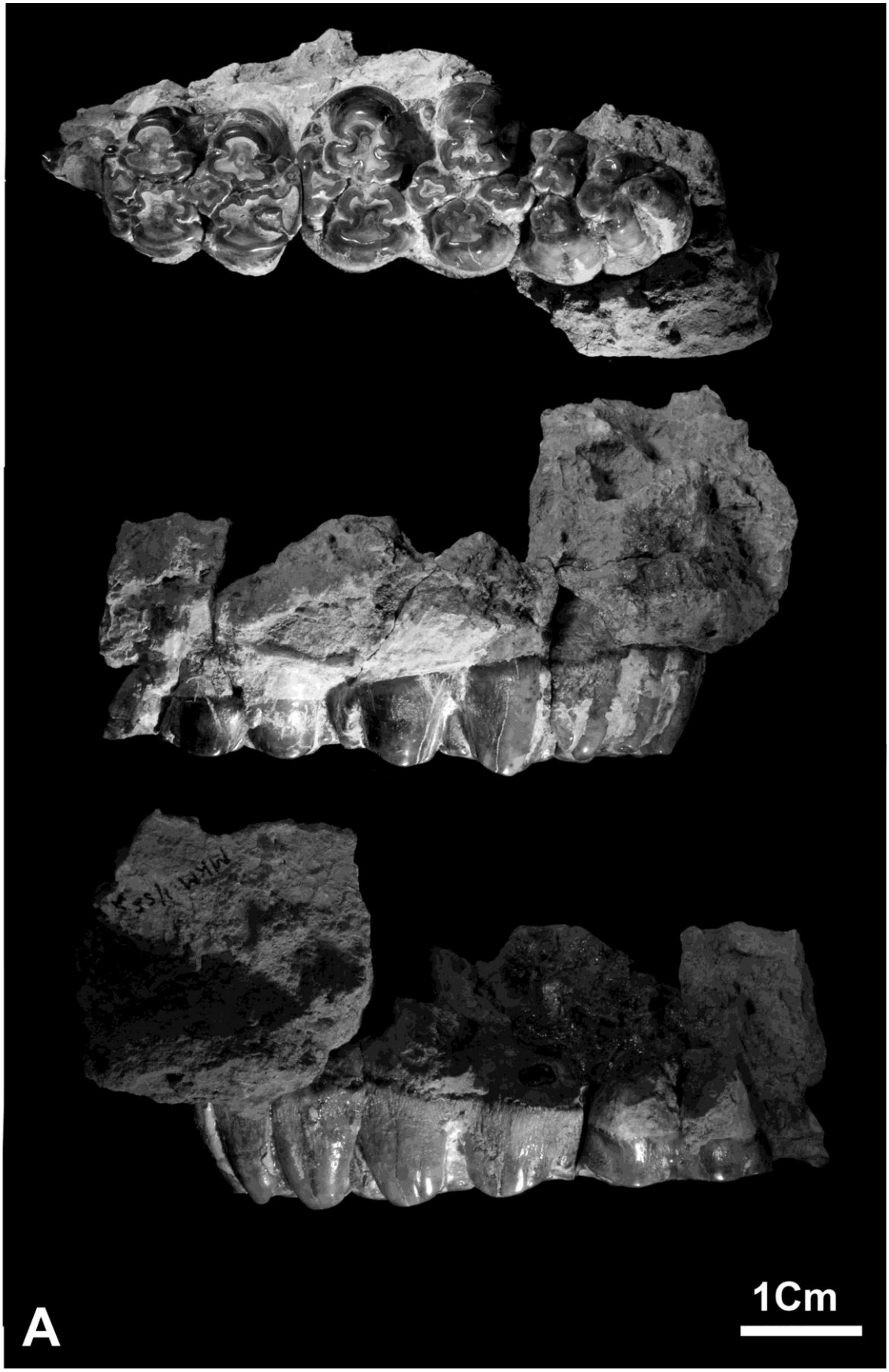

Plate 10. *Notochoerus euilus*. Occlusal, buccal and lingual views: A) MKM-VP-1/55, left maxillary fragment (M2-M3)

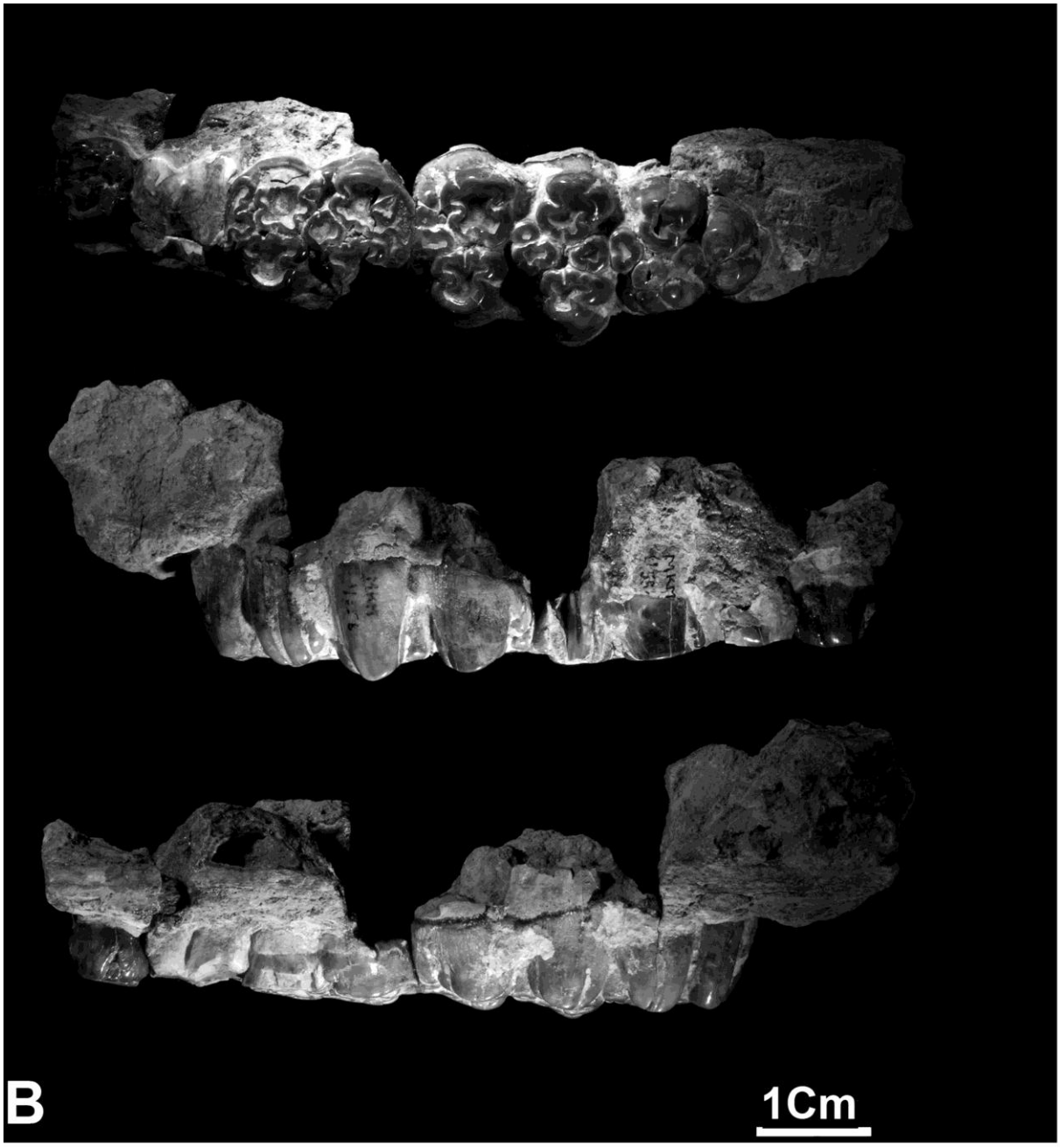

Plate 10 continued. B) MKM-VP-1/55, right maxillary fragment (P4-M3)

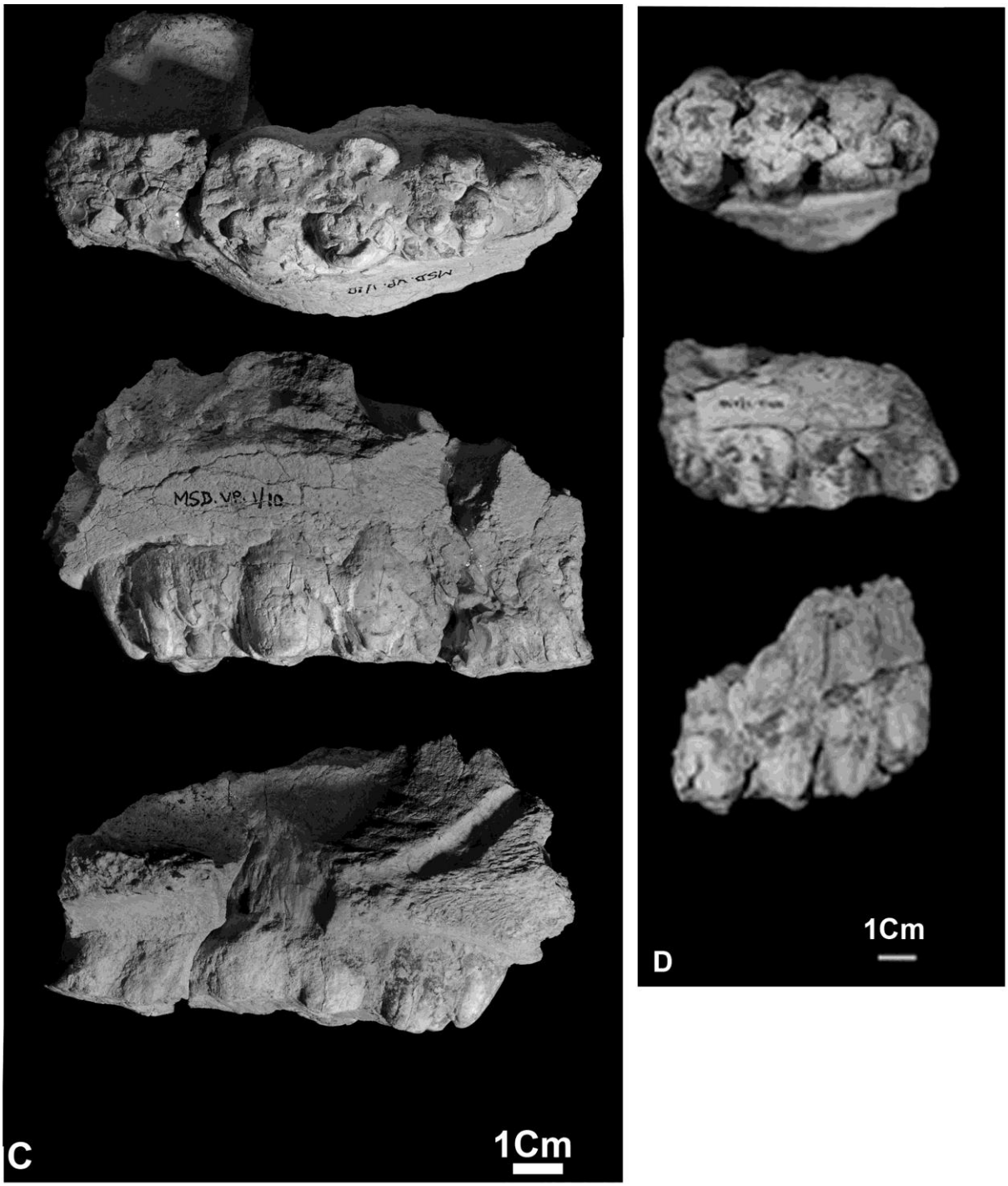

Plate 10 continued. C) MSD-VP-1/10, right maxillary fragment (M2-M3); D) ARI-VP-1/299, right upper third molar

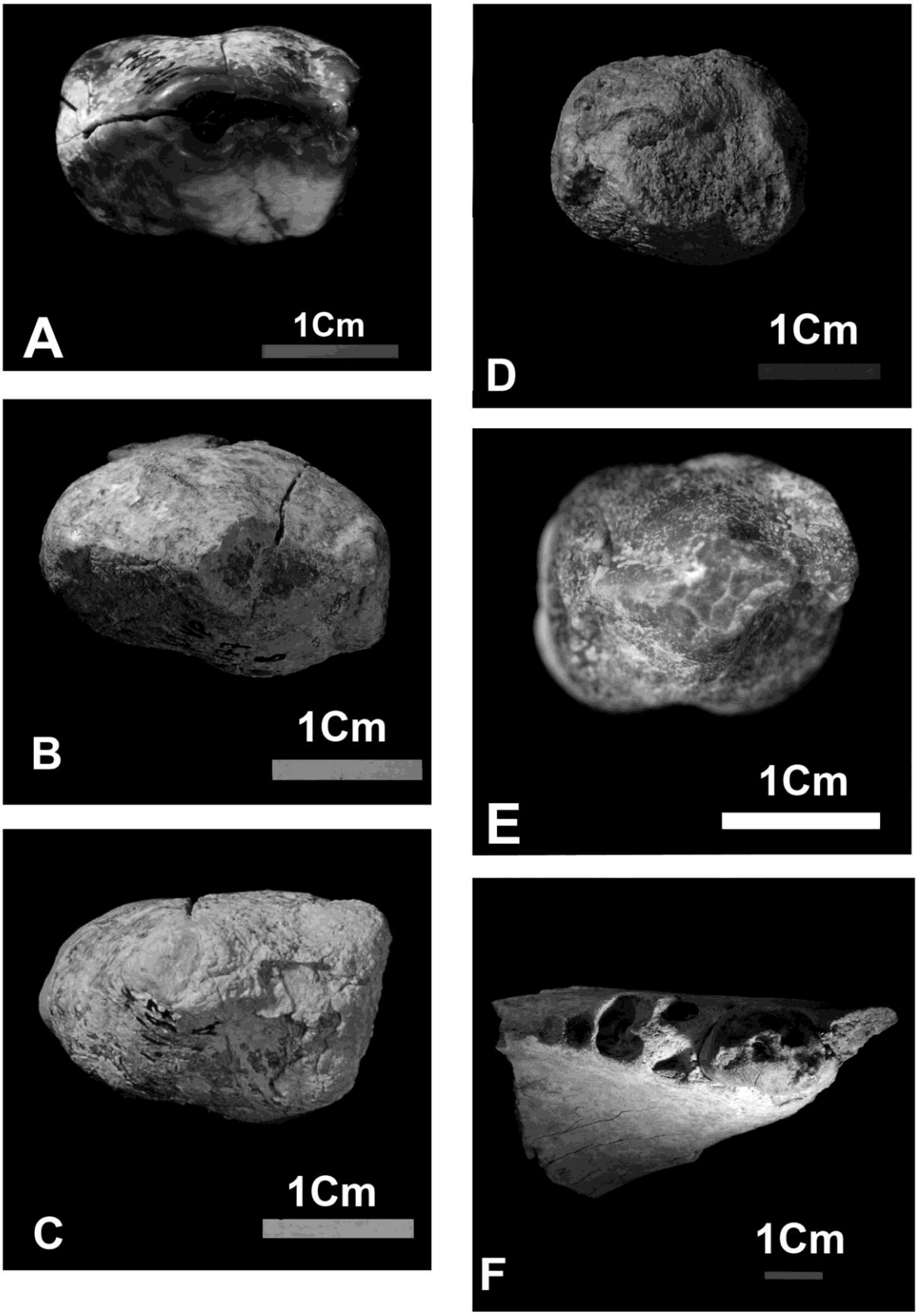

Plate 11. *Notochoerus euilus*. Occlusal views: A) MSD-VP-3/8,left lower third premolar; B) MSD-VP-2/177,right lower third premolar; C) MSD-VP-2/70,left lower third premolar; D) MSD-VP-2/70,right lower fourth premolar; E) MSD-VP-3/9,left lower fourth premolar; F) MSD-VP-2/225,right mandibular fragment (p4)

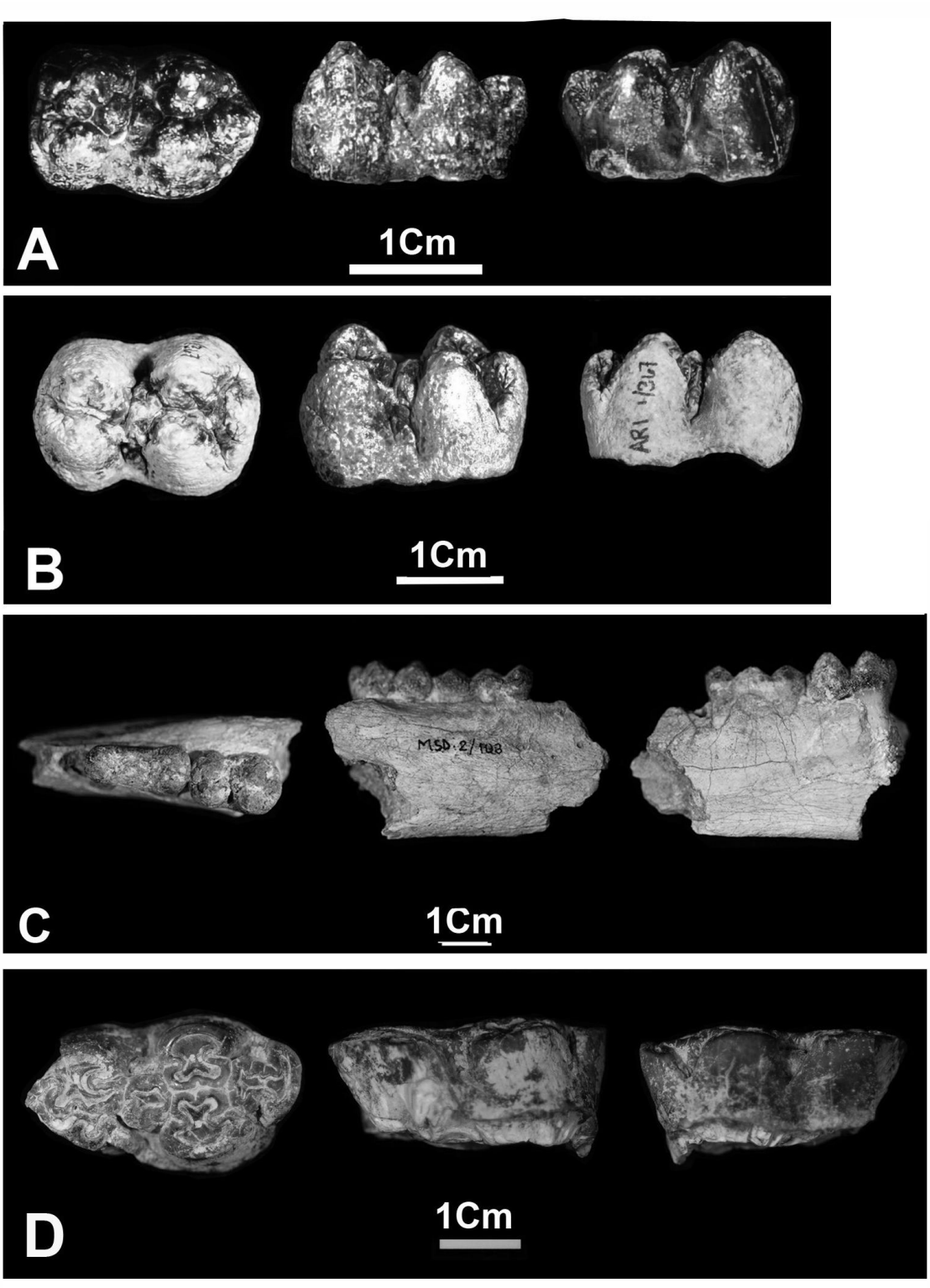

Plate 12. *Notochoerus euilus*. Occlusal, buccal, and lingual views: A) AMA-VP-2/10, left lower first molar; B) ARI-VP-1/367, left lower first molar; C) MSD-VP-2/103, right mandibular fragment (dp4-m1); D) MSD-VP-3/9, left lower second molar

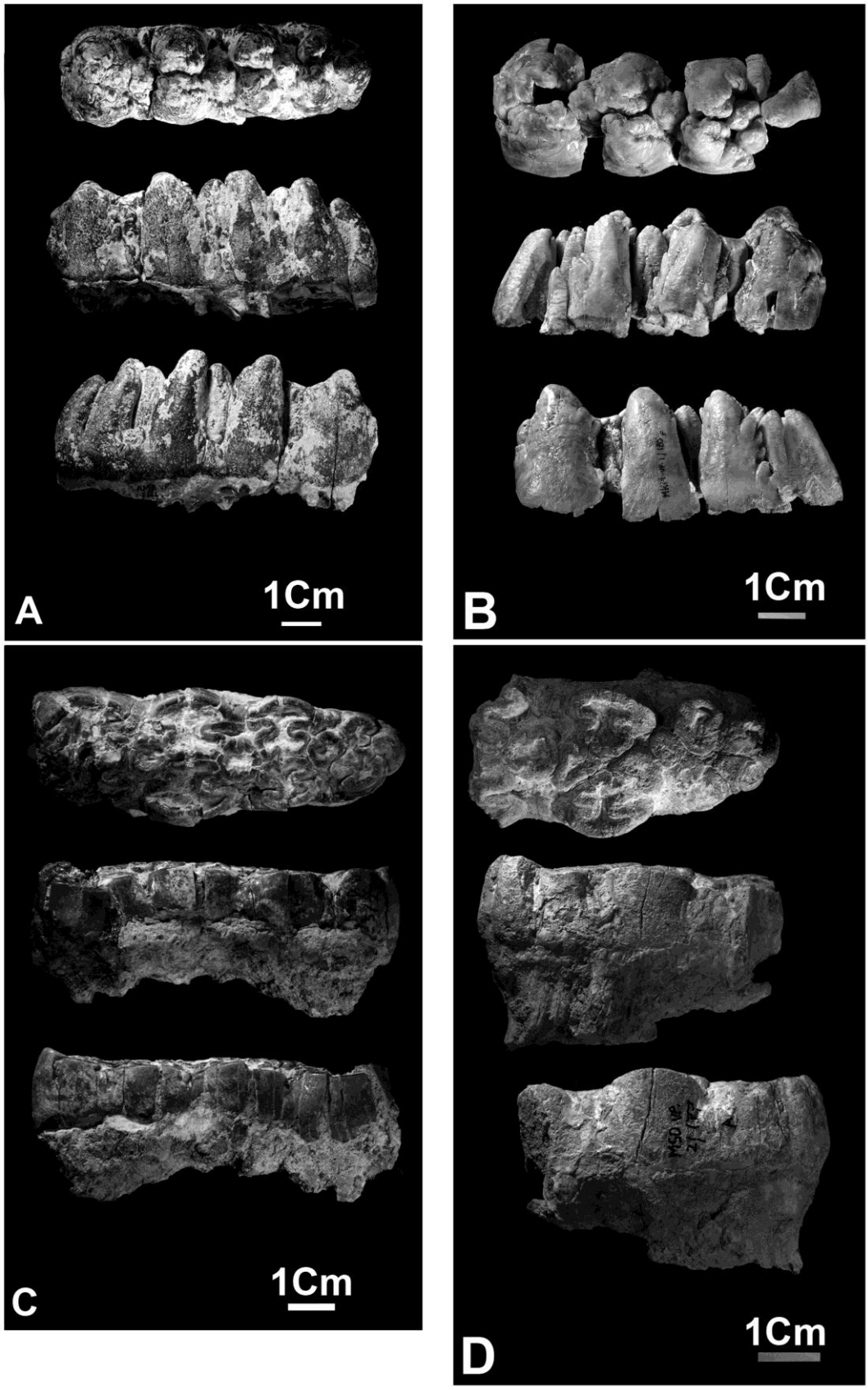

Plate 13. *Notchoerus euilus*. Occlusal, buccal and lingual views: A) AMA-VP-2/44-left lower third molar; B) MKM-VP-1/185,right lower third molar; C) MSD-VP-5/27,left lower third molar; D) MSD-VP-2/177,right mandibular fragment (m3)

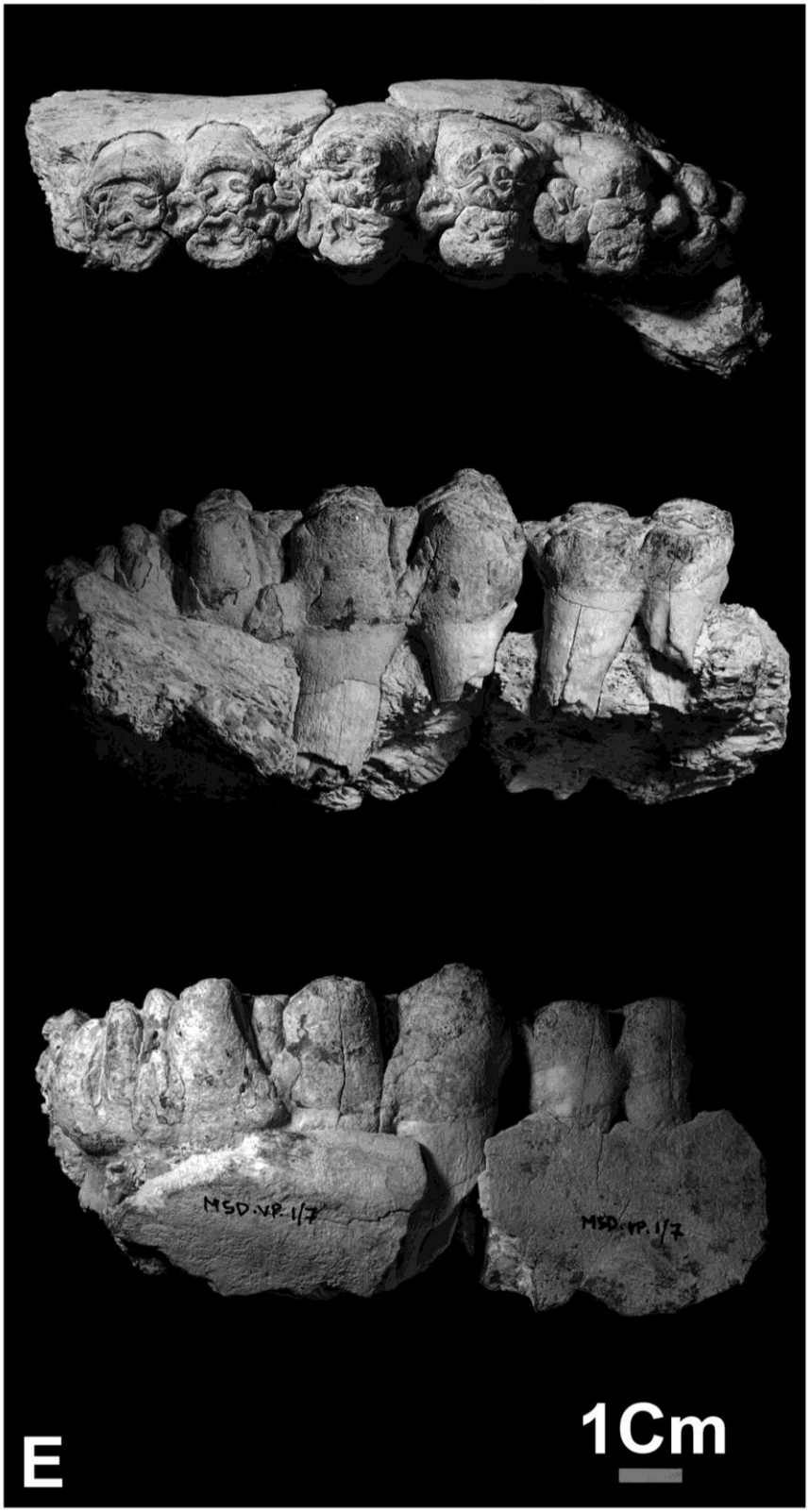

Plate 13 continued. E) MSD-VP-1/7, left mandibular fragment (m2-m3)