Evolution and Paleoecology of Pliocene Suidae (Artiodactyla, Mammalia)

In the Lower Awash Valley (Afar, Ethiopia):

Implications for Hominin Evolution and Paleoenvironments

by

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ABSTRACT

Providing an environmental context to early hominins is as important as describing the hominin fossils themselves, because evolutionary processes are tightly linked to everchanging ecosystems that vary across space and through time. An optimal understanding of ecosystems changes is critical to formulate and test hypotheses regarding human evolution and adaptation. Fortunately, the fossil record has yielded abundant remains of mammals which can be used to explore the possible causal relationships between environmental change and mammal – including hominin – evolution. Although many studies have already been conducted on this topic, most of them are framed at large spatial and temporal scales. Instead, this dissertation focuses on the evolution and paleoecology of only one group of mammals (the Suidae) in a specific geographical area (lower Awash Valley in Ethiopia) and within a constrained time frame (3.8–2.6 Ma). Three dissertation papers address: 1) changes in suid taxonomic composition in relation to Late Pliocene faunal turnover ~2.8 Ma in the Lee-Adoyta basin, Ledi-Geraru; 2) comparisons of suid diets from Hadar (~3.45–2.95 Ma) with respect to those of Kanapoi (~4.1 Ma, West Turkana, Kenya); 3) the dietary ecology of the suids from Woranso-Mille (~3.8–3.2 Ma). Results of these papers show that 1) after ~2.8 Ma there is a replacement of suid species that is coupled with low relative abundance of suids. This is compatible with more open and/or arid environments at this time; 2) suid dietary breadth was broader in Hadar than in Kanapoi, but this is mostly driven by the dietary niche space occupied by *Kolpochoerus* in Hadar, a suid genus absent from Kanapoi; 3) suid diets vary both temporally and geographically within the lower Awash Valley. *Kolpochoerus* incorporates more C_4 resources (e.g., grasses) in its diet after ~3.5 Ma and in general, suids after ~3.5 Ma in Woranso-Mille had C_4-enriched diets in comparison with those from nearby Hadar and Dikika. Presumably, the changes in suid communities (relative abundance and taxonomic composition) and dietary shifts observed in suids were triggered by climatic and habitat changes that also contributed to shape the behavioural and morphological evolution of early hominins.

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CHAPTER 1. INTRODUCTION

1. Introduction

Hominin evolutionary history is marked by a series of events that shaped the morphological and behavioral characteristics of different hominin species. All organisms – including hominins – are tightly linked to their environmental surroundings, upon which their survival depends, and therefore human evolution and behavioral development was influenced by the environments in which hominins evolved. Kingston (2007, p.2) notes that "developing adaptive or causal perspectives on the morphological and behavioral variability documented in the human fossil record requires establishing a comprehensive paleoenvironmental context". Unfortunately, this is an extremely challenging endeavor. Our efforts to understand the relationship between environmental change and the evolution of hominins and other biota are hampered by the intrinsic biases in the fossil record, the complexities of modern analog ecosystems, and the analysis of species that are long-ago extinct.

To effectively grapple with the complexities of past environments, paleoecology has adopted a multidisciplinary approach. Ocean drilling, analyses of pedogenic carbonates, oxygen isotope values, pollen records, faunal analysis, etc., all suggest that there were a series of climate oscillations in the trend towards more arid, cooler, and more seasonal climates during the last part of the Cenozoic in Africa (Bonnefille and Mohammed, 1994; DeMenocal, 1995; Reed, 1997, 2008; Potts, 1998; Bobe et al., 2002; Bonnefille et al., 2004; deMenocal, 2004; Trauth et al., 2007; Bonnefille, 2010; Levin et al., 2011; Maslin et al., 2014; Robinson et al., 2017). The goal of incorporating paleoecology into the study of human evolution is to provide a window on the interplay of the hominid lineage and its environmental context through time. Some researchers have tried to draw direct associations between climatic oscillations and key events in hominin evolution, such as the origin of bipedalism, the emergence of the genus *Homo*, the first use of stone tools, and increases in brain size (DeMenocal, 1995, 2004; Potts, 1998; Trauth et al., 2007; Maslin et al., 2014). These studies are conducted at large macroevolutionary scales and lack the resolution at which hominins interact with the ecosystem, with the result that the effect of the environment on hominin evolution remains speculative.

Fortunately for paleoanthropologists, early hominins coevolved with other large mammals, which are generally more diverse, and their fossil remains more abundant than those of our early ancestors. These fossils represent an opportunity for scientific research to improve our understanding of how environmental change may have driven hominin evolution. To adequately examine the relationship between environmental change and hominin evolution, I propose to use a paleoecological approach at a regional scale and in a group distantly related to hominins, the Suidae (pigs, hogs). The aim of this dissertation is to examine suid evolution and paleoecology in an area of extensive fossiliferous deposits known as the lower Awash Valley (LAV), in the Afar region of Ethiopia, and establish a fine-grained scenario of the habitat shifts that likely affected the course of both suid and hominin evolution from the mid-Pliocene to the early Pleistocene (~3.8–2.3 Ma).

2. The lower Awash Valley

The LAV in the Afar of Ethiopia has been the focus of paleoanthropological fieldwork for decades, leading to the recovery of hundreds of hominin fossils between ~5.3–2.6 Ma. Some of the first geological surveys in the remote lands of the Afar Triangle, approximately 400 km northeast of Addis Ababa, were initiated by Maurice Taieb in the late 1960's (Taieb et al., 1972). One of the first locations targeted by Taieb and colleagues was an area of fossil-rich and extensive sedimentary deposits in the northwestern part of the central Afar region called Hadar. From 1973 to 1977, the International Afar Research Expedition (IARE), under the leadership of Taieb, Donald Johanson, and Yves Coppens, recovered tens of thousands of vertebrate fossils and some 250 fossil hominins now known to date to ~3.45–2.95 Ma (Campisano, 2007, 2012; Campisano and Feibel, 2008). These finds include the partial skeleton of "Lucy" (A. L. 288-1) and numerous hominin remains from a single locality (A.L. 333/333w) which became known as the "First Family" (Taieb et al., 1976; Johanson et al., 1982), representing at least 17 individuals (Behrensmeyer et al., 2003).

The discovery of the Hadar fossil remains (and others from Laetoli, Tanzania) resulted in the naming of a new hominin species, *Australopithecus afarensis* (Johanson and White, 1979), which is today considered to be the likely ancestor of later hominin lineages, including *Homo* (Villmoare et al., 2015) and possibly *Paranthropus* (Rak et al., 2007). More than 90% of the fossils of the *A. afarensis* hypodigm have been recovered from the Hadar Formation at Hadar (Kimbel et al., 2004; Kimbel and Delezene, 2009; Johanson, 2017) but other sites in the LAV have also contributed to our understanding of the evolution and paleobiology of this species. The best example is the partial skeleton of a juvenile of *A. afarensis* dubbed “Selam”, which was found in 2006 at Dikika, an area south of Hadar (Alemseged et al., 2006; Wynn et al., 2006).

It is hypothesized that *A. afarensis* constitutes a single evolving lineage with its putative phyletic ancestor, *A. anamensis* (Kimbel et al., 2006). The latter is best-known from the site of Kanapoi (~4.1 Ma) in the Turkana Basin, Kenya (Leakey et al., 1995; Ward et al., 2013), but is also present in the Afar at Asa Issie (White et al., 2006) and in the LAV at Woranso-Mille (Haile-Selassie et al., 2010a, 2010b). Fossils of both *A. anamensis* and *A. afarensis*, for example, are present in the LAV at the Woranso-Mille research area, where the transition of one species into the other can be tracked through the sequence (Haile-Selassie et al., 2010a). The Woranso-Mille paleontological study area is located less than 50 km north of Hadar and has been under investigation by the Woranso-Mille Paleontological Research Project since 2005, under the direction of Yohannes Haile-Selassie (Haile-Selassie et al., 2007; Deino et al., 2010). Over 13 field seasons have resulted in the collection of more than 6,000 fossils of Pliocene age, including a newly described hominin species, *A. deyiremeda*, and an enigmatic foot (the Burtele foot) with primitive *Ardipithecus*-like features (Haile-Selassie et al., 2012, 2016; Haile-Selassie and Melillo, 2015). The Woranso-Mille study area is divided into a series of localities with ages that range from ~3.76 to ~3.2 Ma, though there are unpublished localities of uncertain age that could expand this temporal span further (Haile-Selassie et al., 2007; Deino et al., 2010; Saylor et al., 2016).

The LAV has also yielded important fossil evidence <3.0 Ma, which has been particularly informative regarding the origin of the genus *Homo*. One of the most important fossil specimens of early *Homo* is the maxilla A.L. 666-1. It was found in association with Oldowan lithic technology in some of the few exposures ~2.3 Ma of the Busidima Formation at Hadar (Kimbel et al., 1996, 1997). Some of the oldest Oldowan stone tools (~2.6 Ma) come from a nearby area known as Gona and they still constitute some of the oldest lithic technology found to date (Semaw et al., 1997; Semaw, 2000). The time interval between ~3.0–2.6 Ma, however, remained virtually unknown in the area until recently. Filling this gap was the motivation of Kaye Reed and colleagues when they surveyed an area east of Hadar known as Ledi-Geraru. In 2013, the Ledi-Geraru Research Project (LGRP) found a partial mandible (LD 350-1), which now constitutes the earliest specimens attributed to the genus Homo at ~2.8 Ma (DiMaggio et al., 2015; Villmoare et al., 2015). As fieldwork continues, recent surveys in the Mille-Logya area, north of Woranso-Mille, may provide even more evidence in this and other time periods in the near future.

In sum, the LAV can be divided into six main research project areas: Dikika, Gona, Hadar, Ledi-Geraru, Mille-Logya, and Woranso-Mille. Of these, the suids from Woranso-Mille, Hadar, and Ledi-Geraru research areas will be discussed studied in this dissertation. Together, these three areas provide a relatively continuous and stratigraphically well-constrained sequence of fossils from ~3.8 to ~2.6 Ma (Deino et al., 2010; Campisano, 2012). The rich fossil deposits in the LAV allow investigating questions related to the context of hominin evolution at regional scales. For example, what were the habitats occupied by hominins in the LAV through the Plio-Pleistocene? Did habitat change influence the diversification and extinction of early hominins?

Previous habitat reconstructions in the LAV suggest that from ~3.8 to 2.95 Ma the LAV was mostly a woodland/bushland mosaic that fluctuated from more covered/mesic to more open/arid habitats (Reed, 1997, 2008; Curran and Haile-Selassie, 2016; Robinson et al., 2017). Although there were fluctuations, there appears to be a general trend towards more open habitats in the late Pliocene (DiMaggio et al., 2015). *Australopithecus afarensis* is hypothesized to be a generalist species (Reed, 2008), adapted to a diversity of habitats, and capable of exploiting a wide variety of dietary resources (Ungar et al., 2010; Wynn et al., 2013). The middle to top part of the Hadar sequence, between ~3.24 Ma and 2.95 Ma, is probably more open and formed primarily by edaphic grasslands and floodplains at the beginning (in DD) and shrubland-like habitats associated with a riverine forest later (in KH) (Bonnefille et al., 2004; Reed, 2008). While there are few sediments between 2.95 Ma and 2.8 Ma, there was a large faunal turnover at ~2.8 Ma that provides evidence of a more open habitat during the first appearance of *Homo* in the LAV at 2.8 Ma (DiMaggio et al., 2015; Bibi et al., 2017; Rowan et al., 2017). It is possible that this open habitat in the LAV was not suitable for *A. afarensis*, and that the inferred habitat change either catalyzed the evolution of early *Homo* or favored its dispersal into the area. In this work, I contribute to our understanding of mammal evolution and habitats in the LAV some of these issues from the perspective of suid evolution.

3. The importance of African Suidae in human evolutionary studies

The extinct relatives of pigs and hogs (family Suidae) were an important component of eastern African faunal communities during the Pliocene, as evidenced by the large number of fossil suid specimens recovered from paleontological sites (Cooke and Ewer, 1972; Cooke, 1978a, 1978b, 2007; Harris and White, 1979; Harris, 1983;

Cooke and Hendey, 1992; White, 1995; Bishop et al., 1999; Made, 1999; Harris et al., 2003; Pickford, 2006; Bishop, 2010; Geraads and Bobe, 2017; Reda et al., 2017; Lazagabaster et al., 2018). Suids first rose to importance in human evolutionary studies when they helped to solve the KBS Tuff controversy in the 1970s regarding the age of an early *Homo* specimen (KNM-ER 1470) recovered from Koobi Fora on the eastern shores of Lake Turkana, Kenya (White, 1995). As such, suids have been intensively used as biochronological markers (White and Harris, 1977; Cooke, 1978b, 1985; Harris and White, 1979), but have also emerged as important indicator taxa for paleohabitat reconstructions (Bishop, 1994, 1999; Cuddahee, 2008) and a model clade for studying species turnover and paleoecological change in the mammalian fossil record, thus providing a comparative record for human evolution (White, 1995; Cooke, 2007; Souron, 2012).

Harris and White (1979) provide the best example of how the study of suids is relevant in paleoanthropology. While improving the chronology of hominin-bearing sites, Harris and White (1979) reorganized much of the taxonomy of fossil African Suidae, built phylogenetic hypotheses that largely stand today, and discussed the most important evolutionary trends of the group during the past seven million years. The main evolutionary trends are demonstrated by extreme changes in the morphology of the masticatory complex (e.g., increase in length and height of third molars) (Harris and White, 1979; Made, 1999). These morphological changes are hypothesized to be adaptations to more abrasive diets, such as grasses (Harris and Cerling, 2002) or grit (Janis 2008), that became more prevalent as C_4 grasslands spread since at least six million years ago (Cerling et al., 2011). However, other contemporaneous suid lineages retained less specialized, bunodont dentitions and likely had generalized omnivorous diets (Harris and White, 1979; Cooke, 2007; Souron, 2012).

4. Proxies for the study of the paleoecology of African Suidae

Suidae are artiodactyl mammals and together with the Tayassuidae and their fossil kin, the extinct Palaeochoeridae, constitute the superfamily Suoidea (Made, 1996, 2010). Modern suids are mostly associated with forested and mixed habitats, or at least where there is some tall vegetation cover (Nowak, 1999; Meijaard et al., 2011). Even modern warthogs (*Phacochoerus* spp.), which are well-adapted to the grasslands and scrublands of Africa, prefer to exploit resources in regions with some tree, bush, or tall grass cover with high water availability (Cumming, 1975, 2013; Butynski and de Jong, 2017). Most extant suids are generalized omnivores, capable of exploiting a wide variety of food resources (Nowak, 1999; Meijaard et al., 2011). These include underground resources (e.g., roots), which they access using their long snouts and anterior dentition. This feeding behavior, known as rooting, is variable among modern suid species and may have evolved in different suid lineages in response to food scarcity due to increased seasonality and changes in vegetation structure (Lazagabaster, 2013).

Because of their importance for biochronological purposes, the taxonomy of Suidae is well-established in eastern Africa (White and Harris, 1977; Harris and White, 1979; Cooke, 1997, 2007; Made, 1999; Bishop, 2010; Souron, 2012). However, the paleoecology of the group is comparatively understudied. Some researchers consider suids as part of the herbivore guild (Cooke, 1978a; Harris and Cerling, 2002; Bishop, 2010) and while this is in part true, the fact is that their feeding behaviors, their foraging ecology, and their digestive system are different from those of other ungulates. Due to their great dietary flexibility and adaptability, dietary inference in fossil suids is challenging. Furthermore, some extinct suids, like the tetraconodontines found in the LAV, had very different craniodental adaptations compared to modern suids. While suid paleodietary reconstructions can be difficult, suid paleodiet may also offer detailed insights into hominin habitats where other mammal groups can only offer limited information. For instance, the majority of African bovids are specialized browsers or grazers, or combine both browsing and grazing feeding behaviors, i.e., mixed-feeders (Lazagabaster et al., 2016). When specialist grazing bovids, such as reduncins or alcelaphins, are found in a certain fossil assemblage, the habitat is usually reconstructed as including grasslands, either arid or mesic (e.g., Reed, 2008). In general, techniques of paleodietary inference (stable isotopes or dental microwear) only confirm that these bovid taxa were grazing and, though valuable, such studies rarely offer additional information on the paleohabitat (e.g., Scott, 2012). This is important because grass is a ground cover in all African savannas and many alcelaphins are found in those habitats rather than open grasslands.

To improve suid paleodietary inferences, the best procedure is to use as many independent approaches as possible and to do so at the species level. It is fundamental to know how diet was changing in specific suid lineages to improve our understanding of the influence that possible habitat change had on suid adaptations, and to make better associations between specific craniodental morphologies and diet. For the reconstruction of fossil suid diets, there are two techniques that are widely used in paleodietary studies: carbon stable isotope analyses and dental microwear texture analyses (a newer version of more classic dental microwear methodologies). Carbon stable isotope analysis is a paleodietary technique that allows for the determination of the proportion of diet derived from plants using the C_3 photosynthetic pathway (trees, shrubs, and high-altitude grasses above 2,000 m) and the C_4 photosynthetic pathway (most low elevation tropical grasses in Africa). C_3 plants have $\delta^{13}C$ values ranging from -22‰ to -36‰ with a mean of -27.4±2.0‰ in tropical Africa and C_4 grasses have a mean of -12.7±1.2‰ with a range of -11‰ to -14‰ (Tieszen et al., 1979, 1983; O'Leary, 1981; Ambrose and DeNiro, 1986; Heaton, 1999; Cerling et al., 2003, 2015; Passey et al., 2005; Kohn, 2010). CAM (Crassulacian acid metabolism) pathway plants, predominantly succulents, have $\delta^{13}C$ values between those of C_3 and C_4 biomass (O'Leary, 1981, 1988; Heaton, 1999), though it is unlikely that they comprised a significant portion of herbivore diet in eastern Africa during the Pliocene. There is abundant carbon stable isotopic data from the LAV, which includes data for suids (Levin et al., 2015; Wynn et al., 2016; Robinson et al., 2017).

Dental microwear texture analyses is a technique that consists in analyzing the occlusal surface of teeth at a microscopical resolution, in search of modification of the enamel imprinted by food particles during mastication in the last days or weeks of life of the individual (Teaford and Glander, 1991). Variation in microscopic wear is the consequence of the physical properties of different food items. Dental microwear texture uses confocal microscopy, which allows for faster, more accurate and replicable analyses (Grine et al., 2006; Scott et al., 2006, 2012; Ungar et al., 2008; Souron et al., 2015). The data analyses are based on variables derived from the topograpy of dental occlusal facets at a microscopic level. Some of the most important variables are discussed briefly here. Complexity (*Asfc*) reflects the change in surface roughness across different scales of observation. Anisotropy (*epLsar*) reflects the orientation of wear striations. The scale of maximum complexity (*Smc*) reflects the size of the microwear features. Textural fill volume (*Tfv*) reflects the geometric shape and depth of wear features (Scott et al., 2005, 2006). In general, grazing animals show lower values of anisotropy and heterogeneity. No dental microwear studies exist thus far on the suids from the LAV, but analysis of the fossil suids from Kanapoi has been successful in differentiating niche partitioning among suids and in reconstructing their habitats (Ungar et al., 2017).

5. Goals and questions

The overarching goal of this dissertation is to refine current knowledge about environmental and faunal change in early hominin evolution through the study of the evolutionary and paleoecological changes in suid lineages of the LAV from ~3.8–2.6 Ma. I focus mainly on suid dietary reconstruction and changes in diet through time, as the most important evolutionary trends in Pliocene eastern African suids occurred in the masticatory complex (Harris and White, 1979). In turn, suid diets are a proxy for habitat reconstruction because diet and habitat are tightly correlated: one cannot eat what is not available in the environment (Ungar, 2010). The critical challenge, however, is to discern what suids actually eat from what it is available in the environment. In this dissertation, I discuss the results of two techniques of paleodietary reconstruction, stable isotope analyses and dental microwear texture analyses. The abundance of different suid species are also important in understanding habitat diversity because suids can be adapted to specific types of habitat or can ecologically partition the available habitat in different ways. It is expected that if a specific type of environment becomes more dominant, then those species with a particular trait that are better adapted to that condition (e.g., hypsodont molars to grind down grasses in open habitats) will become more abundant. While this formula is simplistic, it does explain the trend in the composition of suid communities through time.

This dissertation consists of three papers, each of which analyze suid assemblages in three different but geographically and temporally proximate sites in the LAV: Ledi Geraru (Lee Adoyta), Hadar, and Woranso-Mille (Figure 1.1).

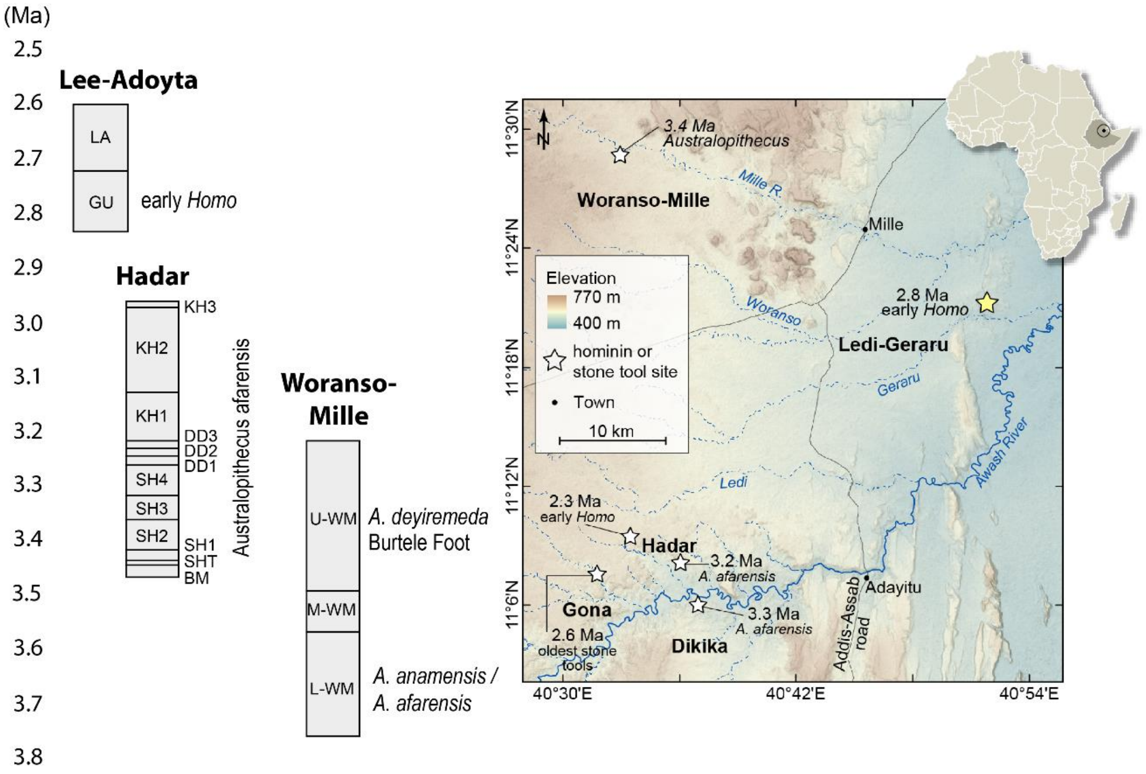

Figure 1.1. Temporal and geographical distribution of the three main sites in the lower Awash Valley (Afar, Ethiopia) studied in this work.

Paper I ('Fossil Suidae (Mammalia, Artiodactyla) from Lee Adoyta, Ledi-Geraru, lower Awash Valley, Ethiopia: implications for late Pliocene turnover and paleoecology') provides a taxonomic and paleoecological study of the suid fossils from the Lee Adoyta drainage, Ledi-Geraru. The Lee Adoyta sub-basin has produced abundant faunal fossil remains dated to ~2.84–2.6 Ma, including the earliest fossil attributable to the genus *Homo* (DiMaggio et al., 2015; Villmoare et al., 2015). Studies of the bovids and giraffids have provided new evidence for late Pliocene faunal turnover and paleoecological change in the Awash Valley, with shifts towards open habitats and grazer-dominated faunas by at least 2.8 Ma (Bibi et al., 2017; Robinson et al., 2017; Rowan et al., 2017). In Paper I, the goal is to understand whether faunal turnover and a transition to diets dominated by C_4 plants (grasses) that occurred in bovids, giraffids, and other mammal clades (DiMaggio et al., 2015; Bibi et al., 2017; Robinson et al., 2017; Rowan et al., 2017) are also reflected in suid lineages and how such shifts relate to broader environmental change in the region during this time. Suid specimens are scarce in the Lee-Adoyta but they are described and compared, especially with respect to the older suid fossils from the Hadar Formation (~3.45–2.95 Ma). Carbon stable isotope and relative abundance data add to the taxonomic analysis and provide a synthetic picture of suid evolution in the LAV that is later complimented by the other two papers.

Q_1: Is there evidence for a taxonomic turnover in Late Pliocene suids in the LAV?

- **Prediction #1:** Suids recovered from the Lee-Adoyta sub-basin <2.82 Ma are different species from those in Hadar <2.95 Ma.

Paper II ('Dental microwear texture analysis of Pliocene Suidae from Hadar sheds light on the dietary breadth expansion in early hominins') uses three-dimensional microwear texture analyses to reconstruct the diet of the suids from Pliocene Hadar (~3.45–2.95 Ma) and compare the results with those from Kanapoi (~4.1 Ma), which is located outside of the LAV, in the Turkana Basin, Kenya. Data from paleodietary proxies of *Australopithecus anamensis* and *A. afarensis* indicate marked differences in dietary breadth between these chronospecies (Sponheimer and Dufour, 2009; Ungar and Sponheimer, 2011; Sponheimer et al., 2013). The Kanapoi sample of *A. anamensis* has a narrow C_3-dominated isotopic signal, while the Hadar sample of *A. afarensis* shows significant dietary breadth and the consumption of both C_3 and C_4 resources (Ungar and Sponheimer, 2011; Sponheimer et al., 2013). However, dental microwear texture analsyes did not find any significant differences between these two species (Ungar et al., 2010). In paper II, I test whether different suid lineages also shifted from narrower diets at Kanapoi to broader ones at Hadar. In particular I predict that the microwear data of the suid genus *Kolpochoerus* will be different from the other two suid genera present in Hadar, *Nyanzachoerus* and *Notochoerus*, providing evidence of niche partitioning among suids. *Kolpochoerus* is not present in Kanapoi, and this absence may be due to the lack of certain food resources in Kanapoi that were available in Hadar.

Q_2: Do suids exploit a broader range of food resources in Hadar than in Kanapoi?

- **Prediction #2:** Suids recovered from Hadar exploit a broader range of resources, especially due to the presence of *Kolpochoerus* in Hadar, which likely occupies a different dietary niche to *Nyanzachoerus* and *Notochoerus.*

Paper III ('Dietary ecology of Pliocene Suidae (Mammalia, Artiodactyla): isotopic evidence from Woranso-Mille, Afar, Ethiopia') uses carbon and oxygen stable isotope analyses to inform about the diet of the suids from Woranso-Mille. Currently available fossil evidence indicates the possible presence of as many as four hominin species between ~3.8 and ~3.2 Ma in different parts of eastern Africa: *A. afarensis*, *A. bahrelghazali*, *K. platyops*, and *A. deyiremeda*, in addition to the Burtele foot. This foot was found in the Burtele locality of Woranso-Mille and dated to ca. 3.4 Ma. Its morphology, including its opposable hallux, is different from *A. afarensis* and more similar to the more primitive (and possibly semi-arboreal) morphological adaptations of the foot of *Ardipithecus* (Haile-Selassie et al., 2012). In the same Burtele locality, a new species, *A. deyiremeda* has recently been named though its taxonomic validity is still being debated (Haile-Selassie et al., 2015). In addition, hominin dentognathic material from Woranso-Mille localities with a chronology of ~3.8 to ~3.6 Ma have been argued to show intermediate characteristics between *A. anamensis* and *A. afarensis* (Haile-Selassie et al., 2010a; Haile-Selassie and Melillo, 2015). In this project I want to explore possible suid diet changes through time and across space that could reflect habitat differences between Burtele and other localities of the same and different age. Relative abundance of different suid taxa area also compared throughout the sequence. Finally, carbon stable isotope data of other sites in eastern Africa are compiled from the literature and compared with Woranso-Mille.

Q₃: How do the diets of suids vary across space and time in the mid-Pliocene of the LAV?

- **Prediction #3:** Suid diets change through the Woranso-Mille sequence (~3.76–3.2 Ma).
- **Prediction #4:** Suid diets are different between Woranso-Mille and other eastern African sites of the same chronology.

Together, the results of the three papers are synthesized and discussed in the context of Pliocene hominin evolution and environmental change in eastern Africa. These results shed light on fundamental issues of environment-mammal community relationships and open a window into the landscapes navigated by our ancestors through the lens of suid evolution and paleoecology.

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CHAPTER 2. FOSSIL SUIDAE (MAMMALIA, ARTIODACTYLA) FROM LEE ADOYTA, LEDI-GERARU, LOWER AWASH VALLEY, ETHIOPIA: IMPLICATIONS FOR LATE PLIOCENE TURNOVER AND PALEOECOLOGY

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Abstract

The fossiliferous late Pliocene deposits of the Lee Adoyta sub-basin, lower Awash Valley (LAV), Ethiopia, sample a poorly-known time interval in this region (~2.82 to <2.5 Ma). Recent fieldwork in Lee Adoyta by the Ledi-Geraru Research Project has produced a rich mammalian fauna, including the earliest specimen of the genus *Homo*. Here, the fossil Suidae (pigs) are described and taxonomical and paleoecological comparisons with other sites in the LAV (e.g., Hadar, Woranso-Mille) are provided. The Lee Adoyta suid fossils document the presence of at least three species, including *Notochoerus* cf. *No. capensis*, *Kolpochoerus phillipi*, and *Metridiochoerus andrewsi*, all of which are absent from the older deposits in the LAV (>2.95 Ma). However, two of these species (*No*. cf. *No. capensis* and *K. phillipi*) have likely ancestors known from the Hadar Formation (*No. euilus* and *K. afarensis*), implying a continuity of suid lineages through the Pliocene LAV. A compilation of stable carbon isotope ($\delta^{13}C$) data show a trend from C_3-C_4 mixed diets at Hadar to C_4-dominated diets by ~2.82 Ma at Lee Adoyta, most likely C_4 grasses. Suids decline in abundance almost linearly from ~3.76 to <2.5 Ma in the LAV, which I propose is related to the expansion of open, grassier habitats during this time.

Keywords – eastern Africa; hominin environments; mammal evolution; stable carbon isotopes

1. Introduction

The time interval between 3.0 Ma and 2.6 Ma in the late Pliocene has been a primary focus of studies testing for causal links between climatic change and mammalian evolution in eastern Africa. Several authors have analyzed late Pliocene faunal turnover in eastern Africa in the context of the onset of high latitude glacial cycles (i.e., the Ice Ages), which were expressed as a general trend towards increased aridity, seasonality, and cooling in the region (Vrba, 1995; Bobe et al., 2002; Bobe and Behrensmeyer, 2004; deMenocal, 2004; Kita et al., 2014; DiMaggio et al., 2015). Evidence for widespread late

Pliocene faunal turnover, however, is hampered by the scarcity of fossiliferous sediments dating to ~3.0–2.6 Ma. To date, most studies have focused on the Shungura Formation in the northern end of the Turkana Basin in southwestern Ethiopia, which provides the most continuous and rich fossil record during this time (Boisserie et al., 2008). Evidence from the Shungura fossil record indicates the replacement of taxa favoring closed and mesic habitats by those adapted to more open and arid habitats during this time (Wesselman, 1984; Bobe and Eck, 2001; Bobe and Behrensmeyer, 2004; Barr, 2015), but the degree to which the Shungura record is characteristic of eastern African faunas as a whole is poorly known.

Recent fieldwork in the Lee Adoyta sub-basin of Ledi-Geraru, lower Awash Valley (LAV), northeastern Ethiopia (Figure 2.1), has provided a new record of late Pliocene faunas dating to ~2.8 to <2.5 Ma. The Lee Adoyta faunas are both abundant (n >1,300 vertebrate fossils as of the 2018 field season) and taxonomically rich and have produced the earliest fossil attributable to the genus *Homo* (DiMaggio et al., 2015; Villmoare et al., 2015). Studies of the bovids and giraffids have provided new evidence for late Pliocene faunal turnover and paleoecological change in the Awash Valley, with shifts towards open habitats and grazer-dominated faunas by at least 2.8 Ma (Bibi et al., 2017; Robinson et al., 2017; Rowan et al., 2017).

Here, I describe the fossil Suidae (pigs) from Lee Adoyta, filling a critical gap in our knowledge of suid evolution during the late Pliocene. I provide detailed taxonomic and paleoecological comparisons of the Lee Adoyta suids with those from the nearby Hadar Formation at Hadar (Figure 2.1) and document dietary changes in different suid lineages through time using the Pliocene LAV records of Woranso-Mille (~3.76–3.56

Ma), Hadar (~ 3.42–2.95 Ma), and Lee Adoyta (~2.82 to <2.5 Ma). I aim to understand whether faunal turnover and a transition to diets dominated by C_4 plants (presumably grasses) that occurred in bovids, giraffids, and other mammal clades (DiMaggio et al., 2015; Bibi et al., 2017; Robinson et al., 2017; Rowan et al., 2017) are also reflected in suid lineages and how such shifts relate to broader environmental change in the region during this time.

2. Geological context

The Ledi-Geraru Research Project area lies in the LAV of the Afar Depression, northeast of the Hadar, Gona, and Dikika paleontological sites and south of the Woranso-Mille and Mille-Logya paleontological sites. The Lee Adoyta sub-basin exposures in the eastern Ledi-Geraru area preserve a sedimentary sequence ~70 m thick that span >2.84 Ma to <2.5 Ma (DiMaggio et al., 2015). Post-depositional faulting of the Lee Adoyta sub-basin has divided the sequence into four major fault-bounded blocks, each of which comprises a discrete sedimentary package. From oldest to youngest, these are the Bulinan, Gurumaha, Lee Adoyta, and Ogoyta fault blocks (DiMaggio et al., 2015) (Figure 2.1). The Bulinan sediments include the Bulinan Tuff dated to 2.842 ± 0.010 Ma and are lacustrine deposits with few vertebrate fossils. The Gurumaha fault block (GU), from which most of the paleontological specimens included in this study are derived, includes the Gurumaha Tuff dated to 2.822 ± 0.006 Ma and spans from less than 2.84 Ma to ~2.75 Ma. These sediments reflect a regression of the Bulinan lake phase to channel and overbank deposits of a nearshore delta plain. The Lee Adoyta fault block (LA) includes the 2.669 ± 0.011 Ma Lee Adoyta Tuff and spans from ~2.7 Ma to <2.58 Ma and represents fluvial channel and floodplain deposits (DiMaggio et al., 2015). The Ogoyta fault block (OG) is younger than the Gurumaha and Lee Adoyta packages based on faunal biostratigraphy, but its exact age is still under investigation (although almost certainly <2.5 Ma). To prevent confusion, I refer to the entire Lee Adoyta sub-basin as ‘Lee Adoyta’ and the fault blocks by their acronyms (GU, LA, OG), which includes the Lee Adoyta fault block (=LA).

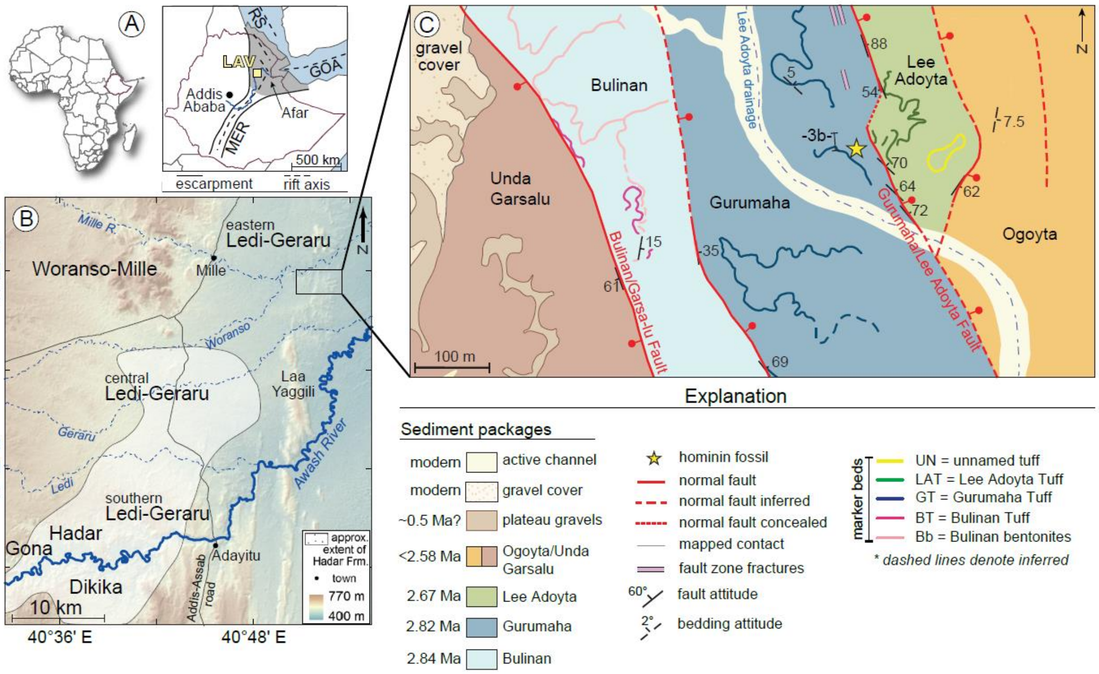

Figure 2.1. Geographic and geological context of the Lee Adoyta. A) Map indicating the position of the lower Awash Valley (in yellow) within the Afar depression (in grey) of Ethiopia (in purple outline). Abbreviations: LAV, lower Awash Valley; RS, Red Sea; GOA, Gulf of Aden; MER, Main Ethiopian Rift. B) Main LAV project areas and the approximate mapped extent of the Hadar Formation. C) Geologic map of the region surrounding the Lee Adoyta hominin site (yellow star indicates the location where LD 350-1 was found) showing NW-SE–oriented faults dissecting sedimentary packages into discrete blocks. Map courtesy of E. DiMaggio.

3. Materials and methods

3.1 Fossil collection

The suid fossils from Lee Adoyta (*n* = 64) were surface-collected during field surveys by the Ledi-Geraru Research Project in 2012, 2013, 2015, and 2018. The total 64 specimens account for 53 unique catalog numbers, as some of the specimens represent the same individual and are labelled as -a, -b, -c, etc. A complete list of specimens is provided in Appendix A, Table SI 1. All suid fossils were measured, photographed, and analyzed, but only 26 specimens are preserved well enough to warrant description here. All fossils collected by the Ledi-Geraru Research Project are housed at the National Museum of Ethiopia, Addis Ababa, under the Authority for Research and Conservation of Cultural Heritage (ARCCH).

3.2 Institutional abbreviations

A.L., 'Afar Locality', specimens collected by the International Afar Research Expedition (IARE) and Hadar Research Project (HRP), housed in the National Museum of Ethiopia, Addis Ababa. KNM, specimens housed in the National Museums of Kenya, Nairobi. LD, specimens collected from Lee Adoyta by the Ledi-Geraru Research Project, housed in the National Museum of Ethiopia, Addis Ababa. OMO-, L-, P-, F-, specimens collected by the International Omo Research Expedition, housed in the National Museum of Ethiopia, Addis Ababa.

3.3 Geological abbreviations

GU, Gurumaha fault block; LA, Lee Adoyta fault block; OG, Ogoyta fault block; SH, Sidi Hakoma Member (Hadar); DD, Denen Dora Member (Hadar); KH, Kada Hadar Member (Hadar); WM, Woranso-Mille.

3.4 Morphological abbreviations, nomenclature, and measurements

Dentition: d, deciduous tooth. MD, mesiodistal diameter measured at the base (enamel-dentine junction). MDmax, maximum anteroposterior diameter. BL, buccolingual diameter of the first lophe/lophid. BLp, buccolingual diameter of second lophe/lophid. BLpp, buccolingual diameter of the third lophe/lophid. Hling, maximum height of the crown in the lingual side. Hbucc, maximum height of the crown in the buccal side. M or m, molar, upper (M) or lower (m). P or p, premolar, upper (P) or lower (p). R or L, right or left; 1-, 2-, 3-, 4- denote tooth position (e.g., m2 indicates lower second molar). Dental nomenclature used here follows Harris and White (1979) and Made (1999). I use Kullmer' s (1999) wear stage recording system to evaluate wear on the third molars that preserve at least the mesial part of the tooth (the first and second lophs/lophids). Wear stages are abbreviated WS followed by a number (1-11) indicating the wear stage from unworn (stage 1) to very worn (stage 11).

Postcrania: MC, metacarpal; II, III, IV, V, denote MC position; DTd, transversal diameter of the astragalus measured distally; Lex, maximum length of the astragalus measured in the external (lateral) side.

All measurements were taken with digital calipers to the nearest 0.1 mm.

3.5 Paleoecological analyses

I combined suid stable carbon isotope ($\delta^{13}C$) and faunal abundance data from Lee Adoyta (Ledi-Geraru), the Hadar Formation (Dikika/Hadar), and Woranso-Mille to construct a record of suid paleoecology in the LAV from ~3.7 to <2.5 Ma. Stable carbon isotope data from suid tooth enamel were collected from Robinson et al. (2017) for Lee Adoyta, Bedaso et al. (2013) and Wynn et al. (2016) for the Hadar Formation, and Levin et al. (2015) for Woranso-Mille. Faunal abundance data were collected from the Hadar Geoinformatics Database (Institute of Human Origins, Arizona State University) for Lee Adoyta and Hadar, and Curran and Haile-Selassie (2016) for Woranso-Mille.

4. Systematic paleontology

4.1 *Notochoerus*

Family Suidae Gray, 1821

Subfamily Tetraconodontinae Lydekker, 1876

Genus *Notochoerus* Broom, 1925

Generic diagnosis: Modified from Harris and White (1979). Tetraconodont suids characterized by their general large size and by having craniodental characters derived with respect to other tetraconodontines (e.g., *Nyanzachoerus*), such as elongated crania, longer and taller third molars, and smaller premolars. The enamel of the lateral main molar pillars is strongly folded, producing H-shaped dentine lakes in occlusal view when worn. In lateral view, the enamel tends to be corrugated and may have a layer of cementum cover. Derived notochoeres, such as *No. capensis* and *No. scotti*, tend to have buccolingually compressed, elongated and taller third molars, smaller premolars, and thinner, more corrugated enamel, than those seen in the comparatively primitive *No. euilus*.

Notochoerus cf. *No. capensis* Broom, 1925

Diagnosis: Modified from Harris and White (1979). A *Notochoerus* species with a greater number of major talon/id pillars, taller individual molar pillars, and more corrugated enamel on third molars than *No. euilus*. In general, most dental characters are intermediate between *No. euilus* and the more dentally-derived *No. scotti* (Harris and White, 1979).

Referred Specimens: LD 564-1 (LA), right and left maxillary fragments with complete M3s, fragment of mandible with complete Lm3, occipital condyles, and other mandibular and cranial fragments; LD 50-1 (OG), a fragment of right mandible with distal portion of m3; LD 133-2, two fragments of R(?)M3; LD 107-2 (GU), a fragment of Rm3; LD 298-1 (GU), a fragment of LM3.

Description: LD 564-1 was found eroding out of the surface and the recovered pieces are part of a fragmentary skull. The M3s are in an advanced stage of wear (WS 7-8) with an almost complete fusion of the pillars of the trigon/id (Figure 2.2). The M3s have six pairs of lophs and five median pillars that are variable in shape but similar in size. The main lateral pillars are H-shaped but become noticeably irregular distally. The lingual pillars are displaced distally with respect to the buccal pillars, giving an overall asymmetric profile to the talon. The space between lophs is narrow, with no visible ectostyles. The enamel is thin but corrugated and is covered by a thick cementum layer. The m3 has seven pairs of lophids, though the distal two are much smaller (at least at this stage of wear and in occlusal view) and are completed by a single terminal pillar. The second and third pair of main lateral pillars are H-shaped (the first one is not visible) and become irregular in occlusal view distally, as in the M3s, but this is probably because they are less worn. Each pair of main pillars is separated by large diamond-shaped median pillars. There are no visible ectostylids in the m3, at least at this wear stage. Measurements of this specimen are given in Table 2.1.

LD 50-1 is a fragmentary right mandibular corpus with a moderately worn m3 that is missing the first lophid and most of the second lophid, though the extent of the basal portions of the roots of these lophids are visible (Figure 2.2). The preserved talonid consists of six pairs of main lateral pillars, the last of which are only worn at the tip and therefore, at this stage of wear, look smaller in occlusal view. Given that the base of the tooth is inside the mandible, it is not possible to determine if there were any more terminal cusps distally. The main lateral pillars are more separated both lingually and buccally than in LD 564-1. There are irregular median pillars separating each pair of main laterals that decrease in size distally. The mesialmost preserved pair of main lateral pillars (the third lophid) is H-shaped in occlusal view but there is an incipient extra arm to the H towards the middle of the tooth. The distalmost talonid pillars are of irregular shape, as in LD 564-1, but are more buccally displaced. Because the tooth is broken, it is not possible to know its size, but it seems that it would have been slightly larger than LD

564-1 (I estimate an unbroken length of ~85 mm considering the preserved roots in the mesial region). The tooth is heavily covered in cementum, under which strongly corrugated enamel is visible in some areas.

LD 133-2 consist of fragments of the middle and the distalmost portion of a R(?)M3. The fragments were not identified as part of the same tooth when originally collected and given different specimen numbers. Here I refer to the combined specimen as LD 133-2. Most of the preserved main lateral pillars are H-shaped in occlusal view while others are trilobate (with extra arms to the H-shape) (Figure 2.2). Several median pillars that are irregular in shape, but similar in size, are positioned between the lateral pillars. The enamel is strongly corrugated, thinner than in *No. euilus*, and with a thick cementum cover. The distalmost portion of the talon is unworn and is terminated in five small and almost vertical pillars that are strongly packed together. Though worn and fragmented, the tooth would have been taller (minimum preserved height = 46 mm) than known M3s of *No. euilus* and therefore align this specimen better with a more derived species such as *No. capensis*.

LD 107-2 is a distal fragment of Rm3 in moderate wear that preserves two of the last main lateral pillars on the labial side and only one on the lingual side. There is a fragmentary terminal pillar but is impossible to know if there were more pillars distal to it. Though worn, the height of the crown is visibly higher (minimum preserved height = 42 mm) than in *No. euilus* and the lateral pillars are more buccolingually compressed, resembling *No. capensis.*

LD 298-1 is a poorly preserved M3 fragment that is missing both mesial and distal portions. The tooth is moderately worn and poorly preserved, but it was probably taller (minimum preserved height = 35 mm) than *No. euilus*, especially towards the distal part of the tooth. The overall size of the tooth is smaller than LD 133-2 and the lateral pillars are slightly less buccolingually compressed. Some of the lateral pillars are H-shaped but others are star-shaped due to the presence of an extra arm to the H. The median pillars are large and mesiodistally elongated, but there are two instead of one towards the distal end of the fragment. The enamel is thin and corrugated, and probably had a thick cementum cover that is now almost completely gone. As in the case of the teeth described above, these characteristics suggest a species more derived than *No. euilus*.

Comparisons: The third molars of LD 564-1 and LD 50-1 resemble the overall morphology of those of *No. euilus*, although they have several characteristics that align these specimens more closely with derived species and in particular with *No. capensis*. *Notochoerus euilus* typically has four or five lophs in M3 and five or six lophids in m3, whereas the Lee Adoyta teeth have six lophs in M3 and seven lophids in m3, a condition typical of *No. capensis*. The narrow separation of the main pillars in lateral view and the corrugated enamel are also characters that are often more strongly expressed in *No. capensis* than in *No. euilus*. Additionally, the M3s of LD 564-1 have distally displaced lingual pillars, a character noted by Harris and White (1979) in their descriptions of *No. capensis*. Metrically, the M3s and m3 of LD 564-1 (RM3: MD = 71.3 mm, BL = 28.3 mm; Lm3: MD = 80.6 mm, BL = 23.8 mm) fall within the range of variation of the most derived *No. euilus* from the Hadar Formation but are smaller than the few complete specimens of *No. capensis*. For example, one of the most complete specimens (M 2077) from Makapansgat, South Africa, has a m3 with a basal length on the lingual side of

114.4 mm and a length of 93.6 mm at the occlusal wear table. I note, however, that the distal extremity of the m3 measured (LD 564-1) is inside the mandible, so that this value is likely an underestimate of the tooth's total length, which is also the case for the M3s of LD 564-1. Given that these teeth are morphologically outside of the range of variation of *No. euilus* from Hadar and elsewhere and more similar to *No. capensis,* we tentatively assign these specimens to *No.* cf. *No. capensis,* even if they are metrically smaller than the known range of variation of *No. capensis*. Nevertheless, this identification warrants additional fossils for secure identification.

Most of the other notochoere remains from Lee Adoyta are fragmentary third molars. The crown height and morphology of the talon/ids of LD 133-2, LD 107-2, LD 298-1, align these teeth better with *No. capensis* than with *No. euilus*. For example, the occlusal shape of the lateral pillars, as well as the morphology of the distal part of the talon in LD 133-2, resemble some of the specimens assigned to *No. capensis* from Makapansgat and some of the specimens assigned to *No. scotti* from the Shungura Formation, including OMO 90-1972-3 (Shungura Member F, ~2.32–2.27 Ma) and OMO 78-1970-1234 (Shungura G-27/G-28, ~1.95 Ma) (Figure 2.2). Similarly, the overall morphology of LD 107-2 and LD 298-1 is reminiscent of more complete specimens from the Shungura Formation that are assigned to *No. scotti*, like OMO 75-1969-300 (Shungura Member G12/G-13, ~2.27–2.05 Ma). The fragmentary nature of the fragmentary notochoere remains from Lee Adoyta impedes their secure attribution to any one species but considering the intraspecific variability within *Notochoerus* species and the available evidence, it is more parsimonious for the moment to assume a variable population of a single species in the Lee Adoyta, in this case *No.* cf. *No. capensis*.

Discussion: *Notochoerus capensis* has been argued to be an intermediate species between *No. euilus* and *No. scotti* (Harris and White, 1979) but Bishop (2010) suggested that the hypodigm of *No. capensis* should be restricted to the material from South Africa, which comes mainly from Makapansgat (~3.0–2.6 Ma) (Herries et al., 2013) and the Vaal River Gravels (age unknown). The *No*. cf. *No. capensis* specimens from Lee Adoyta are less derived than those from South Africa and can be considered intermediate in morphology between *No. euilus* and the South African specimens. It, therefore, seems reasonable to suggest that the specimens assigned here to *No*. cf. *No. capensis* evolved from the dentally derived populations of *No. euilus* ~3.1–2.95 Ma present in the Hadar Formation or elsewhere in contemporaneous sediments. This hypothesis is compatible with that of White and Suwa (2004), who identify *No. capensis* in Shungura Member B (B-10 and B-11, ~3.0 Ma) (McDougall et al., 2012), in the Malawi Chiwondo Beds (~4.0–2.6 Ma) (Bromage et al., 1995), and in Makapansgat (~3.0–2.6 Ma) (Harris and White, 1979; Herries et al., 2013), and propose that the apparent cladogenesis that led to the more derived *Notochoerus* could have taken place at ~2.9 Ma. Considering that the Lee Adoyta deposits and Makapansgat are roughly contemporaneous (Herries et al., 2013; DiMaggio et al., 2015), the derived *Notochoerus* specimens described here may well indicate continuity between eastern and southern African populations. More remains from Lee Adoyta and a broader analysis of late Pliocene (~3.0 Ma) *Notochoerus* are needed to shed light on this issue.

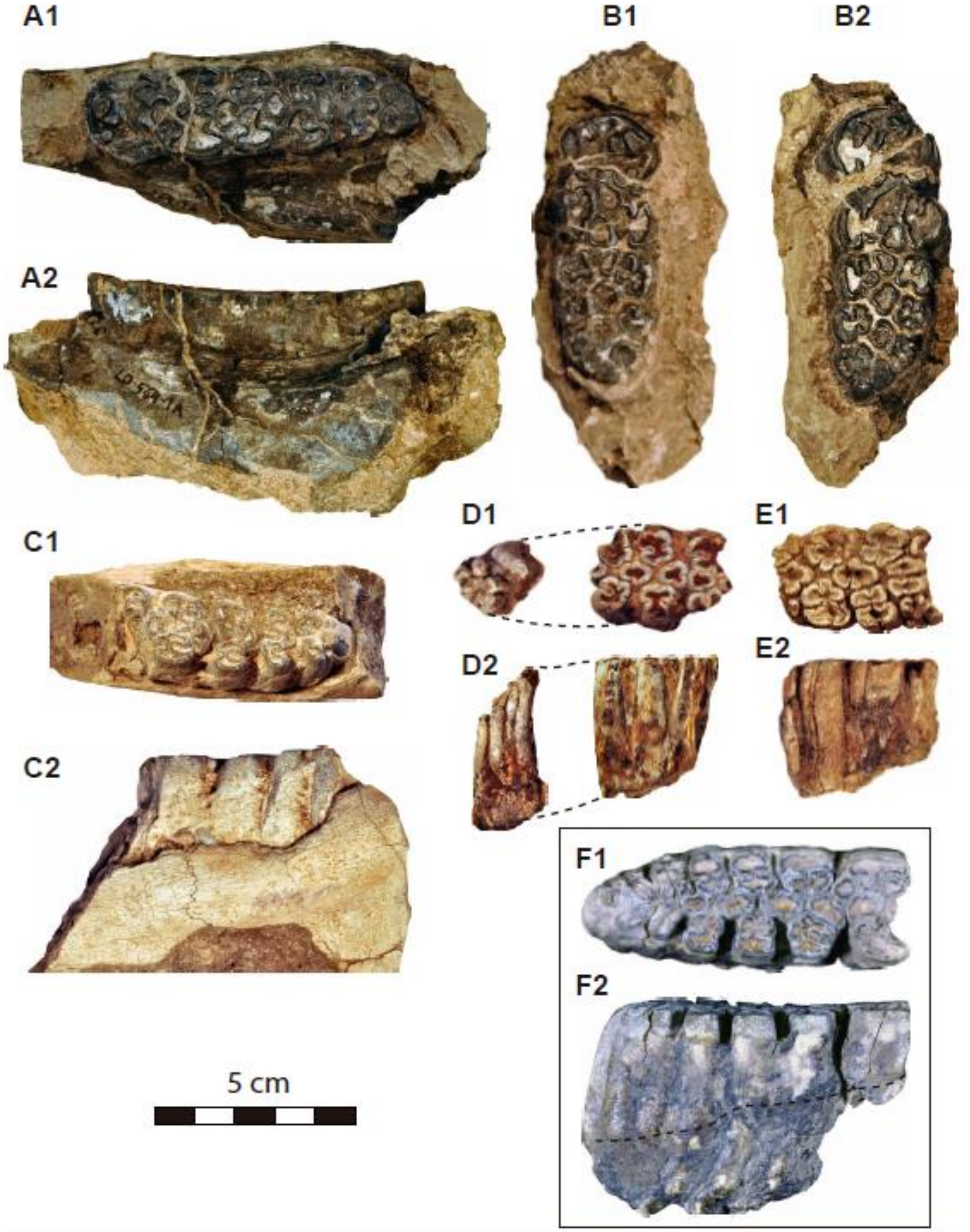

Figure 2.2. Dental remains from Lee Adoyta assigned to *Notochoerus* cf. *No. capensis*. LD 564-1 (LA), Lm3 in occlusal (A1) and labial (A2) views, and right (B1) and left (B2) M3s in occlusal view; LD 50-1 (OG), distal fragment of Rm3 in occlusal (C1) and labial (C2) views; LD 133-2, two fragments of (?R)M3 and reconstruction (dotted lines) in occlusal (D1) and lateral (D2) views; LD 298-1 (GU), fragment of LM3 in occlusal (E1)

and labial (E2) views. A RM3 of *No. scotti* has been included for comparison: OMO 75-1969-300, from Member G 12-13 (~ 2.15-2.05 Ma) for comparison in occlusal (F1) and labial (F2) views. Scale bar = 5 cm.

Table 2.1. Dental measurements (mm) of suid fossils from Lee Adoyta. Abbreviations: GU, Gurumaha. LA, Lee Adoyta. d, deciduous tooth. MD, mesiodistal diameter. MDmax, maximum mesiodistal diameter. BL, transverse diameter of the first lophe/lophid. BLp, transverse diameter of second lophe/lophid. BLpp, transverse diameter of the third lophe/lophid. Hling, maximum height of the crown in the lingual side. Hbucc, maximum height of the crown on the buccal side. M or m, molar, upper (M) or lower (m); P or p, premolar, upper (P) or lower (p). R or L, right or left; 1-, 2-, 3-, 4- denote tooth position; +, indicates minimum preserved height.

Fault block	Specimen number	Species	Tooth	Side	MD	MDmax	BL	BLp	BLpp	Hling	Hbucc
LA	LD 564-1	*Notochoerus* cf. *No. capensis*	M3	R	71.3	71.6	28.3	31.1	27.2	NA	21.2+
LA	LD 564-1	*Notochoerus* cf. *No. capensis*	M3	L	73.2	73.8	29.1	29.6	24.2	19.0+	19.0+
LA	LD 564-1	*Notochoerus* cf. *No. capensis*	m3	L	80.1	81.05	23.5	23.9	22.1	18.4+	13.2+
GU	LD 327-1	*Kolpochoerus phillipi*	m3	R	35.8	36.5	18.1	16.2	13.4	12.7+	10.0+
LA	LD 115356	*Kolpochoerus phillipi*	m3	L	40.1	40.3	NA	18.2	18.25	11.0+	8.5+
GU	LD 327-1	*Kolpochoerus phillipi*	m2	R	19.7	20.9	15.8	15.3	NA	7.3+	6.6+
GU	LD 306-1	*Kolpochoerus phillipi*	p4	R	16.1	16.7	12.6	NA	NA	14.4+	13.2+
LA	LD 586-1	*Kolpochoerus phillipi*	p4	L	16.3	17.25	13.2	NA	NA	13.3+	10.0+
GU	LD 305-1	*Kolpochoerus phillipi*	m1	R	16.4	18.45	12.1	12.2	NA	11.6+	9.4+
GU	LD 133-2	*Kolpochoerus phillipi*	m1	R	17.9	18.5	12	12.2	NA	11	10.2
GU	LD 133-2	*Kolpochoerus phillipi*	dp4	R	19.3	19.4	8.2	8.8	10	6.3+	3.9+
GU	LD 305-1	*Kolpochoerus phillipi*	dp4	R	19.2	20.4	7.65	9.1	10	6.2+	4.0+
GU	LD 381-2	*Kolpochoerus phillipi*	dp4	R	20.85	21.0	7.9	9.2	9.9	7.7+	5.4+
GU	LD 133-2	*Kolpochoerus phillipi*	dp3	R	10.2	10.45	6	NA	NA	6.7+	5.1+
GU	LD 305-1	*Kolpochoerus phillipi*	dp3	R	10.25	10.95	6.1	NA	NA	6.15+	5.5+
GU	LD 115307	*Metridiochoerus andrewsi*	M3	R	48.7	55.7	25.2	25.5	21.7	32.6+	28.1+
GU	LD 445-1	*Metridiochoerus andrewsi*	m3	L	43.9	44.9	18.5	18.2	16.9	20.4+	20.4+

4.2 *Kolpochoerus*

Subfamily Suinae Gray, 1821

Genus *Kolpochoerus* Van Hoepen and Van Hoepen, 1932

Generic Diagnosis: Modified from Harris and White (1979). Suid genus characterized by low-crowned bunodont molars similar in size and morphology to extant *Sus* or *Potamochoerus*, but typically with slightly higher crowns and thicker enamel. Some of the most derived species, such as *K. olduvaiensis* and *K. majus,* have elongated, taller, and more complex third molars. Other craniodental and mandibular features of this genus are discussed in Souron (2012).

Kolpochoerus phillipi Souron et al., 2015

Diagnosis: A species of *Kolpochoerus* with molars characterized by mesiodistally compressed lateral pillars as in *K. majus*. The holotype is an almost complete skull recovered from ~ 2.5 Ma deposits at Matabaietu (Middle Awash, Ethiopia). The M3s resemble those of *K. afarensis, K. majus,* and early *K. limnetes* from members B and C of the Shungura Formation (~ 3.44-2.53 Ma). The m3s are smaller on average than those of *K. majus* and early *K. limnetes* and they have talonids that are intermediate in development between those of *K. afarensis* and *K. majus,* with two symmetrical distal pillars and a small terminal pillar. Other craniodental and mandibular differences between *K. phillipi* and other *Kolpochoerus* are discussed in Souron et al. (2015).

Referred specimens: LD 327-1 (GU), a fragment of right mandibular corpus with m2-m3; LD 115356 (LA), a left mandibular fragment with m3; LD 304-38 (GU), a talonid of Rm3; LD 305-1 (GU), right mandibular fragment of a juvenile individual with deciduous p3-m1; LD 306-1 (GU), a right mandibular fragment an isolated mesial fragment of p3, complete p4, and fragment of m1; LD 586-1 (LA), a Rp4; LD 381-2 (GU), fragment of right mandible with dp4.

Description: LD 327-1 preserves a complete Rm2 and Rm3 together with mandibular fragments that are poorly preserved. Although the two teeth are complete, the occlusal surface shows degradation of the outer layer of the enamel, as well as the superficial layers of the mandibular corpus. The teeth are morphologically typical of Pliocene *Kolpochoerus*, with rounded bunodont and low-crowned cusps, but they are mesiodistally compressed, giving the teeth a bunolophodont aspect (Figure 2.3). The m3 is only slightly worn and has three pairs of well-developed lateral pillars that are similar in size and morphology. The last pair of lateral pillars is roughly symmetrical and is terminated by a small basal terminal pillar. There are two median pillars between the first and second pair of lateral pillars, though the mesial most one is fused to the main mesiolingual cusp. There are two median pillars between the second and third pair of lateral pillars, although the distalmost is not well-separated from the terminal cusp. There is also a buccal ectostylid between the second and third pair of lateral pillars that is almost entirely broken but that was probably well-developed before breakage.

LD 115356 is a left mandibular fragment with a moderately worn Lm3 that is fragmented mesially and missing the entire protoconid. Surface preservation of the enamel is better than in LD 327-1 and the mesiodistal compression of the main lateral pillars is also more obvious than in the former specimen. Overall, the tooth looks wider and more inflated than LD 327-1, which has a talonid that is more triangular and narrows toward its end. Indeed, the second and third lophids in LD 115356 are wider (BLp = 18.2 mm; BLpp = 18.25 mm) in comparison with LD 327-1 (BLp = 16.2 mm; BLpp = 13.4 mm). As in LD 327-1, the talonid of LD 115356 is terminated by two well-developed symmetrical pillars followed by a single central terminal pillar, which is larger than in LD 327-1.

LD 304-38 is a moderately worn distal portion of a Rm3 that preserves part of the talonid. As in LD 327-1, the talonid is composed of two pairs of well-developed symmetrical lateral pillars, the labial pillar being slightly larger than the lingual one, and a smaller terminal pillar. There are two mesiodistally compressed median pillars between the trigonid and the talonid, with the mesial one being much larger. The median pillars are flanked labially by two short ectostylids. The enamel is thick and smooth (Figure 2.3).

LD 305-1 is a well-preserved right mandibular fragment with dp3, dp4, and m1. Although the deciduous dentition is very worn, the first molar is almost unworn and has pillars that are mesiodistally compressed as in other specimens described here.

LD 381-2 preserves a dp4 that is slightly less worn than that of LD 305-1 but is, overall, similar in size and morphology.

LD 306-1 is a right mandibular fragment that preserves a complete p4, a distal fragment of m1, and a p3 that is missing a piece of its distal portion. The occlusal surfaces are well-preserved and display only slight wear, although m1 was likely more worn. The p4 is comprised of a large main central cusp (protoconid) clearly divided in two elements, the mesialmost of which is labially displaced. The tooth has a general blade-like shape, as in *Sus*, and is less expanded buccolingually than those of *Potamochoerus*. The enamel is only slightly crenulated, as in *K. afarensis*. The protoconid is continuous with both mesial and distal cingula, the mesial cingulum being much larger than the distal one.

LD 586-1 is an isolated Rp4 that is similar in size, stage of wear, and morphology to the p4 in LD 306-1. It is slightly larger than LD 306-1, with a stronger development of the distal cingulum and more prominent furrows dividing the protoconid, as well as the protoconid from the cingula (Figure 2.3).

Comparisons: I assign LD 327-1, LD 115356, LD 304-38, and LD 305-1 to *Kolpochoerus phillipi* based largely on the mesiodistal compression of their molar pillars. Additionally, LD 327-1, LD 115356, and LD 304-38 have talonids with a morphology intermediate between *K. afarensis* and *K. majus*. Most of the m3s of *K. afarensis* from Hadar, as well as those from similarly-aged sediments at Maka (~3.4 Ma) in the Middle Awash (White, 1993), differ from the Lee Adoyta specimens in that they lack a terminal basal pillar in the talonid and, in the few exceptions where they do, the talonid pillars are highly asymmetrical (Souron, 2012). The few specimens from Hadar that do have symmetrical talonids never have a terminal basal pillar. This characteristic combination (terminal basal pillar and symmetrical talonid pillars) suggests that the Lee Adoyta specimens are attributable to *K. phillipi*. The size of the m3 (MD = 36.5 mm, BL = 18.9 mm) and m2 (MD = 19.8 mm, BL = 15.7 mm) of LD 327-1 falls within the range of *K.*

phillipi from Matabaeitu ~2.5 Ma (Souron et al., 2015) but also within the range of *K. afarensis*, its most likely ancestor (Cooke, 1978; Souron, 2012) (Table 2.1; Figure 2.3).

LD 306-1 and LD 586-1 are attributed to *K. phillipi* based on the morphology of the p4 crown, specifically the division of the protoconid into two elements. Although this characteristic is not visible in the holotype of *K. phillipi* due to wear, it is present in the paratype (partial mandible MAT-VP-5/1). I note, however, that it also occurs in other suids (e.g., *Sus*). In addition, the p4 of LD 306-1 (MD = 16.6 mm, BL = 12.8 mm) and LD 586-1 (MD = 17.1 mm, BL = 13.2 mm) resemble those of *K. afarensis* in overall size (Table 2.1).

Discussion: *Kolpochoerus phillipi* was named by Souron et al. (2015) based on craniomandibular and dental material from ~2.5 Ma deposits at Matabaietu, in the Middle Awash, Ethiopia. The *Kolpochoerus* material present in the Lee Adoyta is scarce, but the remains described here have characteristics that are intermediate between *K. afarensis* from Hadar and elsewhere and the type material of *K. phillipi* from Matabaietu or the specimens from Konso ~1.9 Ma (Suwa et al., 2014) attributed to *K.* cf. *K. majus*. For example, the Lee Adoyta specimens show only incipient bunolophodonty and an intermediate degree of talonid development in comparison with later representatives of this lineage. The length of the only complete m3 (LD 327-1) falls within the lower range of those of *K. phillipi* (Souron et al., 2015) but also well within the range of variation in the Hadar sample of *K. afarensis* (Figure 2.3). The two complete p4s of LD 306-1 and LD 586-1 are wider than in *K. afarensis* and have a divided and asymmetrical protoconid, a characteristic that is rare in more primitive *Kolpochoerus* but present in the paratype of

K. phillipi. The available evidence suggests that the *Kolpochoerus* specimens from Lee Adoyta are derived from populations of *K. afarensis*, like those from Hadar and Maka, and support the phylogenetic hypothesis proposed by Souron et al. (2015), in which *K. phillipi* represents the earliest species of a clade of “bunolophodont suids” that evolved from *K. afarensis* and which includes the Pleistocene *K. majus* and the extant giant forest hog (*Hylochoerus meinertzhageni*). The Lee Adoyta specimens are the earliest known for *K. phillipi*, extending its first appearance datum to ~2.82 Ma.

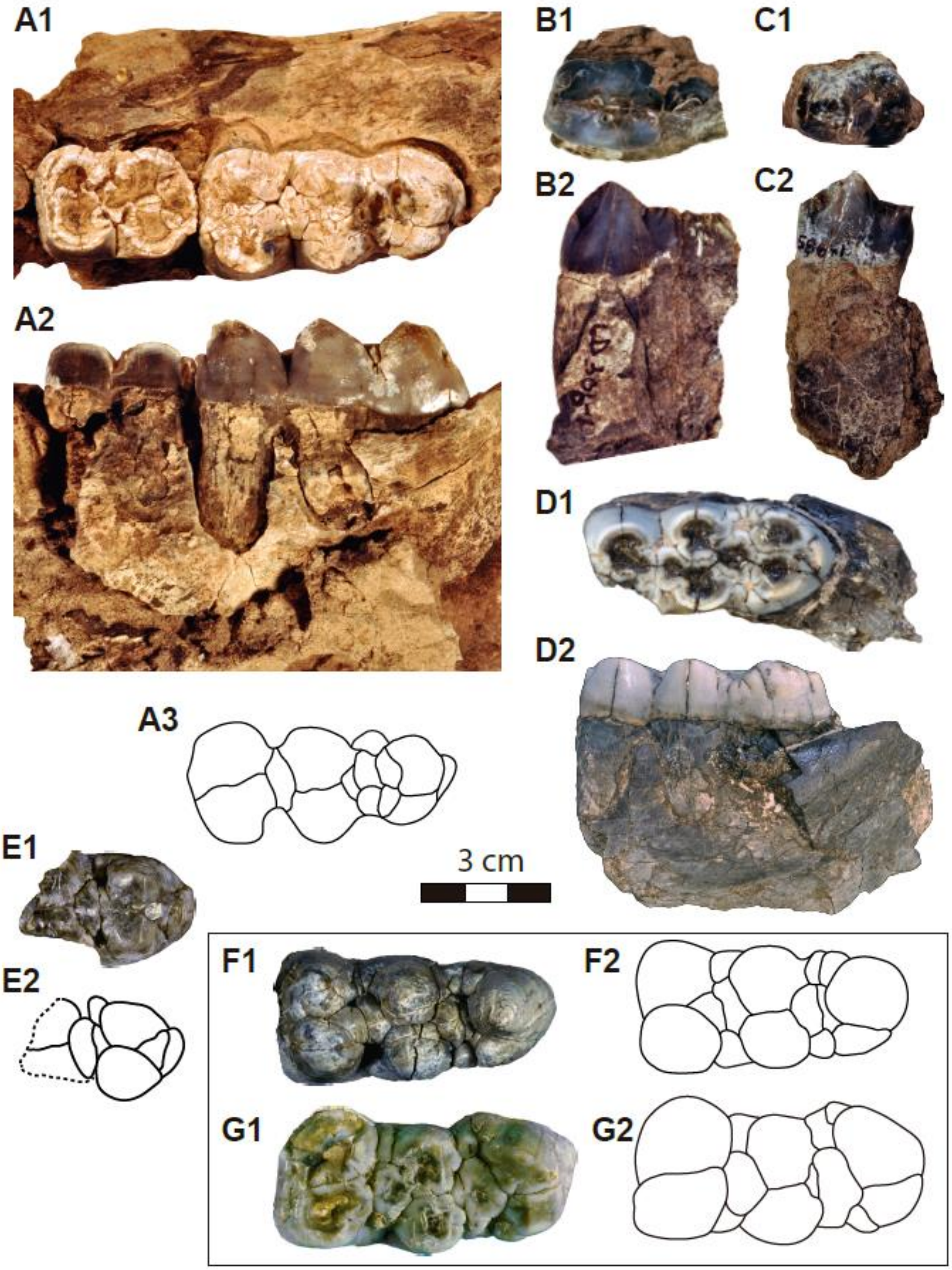

Figure 2.3. Dental and mandibular remains from Lee Adoyta attributed to *Kolpochoerus phillipi*. LD 327-1 (GU), a fragment of right mandible with m2-m3 in occlusal (A1) and lingual (A2) views, and line drawing of cusps in occlusal (A3) view; LD 306-1 (GU), a

right mandibular fragment with p4 in lingual (B1) and occlusal (B2) views; LD 586-1 (LA), a Rp4 in lingual (C1) and occlusal (C2) views; LD 115356, a left mandibular fragment with m3 in occlusal (D1) and lingual (D2) views; LD 304-38 (GU), a talonid of Rm3 in occlusal (E1) view and line drawing (E2) of the same view. Two Rm3s of *K. afarensis* have been included for comparison: A.L. 116-15 (DD-2/DD-3 submember, ~ 3.2 Ma) and A.L. 516-1 (KH-2 submember, ~ 3.0 Ma) from Hadar in occlusal views (F1 and G1) and line drawings of the same views, respectively (F2 and G2). Scale bar = 3 cm.

Kolpochoerus sp.

Referred specimens: LD 305-14 (GU), fragment of Lm3.

Description and comparisons:

LD 305-14 is a small fragment of the distalmost portion of the talonid of a Lm3. The brachydont and bunodont aspect of this fragment aligns this tooth with *Kolpochoerus*. The morphology of the talonid differs from that of the m3s assigned here to *K. phillipi* (LD 327-1, LD 306-1, LD 115356) because the two terminal cusps have different sizes, are asymmetrical, and lack a terminal central cusp.

Discussion: It is likely that all the remains of *Kolpochoerus* from Lee Adoyta belong to *K. phillipi,* as this species is present both in GU and LA, but LD 305-14 is too fragmentary to warrant specific attribution.

4.4 *Metridiochoerus*

Genus *Metridiochoerus* Hopwood, 1926

Generic diagnosis: Modified from Harris and White (1979). Earliest specimens of *Metridiochoerus* are similar to *Kolpochoerus* in overall third molar size and morphology, but advanced forms of *Metridiochoerus* tend to have longer and taller third molars that sometimes exhibit lateral flaring, as well as reduced premolars and incisors. The buccolingual compression of the molars is evident in the morphology of the crown pillars, which also tend to become columnar in more derived species. Other craniodental and mandibular characteristics of this genus are discussed in Harris and White (1979).

Metridiochoerus andrewsi Hopwood, 1926

Diagnosis: Modified from Harris and White (1979). *Metridiochoerus andrewsi* is similar in overall size and dental morphology to *K. afarensis* and *K. limnetes* but differs from the latter in having taller molars with thinner and more plicated enamel that, together with the early fusion of the major molar crown elements, result in a complex crown pattern. The molars may exhibit grooves in the flanks that give the pillars a feather-like appearance. Male crania have well-developed zygomatic knobs that are absent in females. Harris and White (1979) recognize three evolutionary stages in *M. andrewsi*, with the most advanced specimens (stage III) tending to exhibit additional pillars and an increase in both the height and length of the third molars.

Referred specimens: LD 445-1 (GU), Lm3; LD 115307 (GU), a RM3; LD 149-1 (GU), partial cranium; LD 149-2 (GU), fragments of LM3; LD 615-1 (LA), fragment of RM3 or RM2; LD 338-1 (GU) fragment of a third molar.

Description: LD 445-1 is a complete Lm3 in a small mandibular fragment (Figure 2.4). It is well-preserved and in moderate wear (WS 5), which permits a clear view of the occlusal surface. The trigonid is composed of two well-developed lateral pillars which, at this wear stage, display a mushroom or T-shaped wear pattern. The first and second lophids are separated by two circular median pillars, the most mesial of which is fused with the main mesiolingual lateral cusp. The second and third lophids are separated by two median pillars, the last of which distally contacts a large elliptical median pillar. The distal extremity of the tooth bears a smaller distolingual pillar and a well-developed terminal pillar that has mesial curvature towards the tip and is situated slightly buccally, giving an asymmetrical appearance to the distal part of the tooth. The apices of the lateral pillars of the lingual side are well-separated. The main lateral pillars are compressed buccolingually and are slightly convex towards the tip. The lateral edges of the main pillars are flat and on the buccal side they have marked vertical grooves. The enamel is thick and corrugated and there are remains of what was a layer of cementum cover.

LD 115307 is a well-preserved, complete, and lightly worn (WS 3) RM3. In lateral view, the pillars of LD 115307 are flattened in comparison with *Kolpochoerus*, *Potamochoerus*, and *Sus*, and marked by grooves that run vertically along the pillar midline. In comparison with these taxa, there are tall pillars added to the talon and these are packed closely together, which gives an asymmetrical aspect to the distal part of the tooth. The tooth measures 48.7 mm in mesiodistal length and 25.2 mm in buccolingual breadth. The maximum height is 32.6 mm, a value that is likely not far from the original height of the tooth, considering its wear.

LD 149-1 is a partial cranium that preserves the frontals, the parietals, the left orbit, and part of the right orbit (Figure 2.4). It also preserves part of the occipital and the basicranium, but the area bearing the occipital condyles and foramen magnum is broken dorsally, with a large break where the internal braincase is visible. No teeth or alveoli are preserved. A notable feature of this specimen is the presence of a large, well-preserved left zygomatic knob. Zygomatic knobs are structures that develop from the anterior part of the zygomatic. They are filled with a large sinus that is continuous with the rest of the zygomatic and can be large and laterally projecting (most often in males). In LD 149-1, the left knob has an elliptical shape and a size of about 79 mm mediolaterally and 58 mm dorsoventrally. The most lateral part of the knob is characterized by a rugose surface. In this specimen, the zygomatic knobs are oriented approximately at a 75º angle from the sagittal plane. While male zygomatic knobs are frequent within Suidae, the most important characteristic of the LD 149-1 zygomatic knob for taxonomic assignment is its location, which is immediately ventral and anterior to the orbit (there is roughly 30 mm between the inferior part of the orbit and the base of the zygomatic knob).

The orbit is round and small, ~46 mm anteroposteriorly and ~37 mm dorsoventrally and is located high on the cranium but slightly below the line of the nuchal crest. The frontals and parietals are slightly concave between the elevated orbits. The cranium tapers upwards, resembling *Phacochoerus* more so than *Sus* or *Potamochoerus*. However, at the point of minimum distance between the parietals, the posterior part of the cranial roof becomes concave, then slopes ventrally and abruptly turns into a horizontal flat surface that is oriented at a ~60º angle with the occipital. The occipital is concave and continues as a vertical structure up to the dorsal part of the foramen magnum, where the cranium is broken. The supraorbital foramina are visible but fragmented and there is a distance of 165 mm from the posteriormost part of the foramina to the posteromedial portion of the occipital crest. The minimum distance between the orbits is 125 mm while the minimum distance between the temporal lines is 67 mm. There appears to be an antemortem lesion on the top of the cranial vault, 18 mm long (anteroposteriorly) and 9 mm wide (mediolaterally), located approximately 50 mm medially and posteriorly from the top part of the left orbit. The lesion has an elliptical to subtriangular shape and its borders are continuous and rounded, with evidence of some bone healing. These characteristics suggest that the nature of the lesion is traumatic and was produced by impact with a hard-pointed object (see comparisons below).

LD 149-2 is a fragmentary and poorly preserved m3 in two small pieces. This tooth was found near the cranium described above (LD 149-1) and may belong to the same individual. It has a single terminal pillar which is accompanied by two small incipient extra cusps and columnar endostylids and ectostylids separating the terminal pillar from the last main pair of lateral pillars. There is also large median cusp separating the last pair of lateral pillars and the terminal pillar.

LD 615-1 is a mesial fragment of a right upper second or upper third molar in an advanced stage of wear. The buccolingual compression of the lateral pillars, the morphology of the cingulum, and the general aspect and size of the tooth fall within the range of variation of *M. andrewsi* specimens. This tooth was possibly larger than LD 445-1, but it is difficult to determine due to its fragmentary nature.

Comparisons: The morphology and size of LD 445-1 (MD = 44.9 mm, BL = 18.5 mm) and LD 115307 (MD = 48.7 mm, BL = 25.2 mm) are compatible with m3/M3s of early *Metridiochoerus andrewsi* (‘*M. jacksoni*’ sensu Cooke and Wilkinson, 1978) from Shungura Member C (~2.85–2.53 Ma) but slightly smaller than those from Shungura Member D (~2.53–2.40 Ma) based on Cooke's (2007) measurements (Table 2.1; Figure 2.4). The partial cranium LD 149-1 has zygomatic knobs that are typical of *M. andrewsi* males and differ from all other fossil suids. The zygomatic knobs, however, are oriented at a ~75º angle relative to the midline of the skull, which contrasts to the younger specimens of *M. andrewsi* from Koobi Fora, KNM-ER 1210 and KNM-ER 1644 (KBS, ~1.87–1.5 Ma) and KNM-ER 2708 (upper Burgi, ~1.95–1.87 Ma) (McDougall et al., 2012), where these structures are almost perpendicular (~90º angle) (Harris, 1983). A new male cranium UW-88-1300 from Malapa, South Africa (~1.98 Ma), tentatively referred to *M. andrewsi*, also has more perpendicularly-oriented knobs (Lazagabaster et al., 2018) in comparison with LD 149-1. In the Tetraconodontinae and in *Kolpochoerus*, these knobs are located more ventrally in relation to the orbit and further laterally from it.

Discussion: White et al. (2006) described an M3 from the Usno Formation (northern Turkana Basin, Ethiopia) and a mandibular fragment from the Nachukui Formation (West Turkana, Kenya) as belonging to *Metridiochoerus*, both dated to ~3.4 Ma. Cooke (2007) also identified a single specimen of *Metridiochoerus*, attributed to *Metridiochoerus* cf. *M. shawi* in the older deposits of the Shungura Formation (Member B, ~3.44–2.85 Ma). (Cooke, 2007). The first record of *Metridiochoerus* in the Awash Valley is found in the Hata Member of the Bouri Formation ~2.5 Ma (Heinzelin et al., 1999). The remains of

M. andrewsi from the Lee Adoyta described here are the earliest in the Awash Valley, extending its Awash record to ~2.82 Ma. Work in progress, however, suggest the presence of this species in of Hadar KH2, the uppermost member of the Hadar Formation (~3.0 Ma). Furthermore, LD 149-1 is the earliest known cranium of *M. andrewsi* and of the genus *Metridiochoerus* in all eastern Africa. In southern Africa, the earliest known occurrence of *Metridiochoerus* (*M. shawi*) is found at Makapansgat (~3.0–2.6 Ma), (Cooke, 2005; Herries et al., 2013) though some authors contest this genus attribution and instead use *Potamochoeroides* for the Makapansgat specimens (Bender, 1992; Pickford, 2013). The Lee Adoyta *M. andrewsi* cranium already displays the knobs typical of male specimens seen in crania from the Pleistocene deposits of Koobi Fora (upper Burgi and KBS, ~1.95–1.5 Ma) and Malapa (~1.98 Ma), though these knobs are oriented at a lower angle (~75º), suggesting that these structures became more perpendicular through time in the *M. andrewsi* lineage.

The traumatic lesion present on the cranial roof of LD 149-1 may have been caused by the attack of a carnivore or, alternatively, by the lower canine of a rival during male-to-male combat. Such behavior is typical of extant suid species (Meijaard et al., 2011). For example, extant suids with broad heads and long tusks (e.g., giant forest hogs *Hylochoerus* and warthogs *Phacochoerus*) usually engage in fights that can result in severe injuries (Meijaard et al., 2011).

LD 445-1 and LD 115307 third molars from the GU fault block are similar to other specimens of *M. andrewsi* from the earliest members of the Shungura Formation (Member B and C, ~3.44–2.53 Ma). Only one M3 of *M. andrewsi* is known from the LA fault block (LD 615-1) and although it is fragmented, it would possibly have been longer than LD 115307 and more similar to specimens of *M. andrewsi* stage II *sensu* Harris and White (1979) found in Member D through Member G of the Shungura Formation (~2.53–1.90 Ma) (McDougall et al., 2012). This is compatible with the younger age of the LA fault block deposits (~2.67 Ma).

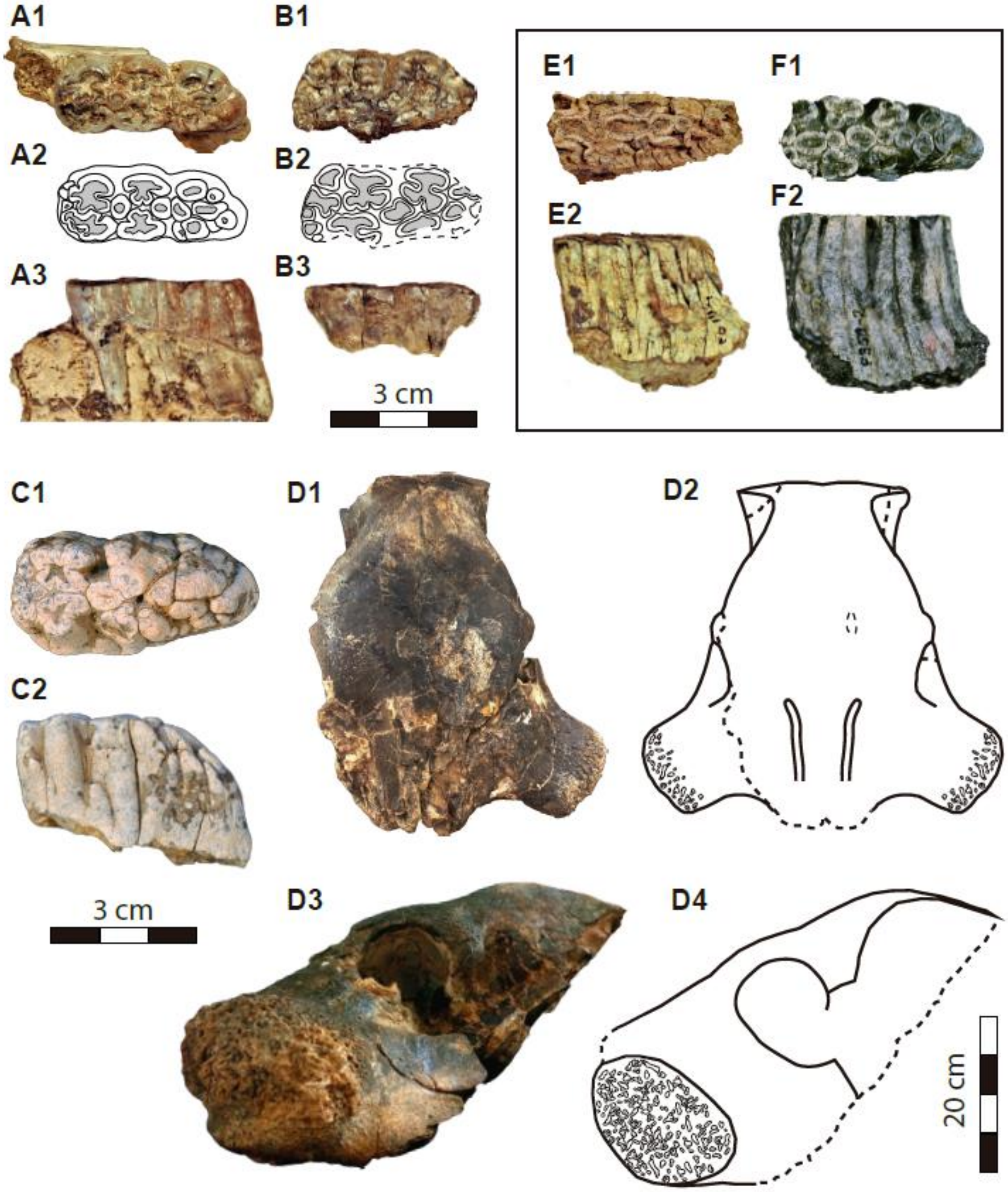

Figure 2.4. Craniodental remains of *Metridiochoerus* from Lee Adoyta. *Metridiochoerus andrewsi*: LD 445-1 (GU), complete Lm3 in occlusal (A1-A2) and lingual (A3) views; LD 615-1 (LA), mesial fragment of Lm3 in occlusal (B1-B2) and lingual (B3) views; LD 115307, RM3 in occlusal (C1) and buccal (C2) views. LD 149-1 (LA), partial male cranium that preserves the left zygomatic knob in dorsal view (D1) and line drawing of mirrored reconstruction in the same view (D2) and left lateral (D3-D4) views.

Metridiochoerus sp.: LD 111-1 (GU), a fragment of (?R)M3 in occlusal (E1) and lingual (E2) views, compared to a (?R)M3 of *M. compactus* from Shungura Member L (~ 1.38-1.05 Ma): F 358-2, in occlusal (E1) and lingual (E2) views. Scale bar = 3 cm except for D1-D4 (= 20 cm).

Metridiochoerus sp.

Referred specimens: LD 111-1 (GU), fragment of a (?L)M3;

Description and comparisons: LD 111-1 is a (?L)M3 that is missing part of the mesial and distal portions of the tooth (Figure 2.4). This specimen is poorly preserved and heavily worn, as evidenced by the large dentine lakes in the occlusal plate due to the fusion of pillars. While the arrangement of the pillars is clearly metridiochoere, this tooth differs from *M. andrewsi*, and in particular from the specimens described above, in several characteristics. First, LD 111-1 would have been mesiodistally longer (if complete) than the complete M3 (LD 115307) from the GU fault block, though how much longer is difficult to determine. Second, LD 111-1 would have been taller (preserved height = 35.0+ mm) than LD 115307 (preserved height = 32.6+ mm), especially when considering that LD 115307 is minimally worn while LD 111-1 is very worn. Third, the base of LD 111-1 flares distally, while the distalmost portion of LD 115307 has a profile that is convex in lateral view. The distal flaring of LD 111-1 is a characteristic only present in derived metridiochoeres and in *Phacochoerus*. Finally, the pillars in LD 111-1 are buccolingually compressed and have a more parallel arrangement than in LD 115307. In general, LD 111-1 has morphological affinities with more derived metridiochoeres, such as *M. hopwoodi* and *M. compactus* (see Figure 2.4 for comparison with *M. compactus* (F 358-2) from Member L of the Shungura Formation ~1.38–1.05 Ma).

Discussion: The height and morphology of this LD 111-1 suggest it belongs to a dentally derived metridiochoere, closer to *M. hopwoodi* or *M. compactus* than to the comparatively primitive *M. andrewsi* (Harris and White, 1979), but its poor preservation prevents further attribution.

4.5 Suidae indet. (postcrania)

Referred specimens: Astragali: (left) LD 573-1 (LA), LD 131-3 (LA), LD 80-1 (LA); (right) LD 709-2 (GU). LD 568-1 (OG), juvenile R navicular, RMC III, RMC IV, RMC V.

Description and comparisons: The Lee Adoyta suid postcrania include four complete astragali. These astragali differ in size and metrically span the entire range of extant African suids and fossil suids from Hadar in my database (Table 2.1; Figure 2.5). LD 573-1 is slightly larger than all astragali from Hadar. The largest suids at Hadar are *No. euilus* and *Nyanzachoerus pattersoni*, but no *Nyanzachoerus* craniodental remains are known from Lee Adoyta, so this astragalus likely belongs to a large *Notochoerus*, possibly a male. LD 131-3 is large and may also belong to *Notochoerus* but, by comparison, is a much smaller individual than LD 573-1. LD 80-1 fits well within the range of extant *Hylochoerus* in overall size, suggesting that this astragalus is more likely to belong to either *Metridiochoerus* or *Kolpochoerus*. Finally, there is a very small astragalus, LD 709-2, comparable in size to a small female of *Potamochoerus* or *Phacochoerus*. Considering the range of variation in extant and fossil suids and strong sexual dimorphism, it is possible that this astragalus belongs to a small individual (likely female) of *Kolpochoerus* or *Metridiochoerus*. It is also possible, however, that this astragalus belongs to a juvenile (astragali have a single center of ossification, so that they get larger through ontogeny but do not show epiphyseal lines as in long bones), but the main facets and morphological features seem already well developed.

LD 568-1 is a group of juvenile right forelimb bones, including a complete MC IV that preserves an unfused distal epiphysis, a MC III missing its distal epiphysis, the proximal part of the MC V, and a complete navicular. Their large size aligns them with known postcrania of *Notochoerus*.

Discussion: Overall, size variation in the Lee Adoyta astragali support the presence of two or possibly three suid taxa with different body sizes, which is consistent with the craniodental evidence: a large *Notochoerus* and one or two suids of medium body size, either *Kolpochoerus* or *Metridiochoerus*. Although I do not formally attribute them to the genus- or species- level, I provide potential identifications based on size in Table 2.2.

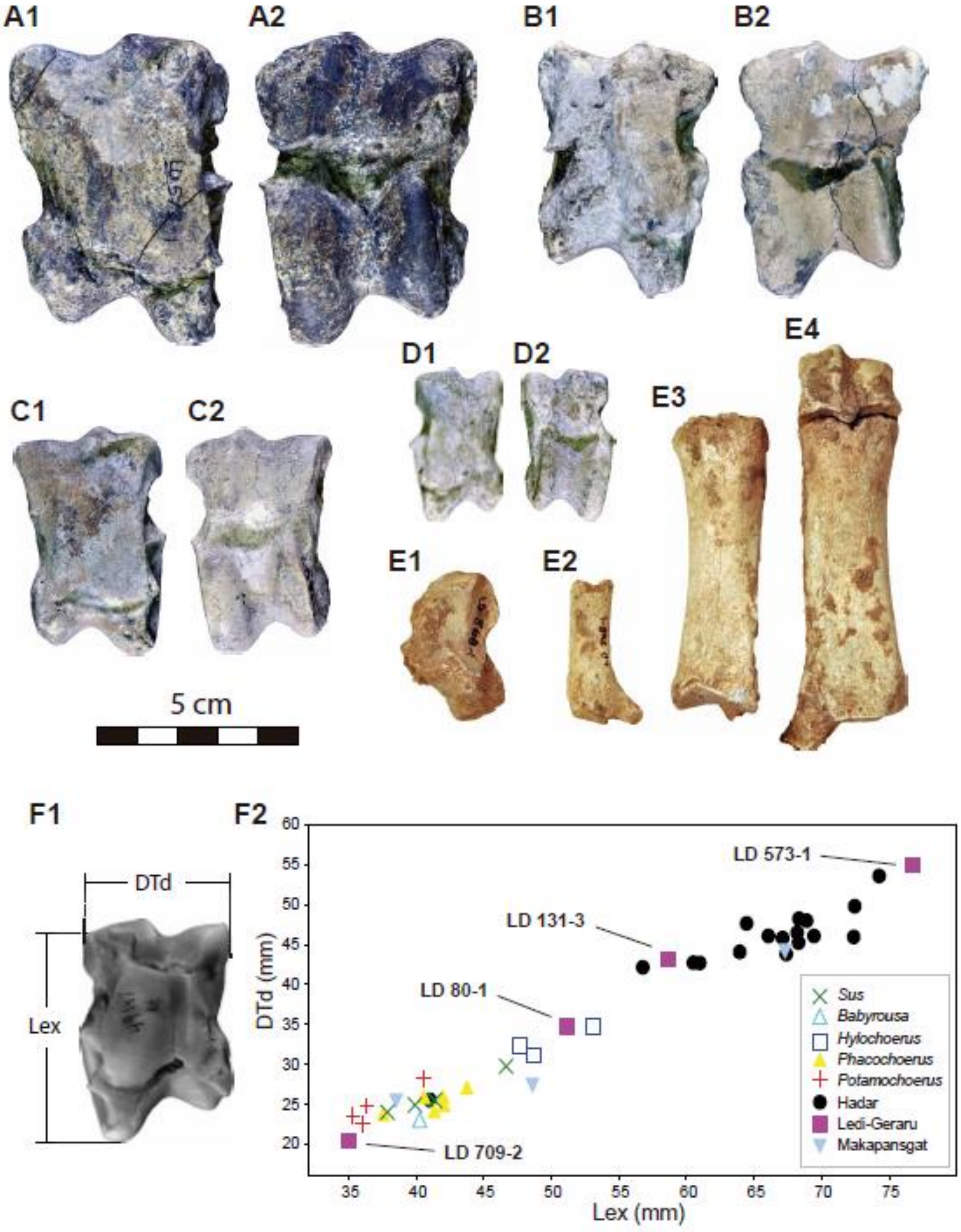

Figure 2.5. Postcranial remains from Lee Adoyta. Astragali in ventral (A1-D1) and dorsal (A2-D2) views: LD 573-1 (LA): left (A1-A2); LD 131-3 (LA): left (B1-B2); LD 80-1 (LA), left (C1-C2); LD 709-2 (GU): right (D1-D2). LD 568-1 (OG), juvenile right navicular (E1), MC V (E2), MC IV (E3), and MC III (E4). Scale bar = 5 cm. Scatter plot of distal transverse width (BLd) and external maximum length (Lex) of astragali from

Lee Adoyta and fossil suid astragali from Hadar and Makapansgat, as well as extant African suid taxa (F1-F2).

Table 2.2. Measurements (mm) for extant and fossil suid astragali. The summary metrics for the astragali that are not from Ledi-Geraru (i.e., extant species and those from Hadar and Makapansgat) are shown as ‘Mean [n; standard deviation]’. Abbreviations: GU, Gurmaha; LA, Lee Adoyta; DTd, transversal diameter of the astragalus measured distally; Lex, maximum length of the astragalus measured in the external (lateral) side; R, right; L, left.

Specimen Number	Site	Fault block	Taxon	Side	Lex	DTd
LD 709-2	Ledi-Geraru	GU	?*Kolpochoerus/Metridiochoerus* sp.	R	35.0	20.5
LD 80-1	Ledi-Geraru	LA	?*Kolpochoerus/Metridiochoerus* sp.	L	51.1	34.7
LD 131-3	Ledi-Geraru	LA	?*Notochoerus* sp.	L	58.7	43.2
LD 573-1	Ledi-Geraru	LA	?*Notochoerus* sp.	L	76.7	54.9
	Hadar		*Notochoerus/Nyanzachoerus* sp.		66.8 [16; 4.6]	66.8 [16; 2.9]
	Hadar		*?Kolpochoerus afarensis*		41.0 [1; NA]	25.6 [1; NA]
	Makapansgat		*Notochoerus capensis*		67.3 [1; NA]	44.2 [1; NA]
	Makapansgat		*Metridiochoerus* (=*Potamochoeroides*) *shawi*		43.5 [2; 7.1]	26.4 [2; 1.4]
	Extant		*Phacochoerus* spp.		41.2 [6; 2.1]	25.4 [6; 1.3]
	Extant		*Potamochoerus* spp.		37.1 [4; 2.4]	24.8 [4; 2.4]
	Extant		*Sus* spp.		41.4 [4; 3.7]	26.1 [4; 2.6]
	Extant		*Babyrousa babyrussa*		40.3 [1; NA]	23.1 [1; NA]
	Extant		*Hylochoerus meinertzhageni*		49.8 [3; 3.7]	32.8 [3; 1.8]

5. Discussion

The fossiliferous sedimentary deposits of the GU, LA, and OG fault blocks of Lee Adoyta sample a time period from the latest Pliocene and earliest Pleistocene of the LAV between ~2.82 and <2.5 Ma that was previously poorly represented (DiMaggio et al., 2015). A preliminary study of the associated fauna revealed a possible faunal turnover and a shift to more open habitats in the LAV between ~2.95 Ma (KH-2, youngest submember of the Hadar Formation) to ~2.82 Ma (DiMaggio et al., 2015). This hypothesis has been supported by extensive studies of the giraffids (Rowan et al., 2017) and bovids from Lee Adoyta (Bibi et al., 2017). Here, I discuss the implications of the fossil Suidae from Lee Adoyta for late Pliocene faunal turnover and paleoecological change by combining isotopic and faunal abundance data from Woranso-Mille (~3.76–3.57 Ma), Hadar (~3.42–2.95 Ma), and Lee Adoyta (~2.82 to <2.5 Ma) to construct a synthetic record of suid evolution in the LAV during this time.

5.1 Taxonomic turnover

The species composition of suids differs between Hadar and Lee Adoyta – Hadar suids are *Nyanzachoerus pattersoni*, *Notochoerus euilus*, and *Kolpochoerus afarensis*, while Lee Adoyta suids are *No.* cf. *No. capensis*, *K. phillipi*, and *Metridiochoerus andrewsi* (Table 2.3; Figure 2.6). Taken at face value, namely on differences in species-level identifications, the Hadar to Lee Adoyta transition between ~2.95–2.82 Ma may appear consistent with high taxonomic turnover during the late Pliocene, as suggested by (Vrba, 1985, 1993, 1995) for large mammals and others (Cooke, 2007) for suids in particular. I emphasize, however, that at the lineage-level the Hadar and Lee Adoyta suid assemblages are actually very similar, as it is likely that Lee Adoyta *No.* cf. *No. capensis* and *K. phillipi* are probably derived from Hadar *No. euilus* and *K. afarensis*, respectively.

The single significant taxonomic difference between the Hadar and Lee Adoyta suid assemblages amounts to the disappearance of *Nyanzachoerus* and the appearance of *Metridiochoerus* (Table 2.3; Figure 2.6). At Hadar, *Nyanzachoerus* is present only in the

Sidi Hakoma and Denen Dora members (though only few specimens have been found in DD; Cooke, 1978) of the Hadar Formation (~3.42–3.20 Ma) and therefore the absence of this primitive tetraconodontine genus at Lee Adoyta is not surprising. The last appearance of *Nyanzachoerus* in all eastern Africa is likely Member B of the Shungura Formation (Boisserie et al., 2008; Bishop, 2010), implying its extinction by at least ~3.0 Ma. On the other hand, the suine genus *Metridiochoerus* first appears in eastern Africa ~3.4 Ma in the Nachukui, Usno, and Shungura Formations (White et al., 2006; Cooke, 2007). The ~2.82 Ma Lee Adoyta specimens represent the earliest record of this genus in the Awash Valley, which – despite having few turnover implications – does have important paleoecological implications, as discussed in Section 5.2 below.

The turnover patterns of Suidae from Hadar to Lee Adoyta are congruent with those described for the bovids and giraffids (Bibi et al., 2017; Rowan et al., 2017). For example, although there are new species of bovids at Lee Adoyta with no immediate ancestors in the Hadar Formation or the LAV in general (e.g., *Beatragus vrbae*, *Kobus sigmoidalis*, and cf. *Menelikia lyrocera*), others have likely ancestors at Hadar (e.g., *Tragelaphus rastafari/nakuae* and possibly the large *Aepyceros*). Furthermore, some bovid taxa persist through the Hadar-Lee Adoyta sequence more or less unchanged (e.g., *Parmularius* aff. *pachyceras* and *Ugandax coryndonae*). The giraffid record is similar, with *Sivatherium maurusium* and the *Giraffa stillei-G. gracilis* lineage persisting through the entire LAV sequence from ~3.42–2.60 Ma. Conclusive evidence for the absence of *G. jumae* at Lee Adoyta is hampered by the small sample size from the late Pliocene sediments (*n* < 20 giraffid fossils), but I consider this likely. Thus, overall, the bovid, giraffid, and suid records show similar turnover patterns across the Hadar-Lee Adoyta sequence: although a handful of new taxa appear in Lee Adoyta, many others clearly sample single lineages through time. This conclusion also applies to the Lee Adoyta early *Homo* mandible (LD 350-1), which possesses a morphology strongly suggestive of its derivation from *Australopithecus afarensis* or an *A. afarensis*-like species during this time (Villmoare et al., 2015).

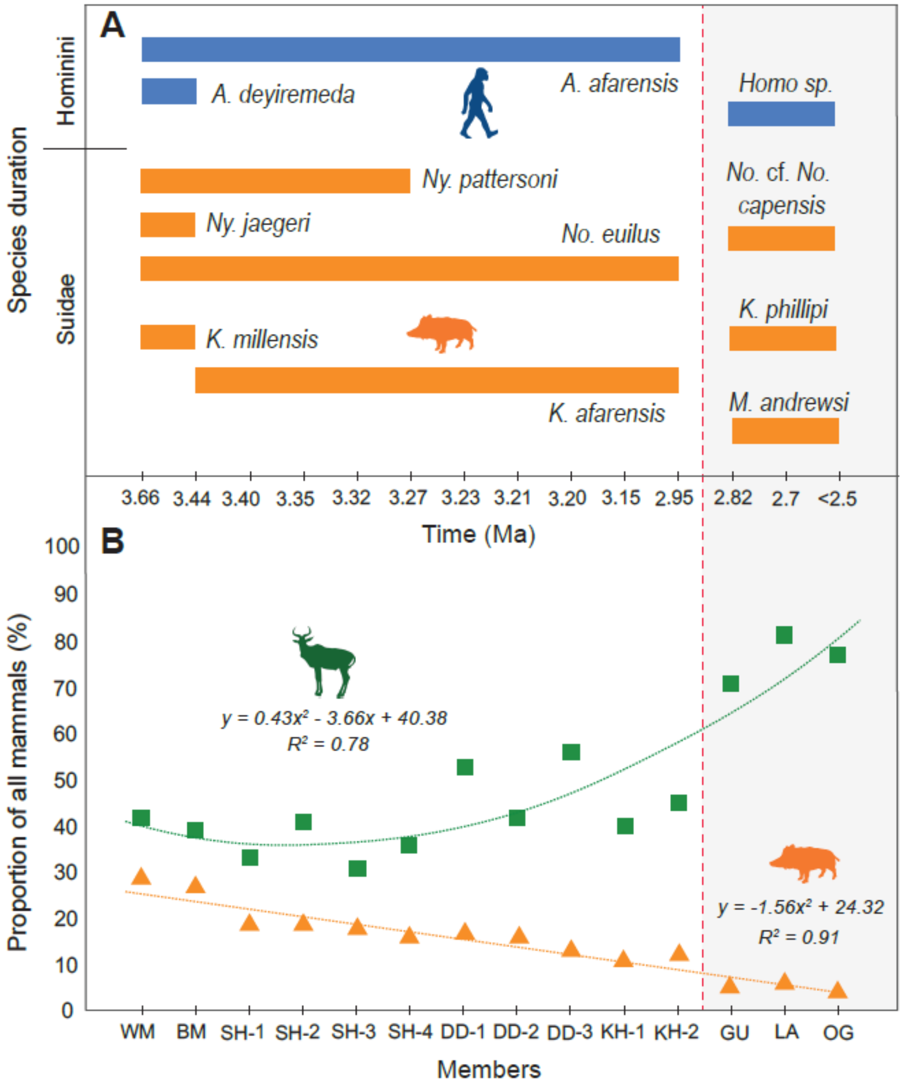

Figure 2.6. Turnover and abundance of suids in the lower Awash Valley. A) Chronogram of species duration of suids (in orange) and hominins (in blue). Abbreviations: A., *Australopithecus*; Ny., *Nyanzachoerus*; No., *Notochoerus*; K., *Kolpochoerus*; M., *Metridiochoerus*. B) Relative abundance in proportion to all mammals, of suids (in orange) and bovids (in green) through time. Note the linear decline of suid abundance through the LAV sequence. The bovid abundance pattern fits better a polynomial trend, with an abundance peak in Lee Adoyta. Abbreviations: WM, Woranso-Mille; BM, Basal Member; SH, Sidi Hakoma Member; DD, Denen Dora Member; KH, Kada Hadar Member; GU, Gurumaha Fault Block; LA, Lee Adoyta Fault Block; OG, Ogoyta Fault Block. The red dotted line indicates the hypothesized turnover in suid species composition and suid abundance, possibly triggered by habitat changes in the LAV ~ 2.95-2.82 Ma.

Table 2.3. Suid taxa present in the lower Awash Valley between ~ 3.76 Ma to < 2.5 Ma, with sites arranged chronologically from oldest to youngest from left to right. Data from Curran and Haile-Selassie (2016), Reda et al. (2017), Cooke (1978, 2007) and this work. Abbreviations: WM, Woranso-Mille; SH, Sidi Hakoma; DD, Denen Dora; KH, Kada Hadar; GU, Gurumaha; LA, Lee Adoyta; OG, Ogoyta.

Species	WM	SH	DD	KH	GU	LA	OG
	3.76-3.57 Ma	3.42-3.24 Ma	3.24-3.20 Ma	3.20-2.95 Ma	2.82 Ma	2.70-2.60 Ma	< 2.50 Ma
Nyanzachoerus pattersoni	X	X	X				
Nyanzachoerus jaegeri	X						
Notochoerus euilus	X	X	X	X			
Notochoerus cf. *No. capensis*					X	X	X
Kolpochoerus millensis	X						
Kolpochoerus afarensis		X	X	X			
Kolpochoerus phillipi					X	X	
Metridiochoerus andrewsi					X	X	

5.2 Dietary change

The compilation of stable carbon isotope ($\delta^{13}C$) data of suid enamel from the LAV is shown in Figure 2.7. The $\delta^{13}C$ data from the ~ 2.82 Ma GU fault block show that Lee Adoyta *K. phillipi* and *No.* cf. *No. capensis* relied heavily on C_4 plants, whereas their Hadar ancestors consumed a greater mixture of C_3 and C_4 plants. For *Kolpochoerus*, there is a steady trend towards a greater incorporation of C_4 resources through time – Sidi Hakoma, Denen Dora, and Kada Hadar specimens of *K. afarensis* have medians that fall within the range of C_3-C_4 mixed feeders but become more positive through time, whereas the upper interquartile and median of Lee Adoyta *K. phillipi* specimens falls close to the breakpoint of grazers and hypergrazers (>1 ‰). For *Notochoerus*, a temporal trend is less clear – Woranso-Mille (~3.7–3.6 Ma) specimens of *No. euilus* consumed a significant proportion of C_4 resources, whereas those from the Hadar Formation fall near the breakpoint of C_4 and C_3-C_4 mixed feeders. Compared to Hadar, however, the ~2.82 Ma GU fault block specimens of *No.* cf. *No. capensis* show a shift to a greater reliance on C_4 grasses compared to *No. euilus* (Figure 2.7). These data are consistent with those of other ungulate lineages, such as *Sivatherium*, which shows a shift in $\delta^{13}C$ values from the Hadar Formation to Lee Adoyta indicating a greater reliance on C_4 resources during the late Pliocene (Robinson et al., 2017).I note that though C_4 resource consumption in suids peaks ~2.82 Ma, specimens from the LA and OG fault blocks did consume a mix of C_3-C_4 vegetation, but this pattern may be due to the small sample size in these fault blocks (see Figure 2.7).

Although I believe that it is likely that the C_4 resources consumed by the Lee Adoyta suids were C_4 grasses, I note other possibilities here. First, it is possible that the C_4 isotope signal comes from succulents (Crassulacean acid metabolism, CAM). However, I consider this explanation unlikely as it has been proposed that CAM plants did not comprise a significant proportion of plant biomass in the eastern African Plio-Pleistocene (Cerling et al., 2003; Kingston, 2011).Second, it is possible that the C_4 isotopic signal of the Lee Adoyta suids comes in part from dicotyledonous shrubs of Chenopodiaceae and Amaranthaceae, which utilize the C_4 photosynthetic pathway. Fossil pollen data suggest that the proportion of Chenopodiaceae and Amaranthaceae varied throughout the eastern African Plio-Pleistocene, with a peak in abundance ~2.6 Ma during a period of marked aridity (Bonnefille, 2010). Extant suids, such as forestdwelling *Hylochoerus meinertzhageni* (d'Huart and Kingdon, 2013), are known to consume these C_4 shrubs, although they are of relatively low in abundance in most savanna landscapes.

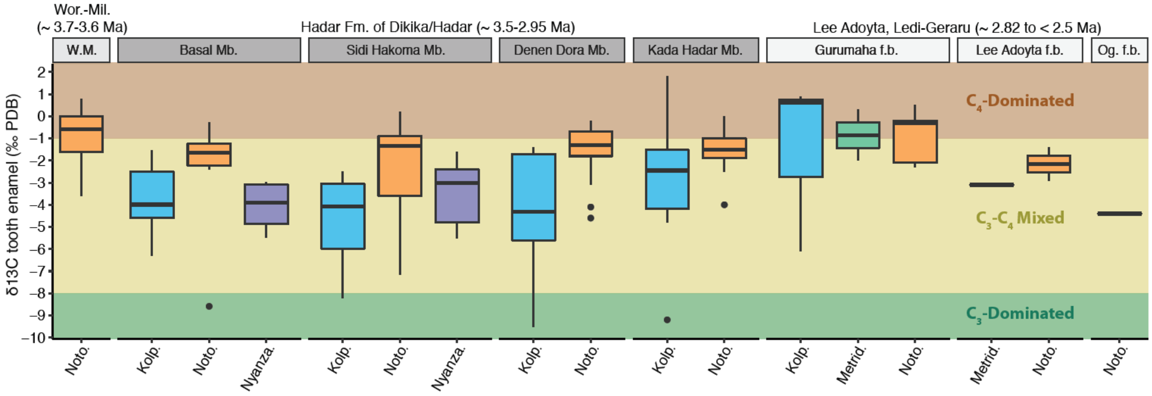

Figure 2.7. Boxplot compilation of enamel δ^{13}C values for suid genera in the lower Awash Valley. The background colors denote C_4-dominated diets (δ^{13}C = -1 to 2 ‰, in brown), C_3-C_4 mixed diets (δ^{13}C = -1 to -8 ‰, in yellow), and C_3-dominated diets (δ^{13}C = -8 to -10 ‰, in green) Abbreviations: Noto, *Notochoerus* (in orange); Kolp, *Kolpochoerus* (in blue); Nyanza, *Nyanzachoerus* (in purple); W.M., Woranso-Mille; Fm., formation; Mb., member; f.b., fault block.

5.3 Late Pliocene paleoecology in the LAV

A shift towards more open and possibly arid environments in the LAV during the late Pliocene has been suggested based on paleoecological studies of the bovids (Bibi et al., 2017), giraffids (Rowan et al., 2017), and mammal faunas as a whole (DiMaggio et al., 2015), as well as stable carbon isotopes (δ13C) of herbivore enamel (Robinson et al., 2017). Here, I build on these studies by discussing in detail the implications of the Lee Adoyta suids for late Pliocene paleoecological change in the LAV from ~3.76 Ma (Woranso-Mille) to <2.5 Ma (OG fault block).

Previous studies using multivariate correspondence analyses of the large mammal functional trait structure of Plio-Pleistocene LAV faunas indicated a shift to lower precipitation and higher temperature seasonality through time, with major differences between the mid-Pliocene and Hadar Formation and the late Pliocene sediments of Lee Adoyta (DiMaggio et al., 2015; Robinson et al., 2017). The Lee Adoyta mammal faunas are dominated by terrestrial grazers, mostly ungulates that favor open and grassy habitats, which contrasts with the older Hadar Formation faunas that are characterized by C_3-C_4 mixed feeders and a taxonomically diverse mixture of terrestrial and arboreal species. For example, the only non-hominin primate species found at Lee Adoyta is the large-bodied, C_4-consuming *Theropithecus*, whereas the Hadar Formation yields a diverse monkey fauna including species of *Parapapio*, *Cercopithecoides*, and cf. *Rhinocolobus*, in addition to *Theropithecus* (Campisano et al., *in press*).

The study of the Lee Adoyta Suidae support the dominance of open, drier, and more seasonal habitats based on both the morphological and isotopic evidence from the *Kolpochoerus* and *Notochoerus* lineages (discussed above in Section 5.2), as well as the first appearance of *Metridiochoerus* in the LAV ~2.82 Ma. The fossil genus *Metridiochoerus* consists of multiple lineages of hypsodont, hyper-grazing suids that gave rise to warthogs (*Phacochoerus* spp.) by at least ~1.0 Ma (Harris and Cerling, 2002; Souron, 2017). Living warthogs are the most arid-adapted of all extant suids, with the desert warthog (*Phacochoerus aethiopicus*) favoring semi-desert bushland and thicket in the Horn of Africa and the common warthog (*Ph. africanus*) favoring mosaics of grassland and open woodlands in eastern and southern Africa savannas (Cumming, 2013; Grubb and D'Huart, 2013). Both *Phacochoerus* species have exaggerated craniodental morphologies related to specialization for the consumption of abrasive grasses and their enamel $\delta^{13}C$ values classify them as C_4 hyper-grazers (Harris and Cerling, 2002). The strong similarities in craniodental morphology and ecology inferred from stable carbon isotopes between fossil species of *Metridiochoerus* and their living descendants *Phacochoerus* (Souron, 2017) implies strong dietary and, by extension, habitat niche conservatism in this lineage since the Pliocene. I therefore propose that the appearance of *Metridiochoerus* in the LAV ~2.82 Ma supports a marked habitat shift at this time because it is unknown at present from the from older LAV sediments, such as those of the mid-Pliocene Hadar Formation, despite having appeared in eastern Africa by at least ~ 3.4 Ma (White et al., 2006; Cooke, 2007) or possibly as early as ~3.8 Ma (Souron, 2012).

Considering the entire LAV sequence from ~3.76 Ma Woranso-Mille to the <2.5 Ma OG fault block, one of the most interesting paleoecological patterns concerns the trends in the relative abundance of suids compared to bovids. For example, in the late Pliocene sediments of Lee Adoyta, suids comprise only 2–4% of the large mammal fauna, whereas they comprise 23–49% of those from the older sediments of Woranso-Mille and Hadar (Figure 2.6). On the other hand, bovids comprise ~28–51% of the Woranso-Mille and Hadar faunas, but overwhelmingly dominate (~64–74%) those from Lee Adoyta. Regression-fitting of these changes through time shows that the abundance patterns of suid decline and bovid increase from the mid- to late Pliocene were markedly different in nature: suid declines are best fit by a linear model ($y = 1.56x^2 + 24.32$, $R^2 = 0.91$) whereas those of bovids are best fit by a polynomial equation ($y = 0.43x^2 – 3.66x + 40.38$, $R^2 = 0.78$), with a spike in bovid abundances between ~2.95–2.82 Ma (Figure 2.6).

A similar pattern was reported from the Shungura Formation by Bobe and Behrensmeyer (2004), who showed a steady decline of suids and an increase in bovid abundances between ~4.0–2.75 Ma. Additional specimens and new analyses of the ~4.0 Ma faunas of the Mursi Formation, lower Omo Valley, support this pattern. The Mursi Formation data presented in Drapeau et al. (2014) show that suids comprise ~44% of the faunas, with a shift towards bovid-dominated faunas in the lower Omo Valley occurring around ~3.0 Ma.

For the LAV, the differences in the regression-fits of suid and bovid abundance patterns through time (Figure 2.6) suggest distinct drivers of paleoecological change in these groups. I propose that the linear decline of suid abundance is related to a steady increase in grassy over woody habitats through time. This grassy trend is supported by comprehensive paleosol datasets from the Awash Valley (Levin et al., 2011) and eastern Africa as a whole (Cerling et al., 2011), as well as from community analyses of the LAV faunas (DiMaggio et al., 2015; Robinson et al., 2017). For example, although the Hadar fauna collectively indicates a mixed grassy-woody environment, multivariate analyses of the large mammal community (Reed, 2008) document a noticeable trend towards the top of the sequence towards drier environments similar to bushland-thicket, especially in the uppermost unit of the Hadar Formation (KH-2 submember). Even KH-2, however, contrasts with the reconstructed environments of Lee Adoyta, which community analyses suggest sample a relatively open grassland like those of the Serengeti Plains today (DiMaggio et al., 2015). Extant suid species, including relatively arid-adapted *Phacochoerus* spp., prefer habitats with some tree cover, and therefore I propose that a trend towards more open habitats is a likely environmental driver behind their gradual decline in abundance through time in the LAV.

In contrast to the linear decline of suids through time, the LAV abundance data show a marked increase in bovid abundances between the ~2.95 Ma KH-2 submember of Hadar and the ~2.82 Ma GU fault block of Lee Adoyta (Figure 2.6). Bovids are a more ecologically diverse clade than suids, with tribes ranging in habitat preference from those favoring relatively woody and mesic environments (e.g., Aepycerotini and Tragelaphini) to those favoring grassy and arid environments (e.g., Alcelaphini and Antilopini) (Kingdon, 2013). Thus, although the shift from woody-grassy habitats at Hadar to open and grassy habitats at Lee Adoyta can explain changes in the relative abundance of bovid tribes (e.g., why Alcelaphini dominate the Lee Adoyta bovid fauna), it cannot explain why bovids are more abundant as a whole during the late Pliocene. I propose that important physiological differences between suids (non-ruminants) and bovids (ruminants) may underlie their divergent patterns of abundance change during the late Pliocene of the LAV. First, ruminants have complex four-chambered stomachs that allow them to uptake more nutrients than single-stomached non-ruminants from a comparable amount of forage (Kingdon and Hoffmann, 2013). Late Pliocene bovids at Lee Adoyta were therefore advantaged over suids because they could generate a greater amount of energy from landscapes more sparsely covered in vegetation and, importantly, extract more nutrients from high-fiber, low-quality forage (i.e., grasses). Second, data from living African ungulates shows that ruminants are significantly more water-independent than non-ruminants (Hempson et al., 2015), implying that arid landscapes favor the former over the latter. Important to note here is that data from terrigenous dust records indicate pulsed aridification in eastern Africa ~2.8 Ma (DeMenocal, 2004), temporally coincident with the shift to bovid-dominated faunas in the LAV as would be predicted. Thus, I conclude that the combination of open, grassy environments and increased aridity drove the marked increase of bovids over suids during the late Pliocene because of their physiological differences in digestion and water-dependence. It would be fruitful for future studies to expand their ecological- and biological- scope beyond hypotheses grounded solely in dietary change, as it may lead to more robust understanding of paleoecological patterns.

6. Conclusions

The taxonomic and paleoecological analysis of the fossil Suidae from Lee Adoyta, Ledi-Geraru, provides important new data on faunal and paleoecological change in the LAV during the late Pliocene. I show that the Lee Adoyta suids belong to at least three species – *Notochoerus* cf. *No. capensis*, *Kolpochoerus phillipi*, and *Metridiochoerus andrewsi* – that exhibit craniodental adaptations (third molar crown height and length) indicative of an increased reliance on abrasive food items. Enamel $\delta^{13}C$ data suggests a heavy reliance of all suid species on C_4 grasses at ~2.82 Ma, following predominantly mixed C_3-C_4 suid diets at Hadar. The taxonomic composition of Lee Adoyta suids differs from that of Hadar, implying a faunal turnover between ~2.95 Ma and ~2.82 Ma, as seen in bovids and giraffids, which is in support of Prediction #1 of this dissertation (Chapter 1, Section 5, p. 14) Morphological affinities between the *Kolpochoerus* and *Notochoerus* species of Lee Adoyta and Hadar, however, suggest that the former is descended from the latter. Lee Adoyta also records the first appearance of *Metridiochoerus* in the LAV and the earliest cranial material of this genus in all eastern Africa. The dietary and morphological changes in the *Notochoerus* and *Kolpochoerus* lineages, as well as the first appearance of hyper-grazing *Metridiochoerus*, supports more arid and open (= grassier) environments in the LAV by ~2.82 Ma. The linear decline in suid abundance from the mid- to late Pliocene, however, suggests gradual rather than punctuated environmental change and faunal turnover throughout this time in the LAV.

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CHAPTER 3. DENTAL MICROWEAR TEXTURE ANALYSIS OF PLIOCENE SUIDAE FROM HADAR SHEDS LIGHT ON THE DIETARY BREADTH EXPANSION IN EARLY HOMININS

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Abstract

Carbon stable isotope data show that early hominins diversified their diet as early as 3.76 Ma. The early hominin *Australopithecus anamensis*, better known from ~4.1 Ma sediments at Kanapoi, West Turkana (Kenya), had a narrow C_3-restricted diet while its descendant *A. afarensis*, better known from ~3.45–2.95 Ma sediments at Hadar, lower Awash Valley (Ethiopia), had a broader diet consisting of a mix of C_3 and C_4 resources. The question is whether the hominin dietary breadth expansion was triggered by environmental changes that influenced, for instance, the food availability present at these two sites. To shed light on this issue, I investigate the diet of suids (family Suidae) using three-dimensional texture microwear analyses. The results show that despite significant dietary overlap, Hadar suids were partitioning the available food resources at Hadar to a certain extent. Based on comparisons with the diet of extant Africa suids, it is inferred that *Nyanzachoerus pattersoni* (*n* = 14) was a mixed feeder, *Notochoerus euilus* (*n* = 61) was a grazer, and *Kolpochoerus afarensis* was an omnivore (*n* = 34). The microwear results also support an expansion of suid's dietary breadth at Hadar in comparison with Kanapoi. Both *Ny. pattersoni* and *No. euilus* at Hadar had more grazing diets than *Ny. pattersoni* and *Ny. jaegeri* at Kanapoi. The suid *K. afarensis* is absent at Kanapoi and has a microwear signal at Hadar that evidences the occasional consumption of hard objects (e.g., nuts, hard fruits) and possibly including underground resources that could have been exploited seasonally. Food availability differed between Hadar and Kanapoi, and Hadar probably had more fragmented habitats and/or more seasonal climate. This study highlights the role of environmental change in hominin evolution during the Pliocene and the importance of examining the paleoecology and evolution of co-occurring mammal lineages to develop a holistic framework in paleoanthropology.

Keywords – *Australopithecus*; paleodiet; mammal; suid; pig; Kanapoi.

1. Introduction

Diet is one of the most fundamental aspects of an organism's biology. Modern humans (*Homo sapiens*) are in part defined by their ability to exploit and consume a wide array of foods, an ecological trait that may have played a critical role during human evolution (Milton, 1987, 2003; Aiello and Wheeler, 1995; Marean and Assefa, 1999; Marean et al., 2007). Available evidence suggests that *Australopithecus afarensis*, which is best known from Pliocene deposits at Hadar (~3.45–2.95 Ma), in the lower Awash Valley (LAV), Ethiopia (Kimbel et al., 1994, 2004; Kimbel and Delezene, 2009; Ward and Kimbel, 2012), had a wide dietary niche breadth (Wynn et al., 2013, 2016).

Australopithecus afarensis is likely the direct descendant of *A. anamensis*, which is best known from Kanapoi (~4.1 Ma), in West Turkana, Kenya (Ward et al., 1999, 2001, 2013; Kimbel et al., 2006; White et al., 2006; Ward, 2010). Carbon stable isotope (δ13C) data from tooth enamel indicate marked differences in dietary breadth between these chronospecies (Sponheimer and Dufour, 2009; Ungar and Sponheimer, 2011; Sponheimer et al., 2013). The *A. anamensis* sample from Kanapoi is characterized by a C_3-dominated isotopic signal, whereas *A. afarensis* from Hadar shows significantly greater dietary breadth and is characterized by the consumption of both C_3 and C_4 plant resources (Sponheimer et al., 2013; Wynn et al., 2013, 2016). Whilst the dietary breadth expansion is supported by biochemical analyses of tooth enamel, this change is not noticeable from the stand point of view of dental microwear analyses. The dental microwear texture data does not support significant differences in the textural properties of the foods consumed by *A. anamensis* and *A. afarensis* and suggest that both species were consuming tough foods (e.g., leaves and the aereal part of grasses). It is important to note that there are only three samples of *A. anamensis* in this study but the sample of *A. afarensis* is much larger (n = 19) and there is no indication that this species was eating hard food items (e.g., fruits, nuts, tubers) (Ungar et al., 2010).

The morphological differences between *A. anamensis* and *A. afarensis* include changes in the anatomy of the midface and the anterior portion of the mandible, and a reduction of the honing facets produced by the interaction of the canines and the third premolars (Ward et al., 1999, 2001, 2013, Kimbel et al., 2004, 2006; White et al., 2006b; Kimbel and Delezene, 2009; Ward, 2010). When contrasted with isotopic evidence, this begs the question: why does *A. afarensis* show an increased dietary niche breadth relative to *A. anamensis*? Are these differences related to the morphological differences in the face and the masticatory complex between these species? Or it might be differential resource availability in the habitats occupied by these hominins? As approximately 90% of *A. afarensis* specimens come from Hadar (Kimbel and Delezene, 2009) and most of the *A. anamensis* fossil material comes from Kanapoi (Kimbel and Delezene, 2009), this question would greatly benefit from a better understanding of the paleohabitats of these two sites and from the study of dietary changes in co-occurring mammalian lineages, particularly herbivores or omnivores whose dietary niches could have overlapped with early hominins.

One of these mammalian lineages comprises the extinct relatives of pigs (family Suidae). The rapid evolution of suid dentitions, their flexible dietary behaviors, and the large number of suid fossils recovered from Plio-Pleistocene eastern African sediments make them an ideal group to examine the relationship between diet shifts and environmental changes. Here, I provide new microwear data bearing on fossil suid diets from late Pliocene Hadar and contributing to paleohabitat reconstructions of *A. afarensis* (Reed, 1997, 2008; Hailemichael, 2000; Hailemichael et al., 2002; Bonnefille et al., 2004; Aronson et al., 2008; Behrensmeyer, 2008; Campisano and Feibel, 2008; Wynn et al., 2016). The dental microwear texture data of Kanapoi fossil suids suggest a diet based mostly on tough food resources (probably mixed feeding with both browsing and grazing). By applying dental microwear texture analyses to fossil suid dentitions from Hadar, I aim to test whether suid lineages also maintained diets with similar food properties in Hadar or if in contrary to hominins, there is a change in the type of foods exploited by suids at this time. If suids were exploiting other foods (e.g., hard objects), then it means those resources were available in the habitats present in Hadar but *A. afarensis* was not exploiting them, which can have implications to our interpretation of diet change in early hominins.

2. Background

2.1 Dietary background of extant African suids

Extant suids occupy a wide range of habitats, but they are mostly associated with forested and mixed grassland-woodland settings (Meijaard et al., 2011). Extant warthogs (*Phacochoerus*), for example, are well-adapted to the savanna grasslands of sub-Saharan Africa but are most often found where there is some tree, bush, or tall grass cover and within range of permanent water sources (Cumming, 1975, 2013). The majority of extant suids are generalized omnivores, capable of exploiting a variety of foods (Leus and MacDonald, 1997; Nowak, 1999; Meijaard et al., 2011), including underground plant parts, which they access using their long snouts and incisal dentition (Ewer, 1958; Lazagabaster, 2013). Extant suid ecology and morphological studies suggest that many fossil suids were also capable of exploiting hard-to-reach resources (Cooke, 1978a; Harris and White, 1979; Harris, 1983; Lazagabaster, 2013; Made, 2013), as has been hypothesized for fossil hominins (Laden and Wrangham, 2005; Dominy et al., 2008; Ungar et al., 2008; Constantino and Wright, 2009).

Five suid species inhabit sub-Saharan Africa today: *Potamochoerus porcus* (red river hog), *Potamochoerus larvatus* (bushpig), *Hylochoerus meinertzhageni* (giant forest hog), *Phacochoerus africanus* (common warthog), and *Phacochoerus aethiopicus* (dessert warthog). Extant species of the genus *Potamochoerus* have a typical, generalized suid dentition like that of wild boars (genus *Sus*) and are characterized by low-crowned bunodont teeth with relatively thick enamel. Modern *Potamochoerus* species are generalist omnivores, capable of effectively exploiting a wide array of foods, including leaves, nuts, tubers, roots, invertebrates, and small vertebrates, among others (Meijaard et al., 2011). They inhabit forested to semi-forested areas, including the humid rainforests of West and Central Africa, as well as riverine or xeric scrub forests and thicket formations from Ethiopia to southern Africa (Breytenbach and Skinner, 1982; Jones, 1984; Seydack, 1990; Meijaard et al., 2011). On the other hand, the other two genera are much more specialized in their dental adaptations and dietary ecologies. The giant forest hog *Hylochoerus* possesses lophodont-like dentition and is primarily a grass and foliage eater (mixed feeder) but it seems to display a great versatility in food selection (Meijaard et al., 2011). *Hylochoerus* has a more restricted geographical distribution and mostly occupies forested habitats (Meijaard et al., 2011; D'Huart and Yohannes, 2014). Finally, *Phacochoerus* species (*P. africanus* and *P. aethiopicus*) are characterized by extremely hypsodont and elongated third molars formed by multiple rows of columnar pillars. In line with the dental evidence, field observations, and isotopic data, show that *Phacochoerus* species are mainly grazers (Cumming, 1975, 2013; Harris and Cerling, 2002; Meijaard et al., 2011), though some populations feed on fruits, nuts, and underground resources seasonally (Cumming, 1975, 2013). In addition, some individuals have been seen feeding on vertebrate prey (Roberts, 2012) and carcasses (Kaye Reed, pers. obs.). *Phacochoerus* species mostly inhabit grasslands, open bushlands, and woodlands in Sub-Saharan Africa (Cumming, 2013), though there are few populations occupying more forested habitats in parts of eastern Africa (Butynski and de Jong, 2017; Teklehaimanot and Balakrishnan, 2017).

2.2 The importance of fossil Suidae in paleoanthropology

Suids initially rose to importance in human evolutionary studies when they helped to resolve a controversy in the 1970s regarding the age of the early *Homo* skull KNM-ER 1470 recovered from Koobi Fora, Kenya (White, 1995). Since then, suid fossils have continued to be intensively studied for biochronological purposes (White and Harris, 1977; Cooke, 1978b, 1985; Harris and White, 1979), but also for hominin habitat reconstructions (Bishop, 1994, 1999; Bishop et al., 1999) and other paleocological issues relevant to human evolution (White, 1995; Cooke, 2007; Souron, 2012; Geraads and Bobe, 2017).

One of the main reasons that suids are so useful in the context of human evolution is that their dentition evolved rapidly and markedly during the Plio-Pleistocene in Africa (Harris and White, 1979; Cooke, 2007), possibly in response to dietary shifts triggered by global and/or regional climatic changes (DeMenocal, 1995, 2004). In fact, the evolution of different suid lineages is a prime example of the impact that the spread of grasslands had on the evolution of the eastern African biota. As C_4 grasslands expanded (Cerling et al., 2011), some suid lineages adapted their masticatory apparatus to consume foods with a higher content of abrasive particles, e.g., silica and grit associated with grasses (Harris and White, 1979; Made, 1999; Cooke, 2007). Thus, most Plio-Pleistocene African suid lineages exhibit parallel and progressive dental evolutionary trends, such as an increase in third molar length and height, a reduction of the premolars and thinner enamel, and changes in the anterior dentition (Harris and White, 1979).

Other synchronous suid lineages retained less-specialized, bunodont dentitions and probably had broader, likely omnivorous diets associated with more wooded habitats (Harris and White, 1979; Harris, 1983; Cooke, 2007; Cuddahee, 2008; Souron, 2012). At sites where fossils of suid taxa with both generalized and specialized craniodental features are found, some degree of niche partitioning between taxa would be expected, at least in terms of diet, if not habitat. Carbon stable isotope analysis have shown, however, that the relationship between C_4 resource consumption (e.g., grasses) and dental morphology (e.g., length and height of the third molar) in suids is not straightforward (Harris and Cerling, 2002), a fact that should not come as a surprise. There are several explanations for this mismatch. First and foremost, dental morphology is driven mostly by food fracture properties and phylogeny (what the animal is capable of eating) whereas carbon stable isotopes depend on the photosynthetic pathway of the plants consumed by the animals and can reveal only what type of plant the animals consumed during a limited timespan during crown formation (juvenile age). Second, most suids—at least the extant ones—are very flexible in terms of diet and capable of exploiting a wide array of dietary resources (Meijaard et al., 2011; Souron, 2017). As mentioned before, even the hypergrazer warthogs (Harris and Cerling, 2002) rely on roots, tubers, or fruits at certain times of the year (Cumming, 1975) and occasionally even consume animal carrion (Roberts, 2012). These reasons complicate the reconstruction of suid diets in the past.

To capture a larger amount of the complexity of suid’s paleodiets, some researchers have used other techniques of paleodietary inference, like dental microwear analyses. In the context of suid paleodiets, dental microwear analyses have been applied to the study of fauna from fossil assemblages (Hunter and Fortelius, 1994) and archaeological sites (Vanpoucke et al., 2009), and have been used in paleoecological studies of human evolution in eastern Africa (Bishop et al., 2006; Medin et al., 2015; Ungar et al., 2017). However, the most recent dental microwear approach, known as three-dimensional microwear texture analysis, has only been applied to the study of suid diets by Souron et al. (2015b) and Ungar et al. (2017). Here, I apply this technique (more information in Section 3.2) to the analysis of Hadar suid diets and compare the microwear metrics with those of the Kanapoi suids first published in Ungar et al. (2017).

2.3 Hadar – Geological background

The Hadar Research Project area is located along the lower course of the Awash River, in the west-central part of the Awash Valley, Ethiopia. The Pliocene deposits of Hadar date to ~3.45–2.95 Ma (Campisano and Feibel, 2008) and are the source of approximately 90% of the specimens attributed to *A. afarensis* (Kimbel and Delezene, 2009), including the partial skeleton A.L. 288-1 ("Lucy"). The ~155 m of Hadar Formation strata consist of floodplain paleosols, fluvial and deltaic sands, and lacustrine clays and silts (Taieb et al., 1976; Campisano and Feibel, 2008). A paleolake existed east and northeast of the Hadar Project research area, but lacustrine transgressions occurred in the region. Most of the vertebrate remains at Hadar, however, are recovered from fluvial-deltaic deposits (Campisano and Feibel, 2008; Campisano, 2012).

The presence of multiple tephra in the Hadar sequence has allowed detailed dating of the sediments. The Sidi Hakoma Tuff (~3.42 Ma) is close to the base of the sequence and the BKT-2 Complex (~2.95) Ma caps the strata at the top of the sequence. The Hadar Formation is divided into four members, the Basal Member (BM, 3.45–3.42 Ma), the Sidi Hakoma Member (SH, ~3.42–3.24 Ma), the Denen Dora Member (DD, ~3.24–3.20 Ma), and the Kada Hadar Member (KH, ~3.20–2.95 Ma) (Campisano and Feibel, 2008; Campisano, 2012). These members - BM, SH, DD, and KH - will be used as geological units in statistical analyses (see Section 3.5)

3. Material and Methods

3.1 Sample

All suitable suid lower third molars from the Hadar collection housed at the National Museum of Ethiopia were examined for this study. The fossils were recovered during several decades of field work by the International Afar Research Expedition and the Hadar Research Project (Kimbel and Delezene, 2009; Johanson, 2017). The lower third molars considered suitable were those that preserved at least the two most mesial pair of main cusps (the first two lophids), were not completely unworn, and had well-preserved enamel on the occlusal surface. Those specimens with obvious postmortem damage or with an obscuring, irremovable layer of matrix or preservative were excluded from the analysis. The lower third molar was chosen as the target of our analysis for several reasons. First, this was the tooth used by Ungar et al. (2017) in the dental microwear analysis of the Kanapoi suids. Second, third molars are the most common teeth in the suid fossil record and the most taxonomically informative (Harris and White, 1979). In addition, the third molar mesial cusps are closer to the center of the molar row (especially in species with elongated third molars), an area targeted in most microwear studies. Furthermore, the adult individuals of some suid species, like modern *Phacochoerus* or fossil *Metridiochoerus*, lose cheek teeth with age, except for the third molars. The selection of third molars, therefore, maximizes the possibility of comparing dental microwear across different suid genera.

A total sample of 148 fossil lower third molars from Hadar were molded, cast, and analyzed under confocal microscopy, but only 109 had well-preserved microwear with no sign of taphonomic alteration and were included in the final analysis. The final fossil sample from Hadar includes the three extinct species represented at the site (Cooke, 1978a), including *Nyanzachoerus pattersoni* (*n* = 14), *Notochoerus euilus* (*n* = 61), and *Kolpochoerus afarensis* (*n* = 34). The collection number and stratigraphical provenience of each of these fossils can be found in Table 3.1.

For comparative purposes, a total of 50 specimens of modern African suid species with known diets were included in the analyses and used as a baseline for fossil comparisons. The modern sample includes four extant suid species, *Hylochoerus meinertzhageni* (*n* = 3), *Phacochoerus* spp. (*n* = 18), *Potamochoerus larvatus* (*n* = 23), and *Po. porcus* (*n* = 6). These molds were taken from skulls kept in the osteological collections of the Field Museum of Natural History (Chicago, USA), the National Museum of Kenya (Nairobi, Kenya), and the National Museum of Ethiopia (Addis Ababa, Ethiopia).

Finally, a total of 19 fossil specimens from Kanapoi were also included in the analyses. These belong to two species, *Ny. pattersoni* (*n* = 15) and *Ny. jaegeri* (*n* = 4). Partial results of the microwear analysis of Kanapoi suids were published in Ungar et al.

(2017). For comparative purposes, *Ny. pattersoni* from Hadar and *Ny. pattersoni* from Kanapoi are treated as different analytical units throughout the rest of this paper.

Table 3.1. List of suid fossil third molars analyzed in this work. Abbreviations: ID, catalog number BM, Basal Member; SHT, Sidi Hakoma Tuff; DD, Denen Dora Member; KH, Kada Hadar Member; R, right; L, left; pro, protoconid; meta, metaconid; Mb, member assigned in this work.

ID	Submember	Mb.	Taxon	Side	Cusp	ID	Submember	Mb.	Taxon	Side	Cusp
AL 401-3	BM/SHT	BM	*Ny. pattersoni*	R	pro	AL 374-1	SH3/SH4	SH	*No. euilus*	R	meta
AL 272-1	BM	BM	*Ny. pattersoni*	L	meta	AL 246-2	SH1/SH2	SH	*No. euilus*	R	pro
AL 124-53	BM/SHT	BM	*Ny. pattersoni*	R	meta	AL 325-5	SH4	SH	*No. euilus*	L	meta
AL 407-3A	BM	BM	*Ny. pattersoni*	L	pro	AL 1248-1	SH1	SH	*No. euilus*	L	pro
AL 142-13A	SH1/SH2	SH	*Ny. pattersoni*	L	pro	AL 128-11	SH1/SH2	SH	*No. euilus*	R	meta
AL 137-36	SH1/SH2	SH	*Ny. pattersoni*	L	pro	AL 254-7A	SH1/SH2	SH	*No. euilus*	R	pro
AL 165-4	SH1/SH2	SH	*Ny. pattersoni*	L	meta	AL 53-18	SH3	SH	*No. euilus*	L	meta
AL 1903-1	SH2	SH	*Ny. pattersoni*	R	meta	AL 198-12	SH1/SH2/SH3	SH	*No. euilus*	L	meta
AL 218-2	SH1/SH2/SHT	SH	*Ny. pattersoni*	L	meta	AL 315-13	DD2/DD3	DD	*No. euilus*	R	pro
AL 1914-1	SH2	SH	*Ny. pattersoni*	R	pro	AL 342-9C	DD2	DD	*No. euilus*	L	pro
AL 142-13B	SH1/SH2	SH	*Ny. pattersoni*	R	pro	AL 1800-1	DD2	DD	*No. euilus*	R	pro
AL 127-7	SH1/SH2	SH	*Ny. pattersoni*	R	pro	AL 315-4	DD2/DD3	DD	*No. euilus*	L	pro
AL 1764-1	SH2	SH	*Ny. pattersoni*	R	pro	AL 768-4	DD3	DD	*No. euilus*	R	meta
AL 126-18	SH1/SH2	SH	*Ny. pattersoni*	L	meta	AL 379-6	DD1/DD2	DD	*No. euilus*	R	pro
AL 401-4	BM/SHT	BM	*K. afarensis*	L	meta	AL 378-1A	DD3	DD	*No. euilus*	R	pro
AL 403-2	BM/SHT	BM	*K. afarensis*	R	meta	AL 635-1e	DD3	DD	*No. euilus*	L	pro
AL 199-7	SH1	SH	*K. afarensis*	R	meta	AL 285-5	DD2	DD	*No. euilus*	R	pro
AL 327-19	SH2	SH	*K. afarensis*	L	pro	AL 362-12	DD3	DD	*No. euilus*	R	pro
AL 142-21B	SH1/SH2	SH	*K. afarensis*	R	pro	AL 157-3	DD3/KH1	DD	*No. euilus*	R	pro
AL 1522-1	SH1	SH	*K. afarensis*	L	pro	AL 154-2	DD2/DD3	DD	*No. euilus*	L	pro
AL 237-4B	SH1/SH2/SH3	SH	*K. afarensis*	L	pro	AL 379-8	DD1/DD2	DD	*No. euilus*	L	pro
AL 129-49	SH1/SH2	SH	*K. afarensis*	R	pro	AL 182-47	DD2	DD	*No. euilus*	L	meta
AL 127-38	SH1/SH2	SH	*K. afarensis*	L	pro	AL 116-142	DD2/DD3	DD	*No. euilus*	R	pro
AL 325-9	SH4	SH	*K. afarensis*	L	meta	AL 135-6A	DD2/DD3	DD	*No. euilus*	R	pro
AL 255-1	SH1/SH2	SH	*K. afarensis*	R	pro	AL 154-20	DD2/DD3	DD	*No. euilus*	L	pro
AL 419-1	SH2/SH3	SH	*K. afarensis*	R	pro	AL 133-34	DD2/DD3	DD	*No. euilus*	L	meta
AL 164-2	SH2	SH	*K. afarensis*	R	pro	AL 167-12	DD2/DD3	DD	*No. euilus*	L	pro
AL 379-3	DD2/DD3	DD	*K. afarensis*	R	meta	AL 190-4	DD2/DD3	DD	*No. euilus*	L	pro
AL 1582-6	DD2/DD3	DD	*K. afarensis*	L	meta	AL 135-11	DD2/DD3	DD	*No. euilus*	L	pro
AL 321-10A	DD2/DD3	DD	*K. afarensis*	R	pro	AL 58-2	DD2	DD	*No. euilus*	R	pro
AL 187-12	DD2/DD3	DD	*K. afarensis*	L	pro	AL 191-4	DD3	DD	*No. euilus*	R	pro
AL 220-2	DD2/DD3	DD	*K. afarensis*	L	pro	AL 134-4	DD2/DD3	DD	*No. euilus*	R	pro
AL 116-26	DD3	DD	*K. afarensis*	L	pro	AL 116-61	DD2/DD3	DD	*No. euilus*	L	pro
AL 168-13	DD2	DD	*K. afarensis*	R	pro	AL 195-4	DD1	DD	*No. euilus*	L	pro

AL 134-7B	DD2/DD3	DD	*K. afarensis*	R	meta	AL 184-4	DD3	DD	*No. euilus*	L	pro
AL 182-48	DD2	DD	*K. afarensis*	L	pro	AL 116-112	DD2/DD3	DD	*No. euilus*	R	meta
AL 183-44	DD2	DD	*K. afarensis*	R	pro	AL 195-35	DD1	DD	*No. euilus*	L	pro
AL 321-10B	DD2/DD3	DD	*K. afarensis*	L	pro	AL 173-20	DD	DD	*No. euilus*	R	pro
AL 385-2A	DD2/DD3	DD	*K. afarensis*	L	pro	AL 187-11	DD2/DD3	DD	*No. euilus*	R	pro
AL 118-6	DD2/DD3	DD	*K. afarensis*	R	meta	AL 58-21B	DD2	DD	*No. euilus*	L	pro
AL 296-1C	DD1/DD2	DD	*K. afarensis*	R	pro	AL 58-25A	DD2	DD	*No. euilus*	R	pro
AL 116-60B	DD2/DD3	DD	*K. afarensis*	L	meta	AL 154-37	DD2/DD3	DD	*No. euilus*	R	meta
AL 56-16bis	DD2/DD3	DD	*K. afarensis*	R	pro	AL 192-19	DD2	DD	*No. euilus*	R	pro
AL 455-1B	KH2	KH	*K. afarensis*	L	pro	AL 182-89	DD2	DD	*No. euilus*	L	meta
AL 516-2	KH2	KH	*K. afarensis*	R	meta	AL 185-8	DD3	DD	*No. euilus*	R	meta
AL 1805-1	KH2	KH	*K. afarensis*	R	pro	AL 122-4	DD2/DD3	DD	*No. euilus*	L	pro
AL 1109-1	KH1	KH	*K. afarensis*	L	pro	AL 176-9	DD	DD	*No. euilus*	R	meta
AL 455-1C	KH2	KH	*K. afarensis*	R	pro	AL 122-5	DD2/DD3	DD	*No. euilus*	R	pro
AL 403-47B	BM/SHT	BM	*No. euilus*	L	meta	AL 191-9	DD3	DD	*No. euilus*	L	pro
AL 124-42B	BM/SHT	BM	*No. euilus*	L	meta	AL 150-86	DD	DD	*No. euilus*	L	meta
AL 398-1B	BM/SHT	BM	*No. euilus*	L	pro	AL 173-9	DD	DD	*No. euilus*	L	pro
AL 124-57	BM/SHT	BM	*No. euilus*	L	pro	AL 932-1	KH2	KH	*No. euilus*	R	pro
AL 360-1	SH3	SH	*No. euilus*	R	pro	AL 694-1	KH2	KH	*No. euilus*	R	pro
AL 348-4	SH4	SH	*No. euilus*	R	pro	AL 282-8	KH1	KH	*No. euilus*	L	pro
AL 1923-1	SH2	SH	*No. euilus*	R	pro						

3.2 Molding and casting procedures

The enamel on the occlusal surfaces of all third molars was assessed visually using a hand-held magnification glass. Molars deemed suitable for microwear analysis were cleaned using alcohol-soaked cotton swabs or a very soft brush, and high-resolution molds were produced using President's Jet regular body polyvinylsiloxane dental impression material (Coltene-Whaledent, Alstatten, Switzerland). High-resolution replicas of specimens were poured into these molds at the University of Arkansas using Epotek 301 epoxy resin and hardener (Epoxy Technologies, Billerica, MA, USA), then allowed to harden before analysis.

3.3 Confocal microscopy

All the epoxy replicas were analyzed under the Sensofar Plμ Neox confocal profiler in white-light mode with a 100x objective at the University of Arkansas. A stitched point cloud of 242 x 181 mm with a lateral spacing (x, y) of 0.17 mm and a published vertical resolution <1 nm was collected for each analyzed surface. This resulted in a cloud of approximately 1.52 million points representing each specimen. Raw point clouds were processed using MountainsMap software (DigitalSurf, Besançon, France) with SensoMAP version 6 (Sensofar Corp., Barcelona, Spain). Surfaces were leveled and any data representing dust or other adherent particles on the original facet were deleted manually prior to analysis. Missing data points were not filled but excluded from analyses. Selected surfaces produced using the process outlined above for each of the suid species analyzed are illustrated in Figure 3.1. The surfaces composed of the resulting point clouds were then analyzed using scale-sensitive fractal analysis software (ToothFrax and SFrax, Surfract Corporation, Norwich, Vermont, USA), which has become a standard for the quantitative characterization of dental microwear surface texture and is the same technique used by Ungar et al (2017). Detailed descriptions of the individual texture attributes generated from the point clouds can be found in Scott et al. (2006).

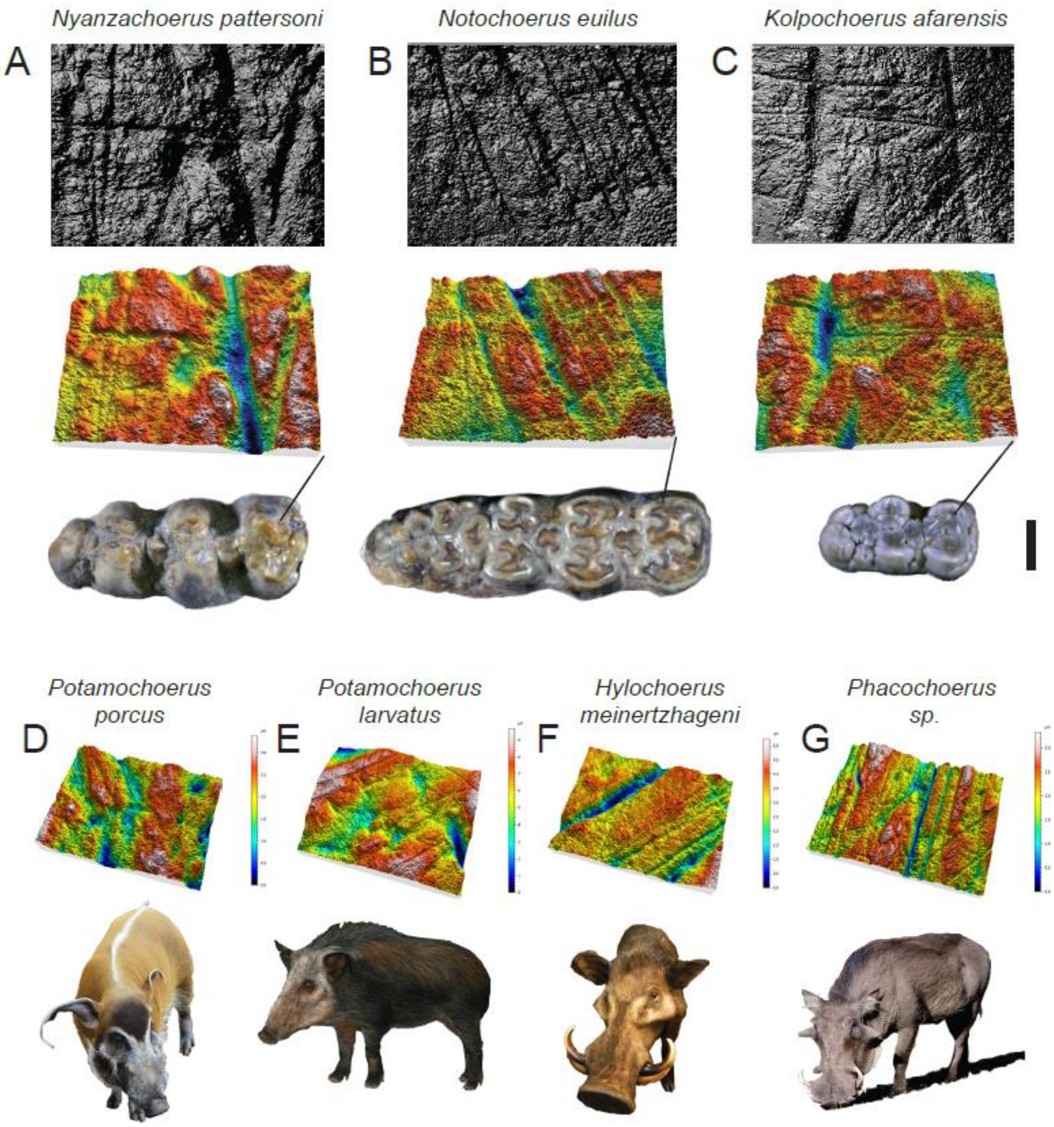

Figure 3.1. Selected topographic surfaces obtained from the Sensofar Plμ Neox confocal profiler in white-light mode with a 100x objective, for each species analyzed in this work. Raw point clouds were processed using MountainsMap software (DigitalSurf, Besançon, France) with the SensoMAP version (Sensofar Corp., Barcelona, Spain). A) *Nyanzachoerus pattersoni* AL 142-11; B) *Notochoerus euilus* AL 135-6A; C) *K. afarensis* AL 408-2A; D) *Potamochoerus porcus* FMNH 38170; E) *Po. larvatus* OM-Pot-NN4; F) *Hylochoerus meinertzhageni* OM 2143; G) *Phacochoerus* sp. OM 4921. All teeth pictured are right lower third molars. The line indicates the facet where the microimage was taken, shown on the occlusal surface of the original specimen. Black scale = 1 cm. The color scale represents different elevations of the topographic surface, from lowest (blue) to highest (red).

3.4 Dental microwear texture variables

A summary of all variables used can be found in Table 3.2. I consider a total of thirteen variables following Delezene et al. (2016) and Ungar et al. (2017). Data for five microwear texture variables were derived from scale-sensitive fractal analysis (SSFA) software programs (ToothFrax and SFrax, Surfract Corp.; Scott et al., 2006; Ungar et al., 2008). These variables include area scale fractal complexity (*Asfc*), anisotropy (*epLsar*), textural fill volume (*Tfv*), and two measures of heterogeneity of complexity ($HAsfc_{9}$ and $HAsfc_{81}$). The procedures used to calculate SSFA variables can be found in Scott et al. (2006). Additionally, surface textures were characterized by eight International Organization for Standardization (2010) (ISO 25178-2) texture measurements, which are increasingly being employed in microwear analyses to complement SSFA (e.g., Calandra et al., 2012; Schulz et al., 2013). The ISO parameters were generated using Sensomap v6 and include five-point pit height (*S5v*), maximum pit height (*Sv*), mean dale area (*Sda*), mean dale volume (*Sdv*), pit void volume (*Vvv*), texture-aspect ratio (*Str*), developed interfacial area ratio (*Sdr*), and skewness (*Ssk*) (ISO/FDIS 25178-2, International Organization for Standardization, 2010; Ţălu et al., 2013). For the ISO variables, the curvature of the scanned surface was removed by using the “form removal” operator of Sensomap.

In summary, the variables analyzed in this study include two measures of feature complexity (*Asfc*, *Sdr*), two measures of feature anisotropy (*epLsar*, *Str*), two measures of heterogeneity of textures ($HAsfc_{9}$, $HAsfc_{81}$), three measures of feature volume (*Tfv*, *Vvv*, *Sdv*), a measure of feature area (*Sda*), two measures of feature depth (*Sv*, *S5v*), and a measure of the density of scratches (*Ssk*).

Table 3.2. Microwear variables used in this work. Abbreviations: Var, variable name abbreviated; SSFA, variables associated with scale-sensitive fractal analysis ISO/FDIS 25178-2, variables associated with the International Organization for Standardization (2010).

Measure	Var.	Variable name	Analysis
Feature complexity	*Asfc*	Complexity	SSFA
	Sdr	Developed interfacial area ratio	ISO/FDIS 25178-2
Feature anisotropy	*epLsar*	Anisotropy	SSFA
	Str	Texture-aspect ratio	ISO/FDIS 25178-2
Texture heterogeneity	$HAsfc_9$		SSFA
	$HAsfc_{81}$		SSFA
Feature volume	*Tfv*	Textural fill volume	SSFA
	Vvv	Pit void volume	ISO/FDIS 25178-2
	Sdv	Mean dale volume	ISO/FDIS 25178-2
Feature area	*Sda*	Mean dale area	ISO/FDIS 25178-2
Feature depth	*Sv*	Maximum pit height	ISO/FDIS 25178-2
	S5v	Five-point pit height	ISO/FDIS 25178-2
Density of scratches	*Ssk*		ISO/FDIS 25178-2

3.5 Geological units

The geological units included in the five temporal bins are constituted by Kanapoi (Ka, ~4.1 Ma) and Hadar members, Basal Member (BM, ~3.45–3.42 Ma), Sidi Hakoma Member (SH, ~3.42–3.24 Ma), Denen Dora Member (DD, ~3.24–3.20 Ma), and Kada

Hadar Member (KH, ~3.20–2.95 Ma) (Campisano and Feibel, 2008; Campisano, 2012) (see also Figure 1.1). All species were pooled together for each of these geological units.

3.6 Data analysis

Statistical analyses follow previous studies of dental microwear texture analyses (Ungar et al., 2008, 2010; Delezene et al., 2013). The data was not normally distributed, as is usually the case with microwear texture variables. Thus, all the statistical analyses were performed on rank-transformed data. First, differences in central tendencies between taxa and between geological units were assessed using a one-way MANOVA for all variables, with individual ANOVAs and multiple comparisons post hoc tests (Dunn's tests) used to determine the sources of significant variation. In addition to comparisons of central tendency, the homogeneity of variances was compared among species using Levene's tests following Plavcan and Cope's (2001) method. In past studies (e.g., Ungar et al., 2017), differences in the homogeneity of variances have been suggested to be important for inferring food preferences and dietary specificity. Finally, multivariate analysis was carried out, using a correlation-based principal component analysis (PCA) on all the variables following Delezene et al. (2013). All statistical analyses were performed in R environment v. 3.4.1.

4. Results

Descriptive statistics are presented in Tables 3.3–3.4 and illustrated in Figures 3.2–3.3. The univariate statistical analyses are summarized in Tables 3.5–3.7. The results of multivariate analysis are presented in Table 3.8 and Figures 3.4–3.5.

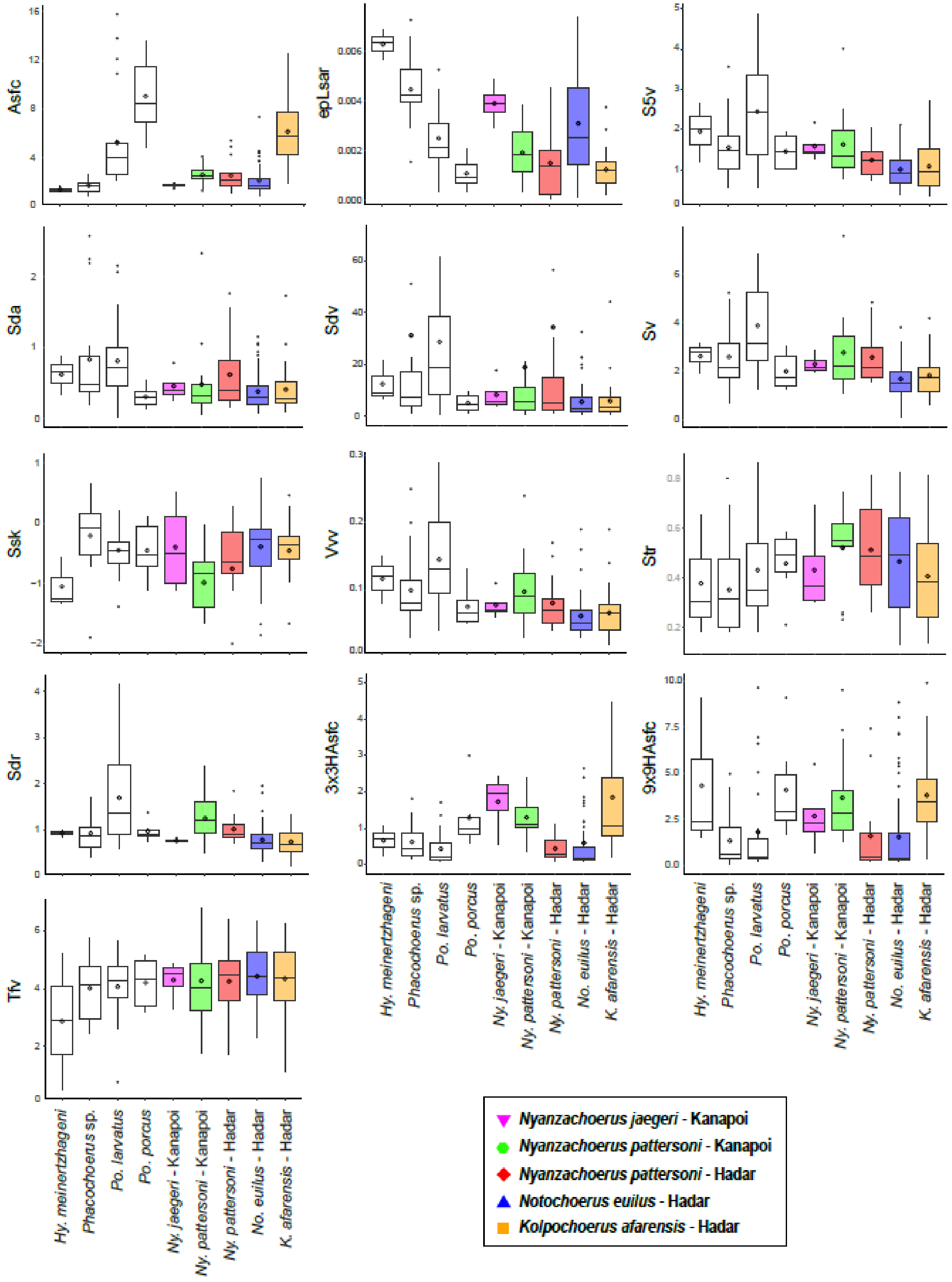

Figure 3.2. Boxplots showing the raw values of all the texture microwear variables for each extant and fossil suid species analyzed in this work.

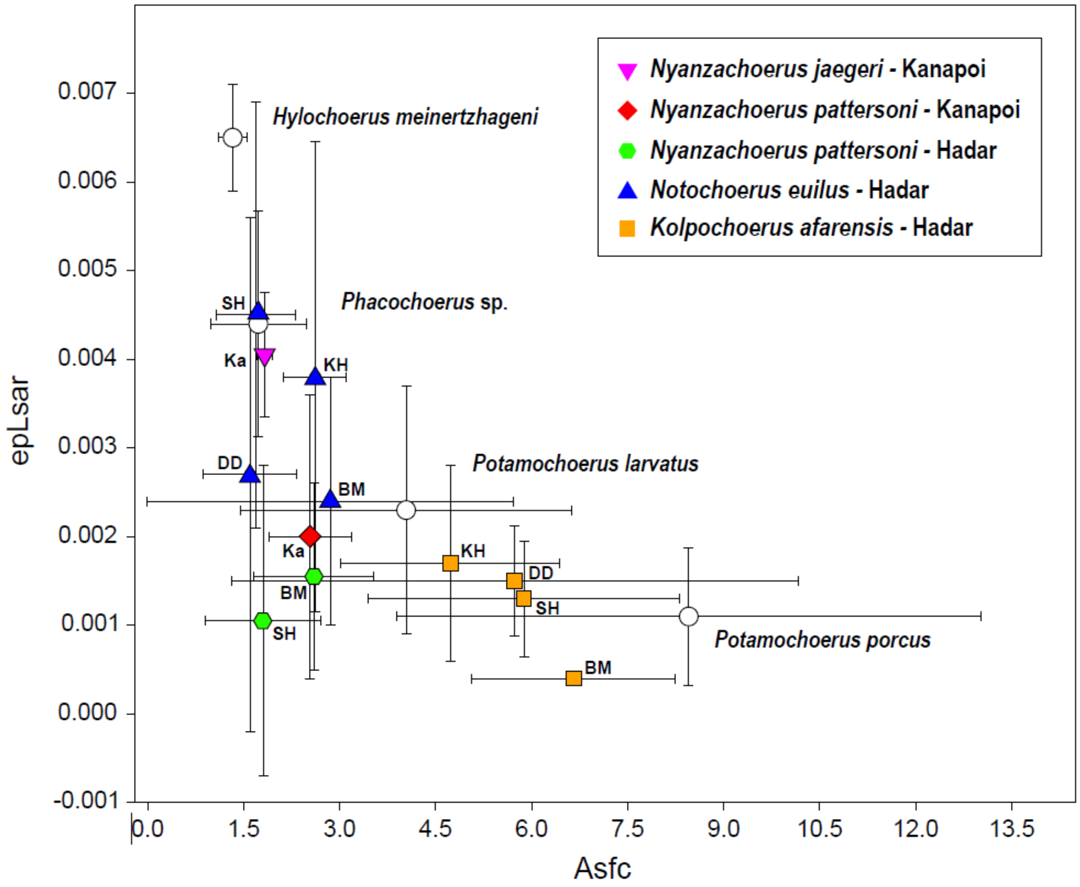

Figure 3.3. Bivariate plot of anisotropy (*epLsar*) and complexity (*Asfc*). Each point represents the median and the lines represent the standard deviation. Abbreviation of geological units: Ka, Kanapoi; BM, Basal Member; SH, Sidi Hakoma; DD, Denen Dora; KH, Kada Hadar.

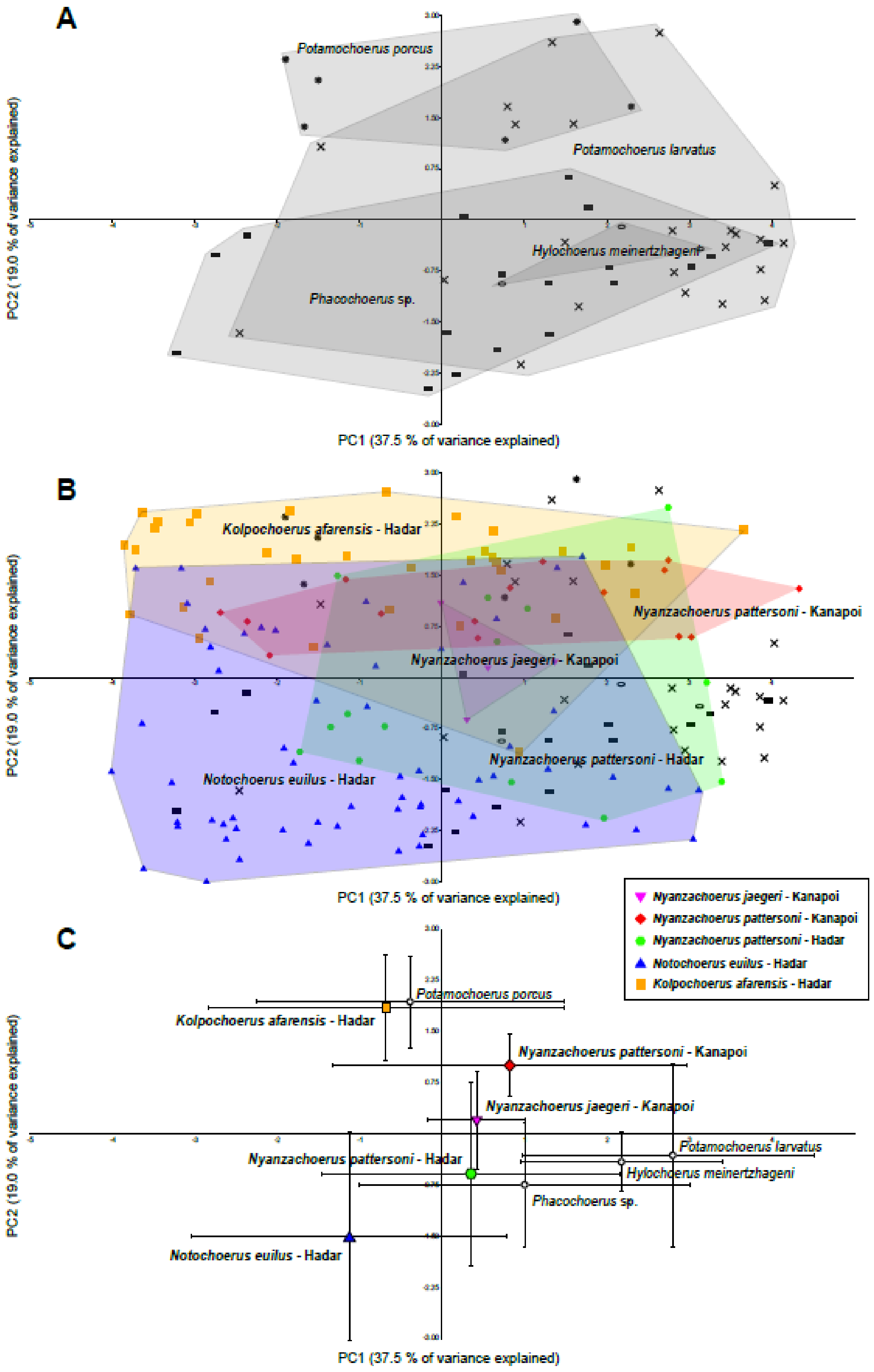
A
Potamochoerus porcus
Potamochoerus larvatus
Hylochoerus meinertzhageni
Phacochoerus sp.
PC2 (19.0 % of variance explained)
PC1 (37.5 % of variance explained)
B
Kolpochoerus afarensis - Hadar
Nyanzachoerus pattersoni - Kanapoi
Nyanzachoerus jaegeri - Kanapoi
Nyanzachoerus pattersoni - Hadar
Notochoerus euilus - Hadar
PC2 (19.0 % of variance explained)
PC1 (37.5 % of variance explained)
▼ Nyanzachoerus jaegeri - Kanapoi
◆ Nyanzachoerus pattersoni - Kanapoi
● Nyanzachoerus pattersoni - Hadar
▲ Notochoerus euilus - Hadar
■ Kolpochoerus afarensis - Hadar
C
Potamochoerus porcus
Kolpochoerus afarensis - Hadar
Nyanzachoerus pattersoni - Kanapoi
Nyanzachoerus jaegeri - Kanapoi
Potamochoerus larvatus
Nyanzachoerus pattersoni - Hadar
Hylochoerus meinertzhageni
Phacochoerus sp.
Notochoerus euilus - Hadar
PC2 (19.0 % of variance explained)
PC1 (37.5 % of variance explained)

Figure 3.4. Principal components analysis (PCA) with all variables included. A) Extant suid taxa (fossil taxa were included in the PCA but the symbols were posteriorly removed) for better visualization). B) Fossil suid taxa (symbols for extant taxa have been included for comparison). C) The points represent medians and the lines standard deviations. All taxa included.

4.1 Extant suid diets

The extant suid species analyzed in this work are distinguished by their *Asfc*, *Sv*, *Ssk*, *Vvv*, $HAsfc_9$, and $HAsfc_{81}$ values (Tables 3.3–3.5). The microwear variables that better differentiate extant suid species ($p<0.0001$, Table 3.5) are complexity (as measured by *Asfc*) and anisotropy (as measured by *epLsar*). The *Asfc* median values of *Potamochoerus porcus* and *Po. larvatus* are 4.04 and 8.46, respectively, which are significantly higher ($p < 0.01$, Table 3.6) than in the grazer *Phacochoerus* (1.33) and the mixed feeder *Hylochoerus meinertzhageni* (1.73) (Table 3.3; Figure 3.2). The other measure of complexity, *Sdr*, is higher in *Po. larvatus* (median value of 1.37), but the values are similar between *Po. porcus* and the other two taxa (*Phacochoerus* and *H. meinertzhageni*). In fact, only the differences in *Sdr* values between *Po. larvatus* and *Phacochoerus* are statistically significant ($p<0.05$; Table 3.6). With respect to feature volume as measured by *Vvv, Po. larvatus* again has the highest median value (0.13), but in this case, it is very close to the median value of *Hy. meinertzhageni* (0.12). Similarly, *Po. larvatus* has the highest median value of feature depth as measured by *Sv* (3.11), in contrast with *Po. porcus* (1.71), which has the lowest (Figure 3.2), while *Phacochoerus* and *Hy. meinertzhageni* have intermediate median values of *Sv*, 2.15 and 2.78, respectively. These two taxa differ in the values of featured skewness (*Ssk*) ($p<0.01$,

Table 3.6); *Hy. meinertzhageni* has a median value of -1.25 while *Phacochoerus* has a value of -0.08. Finally, *Po. porcus* has more heterogeneous surfaces than the other taxa, with median values of $HAsfc_9$, 0.98, and $HAsfc_{81}$, 2.88 that are significantly higher than *Po. larvatus* (0.21 and 0.43 for $HAsfc_9$ and $HAsfc_8$, respectively) ($p<0.05$; Table 3.6).

The analysis of variance using Levene's test uncovered statistical differences in *Asfc*, *epLsar,* and *Sdr* ($p<0.05$; Table 3.5). These results seem to be driven by differences between *Po. larvatus* and two other taxa, *Phacochoerus* and *Hy. meintertzhageni* ($p<0.001$, Table 3.7). Similarly, the results in *Sdr* seem to be driven mostly by differences between *Po. larvatus* and both *Hy. meinertzhageni* and *Po. porcus*.

The differences between variables can be better visualized by a multivariate PCA (Figure 3.4A). Most of the separation between modern taxa seems to occur in the PC2 axis, though this component explains only 19% of the variance. The four variables that load most significantly in PC2 are complexity (*Asfc*), anisotrooy (*epLsar*) and heterogeneity ($HAsfc_9$ and $HAsfc_{81}$). Though there is a lot of overlap, *Po. porcus* is well separated from *Phacochoerus* and *Hy. meinertzhageni*. *Po. larvatus* occupies a large area in the multivariate space, which may reflect the generalized diet of this species

Table 3.3. Summary statistics for all the exant and fossil African suid species analyzed in this work. Abbreviations: *n* = sample size; sd = standard deviation.

Taxon	*n*		*Asfc*	*epLsar*	*S5v*	*Sda*	*Sdv*	*Sv*	*Ssk*	*Vvv*	*Str*	*Sdr*	*HAsfc*$_{9}$	*HAsfc*$_{81}$	*Tfv*
Hylochoerus meinertzhageni	3	median	1.33	0.0065	2.01	655.97	9.02	2.78	-1.25	0.12	0.30	0.93	0.71	2.34	29075.94
		mean	1.40	0.0064	1.96	624.64	12.35	2.60	-1.05	0.12	0.38	0.93	0.66	4.31	28708.69
		sd	0.24	0.0006	0.71	271.33	7.96	0.62	0.42	0.04	0.24	0.08	0.41	4.14	23626.26
Phacochoerus spp.	18	median	1.73	0.0044	1.48	473.42	7.44	2.15	-0.08	0.08	0.32	0.88	0.44	0.58	41136.70
		mean	1.73	0.0046	1.56	834.94	31.18	2.57	-0.21	0.10	0.35	0.93	0.62	1.33	40090.09
		sd	0.57	0.0014	0.76	736.38	63.89	1.28	0.58	0.06	0.16	0.38	0.49	1.50	10751.74
Potamochoerus larvatus	23	median	4.04	0.0023	2.45	724.35	18.84	3.11	-0.46	0.13	0.35	1.37	0.21	0.43	42604.92
		mean	5.24	0.0026	2.45	815.14	28.62	3.86	-0.45	0.15	0.43	1.70	0.43	1.79	40653.02
		sd	3.93	0.0011	1.18	555.23	31.91	1.75	0.39	0.07	0.21	1.02	0.45	2.68	10079.44
Potamochoerus porcus	6	median	8.46	0.0011	1.45	289.85	4.71	1.71	-0.53	0.07	0.49	0.91	0.98	2.88	43159.40
		mean	9.07	0.0012	1.46	307.19	5.08	1.98	-0.45	0.08	0.46	0.97	1.28	4.08	41991.33
		sd	3.35	0.0006	0.46	146.97	3.43	0.77	0.48	0.03	0.14	0.22	0.88	2.80	8953.52
Nyanzachoerus jaegeri - Kanapoi	4	median	1.83	0.0040	1.45	396.44	5.80	2.14	-0.50	0.07	0.37	0.75	1.96	2.26	45206.42
		mean	1.76	0.0041	1.59	457.36	8.24	2.27	-0.40	0.08	0.43	0.77	1.73	2.66	42995.58
		sd	0.19	0.0008	0.40	230.96	6.39	0.40	0.77	0.02	0.18	0.04	0.82	2.02	7006.55
Nyanzachoerus pattersoni - Kanapoi	15	median	2.54	0.0020	1.35	313.13	5.65	2.18	-0.84	0.09	0.55	1.21	1.11	2.84	39410.82
		mean	2.61	0.0021	1.64	482.27	18.83	2.75	-0.98	0.10	0.52	1.25	1.30	3.65	33662.88
		sd	0.82	0.0010	0.83	570.88	46.97	1.62	0.65	0.05	0.15	0.51	0.59	2.41	30717.39
Nyanzachoerus pattersoni - Hadar	14	median	2.12	0.0016	1.25	400.29	4.80	2.12	-0.65	0.07	0.49	0.91	0.29	0.40	40266.00
		mean	2.56	0.0017	1.25	621.84	34.30	2.55	-0.75	0.08	0.51	1.02	0.44	1.57	42692.82
		sd	1.35	0.0015	0.38	515.11	87.79	1.09	0.87	0.04	0.18	0.31	0.35	2.28	14311.35
Notochoerus euilus - Hadar	61	median	1.66	0.0027	0.91	305.54	2.90	1.51	-0.27	0.05	0.49	0.71	0.18	0.35	44306.90
		mean	2.13	0.0032	1.02	382.03	5.53	1.66	-0.39	0.06	0.46	0.79	0.60	1.53	44261.68
		sd	1.21	0.0020	0.44	259.76	6.19	0.70	0.48	0.03	0.20	0.32	1.24	2.25	9745.87
Kolpochoerus afarensis - Hadar	34	median	5.79	0.0014	0.97	281.71	3.64	1.72	-0.37	0.07	0.38	0.70	1.08	3.45	43582.62
		mean	6.15	0.0014	1.09	408.96	5.80	1.81	-0.46	0.07	0.41	0.74	1.85	3.79	43427.66
		sd	2.63	0.0008	0.55	323.07	7.76	0.80	0.50	0.03	0.20	0.30	1.75	2.07	11505.46

Table 3.4. Summary statistics for Kanapoi and the four members of Hadar. Abbreviations: BM, Basal Member; SH, Sidi Hakoma; DD, Denen Dora; KH, Kada Hadar; *n*, sample size.

Site - Member	*n*		*Asfc*	*epLsar*	*S5v*	*Sda*	*Sdv*	*Sv*	*Ssk*	*Vvv*	*Str*	*Sdr*	$HAsfc_9$	$HAsfc_{81}$	*Tfv*
Kanapoi	19	median	2.39	0.0022	1.44	320.10	5.65	2.18	-0.84	0.08	0.54	0.99	1.22	2.67	43440.72
		mean	2.43	0.0025	1.63	477.03	16.60	2.65	-0.86	0.09	0.50	1.15	1.39	3.44	42756.61
		sd	0.81	0.0013	0.75	512.33	41.74	1.45	0.70	0.05	0.16	0.49	0.64	2.32	12942.12
Hadar - BM	10	median	2.81	0.0015	1.01	258.19	2.69	1.71	-0.29	0.05	0.31	0.91	0.21	0.36	42472.33
		mean	3.48	0.0019	1.10	374.25	4.07	1.74	-0.32	0.06	0.32	1.01	0.61	1.42	43097.56
		sd	2.05	0.0016	0.38	318.06	3.42	0.57	0.35	0.020	0.14	0.52	1.01	1.52	10323.30
Hadar -SH	32	median	2.20	0.0017	1.10	391.43	5.27	1.97	-0.50	0.07	0.53	0.83	0.63	1.61	44347.49
		mean	3.54	0.0021	1.17	509.26	18.95	2.13	-0.59	0.07	0.49	0.85	1.10	2.29	44195.07
		sd	2.42	0.0017	0.48	404.33	58.80	0.96	0.62	0.03	0.21	0.28	1.76	2.38	9525.09
Hadar -DD	59	median	1.95	0.0020	0.86	278.07	2.69	1.51	-0.30	0.05	0.46	0.68	0.31	0.47	43220.36
		mean	3.18	0.0027	0.98	353.34	4.86	1.63	-0.42	0.06	0.45	0.75	0.87	2.11	43172.05
		sd	2.57	0.0019	0.43	220.25	4.92	0.72	0.57	0.03	0.19	0.28	1.39	2.50	11358.31
Hadar -KH	8	median	4.22	0.0021	1.21	406.81	4.41	1.98	-0.44	0.08	0.50	0.78	1.20	4.03	48078.02
		mean	4.87	0.0027	1.30	628.59	10.10	2.13	-0.34	0.08	0.51	0.78	1.61	4.02	47322.24
		sd	3.44	0.0021	0.72	524.61	14.17	1.07	0.38	0.05	0.22	0.33	1.33	2.37	9895.37

Table 3.5. Analyses of central tendencies and variance (Levene's test) of suid microwear texture data. Data for analyses of central tendencies was rank-transformed to mitigate violation of assumptions inherent to parametric statistics (Conover & Iman 1981). Microwear data for analyses of variance were transformed for Levene's test ($X' = |X$— mean (X)|) following Plavcan & Cope (2001). Significant results where $p<0.05$ are bolded. Abbreviations: F, F value; p, p value; df, degrees of freedom.

	Extant taxa		Fossil taxa		Geological units	
Central tendencies	**F (df = 3)**	**p**	**F (df = 4)**	**p**	**F (df = 4)**	**p**
MANOVA Wilks' λ	**4.24**	**<0.0001**	**6.15**	**<0.0001**	**2.76**	**<0.0001**
ANOVA *Asfc*	33.48	**<0.0001**	30.08	**<0.0001**	1.64	0.1692
ANOVA *epLsar*	22.09	**<0.0001**	10.55	**<0.0001**	0.81	0.5182
ANOVA *S5v*	1.91	0.1420	**4.45**	**0.0022**	**4.88**	**0.0011**
ANOVA *Sda*	2.68	0.0576	0.83	0.5108	1.62	0.1728
ANOVA *Sdv*	2.69	0.0575	1.65	0.1666	2.12	0.0819
ANOVA *Sv*	**3.26**	**0.0300**	**5.51**	**0.0004**	**4.82**	**0.0012**
ANOVA *Ssk*	**3.20**	**0.0317**	**3.60**	**0.0082**	**3.10**	**0.0181**
ANOVA *Vvv*	**3.13**	**0.0346**	**3.52**	**0.0093**	**4.14**	**0.0035**
ANOVA *Str*	0.91	0.4436	1.56	0.1901	1.81	0.1309
ANOVA *Sdr*	2.54	0.0684	6.32	0.0001	4.14	0.0035
ANOVA $HAsfc_{9}$	**4.66**	**0.0063**	**21.57**	**<0.0001**	**6.04**	**0.0002**
ANOVA $HAsfc_{81}$	**3.27**	**0.0294**	**14.72**	**<0.0001**	**4.12**	**0.0036**
ANOVA *Tfv*	0.28	0.8383	0.20	0.9362	0.33	0.8580
Sample variances (Levene's test)						
MANOVA Wilks' λ	**2.06**	**0.0020**	**1.78**	**0.0011**	0.89	0.6834
ANOVA *Asfc*	**5.28**	**0.0033**	**3.53**	**0.0091**	**3.38**	**0.0117**
ANOVA *epLsar*	**8.85**	**0.0001**	1.50	0.2068	1.56	0.1895
ANOVA *S5v*	1.18	0.3280	2.14	0.0800	0.68	0.6090
ANOVA *Sda*	0.68	0.5705	0.53	0.7169	0.12	0.9750
ANOVA *Sdv*	1.39	0.2578	0.99	0.4171	0.72	0.5785
ANOVA *Sv*	1.20	0.3206	1.56	0.1906	0.83	0.5060
ANOVA *Ssk*	1.33	0.2767	**3.50**	**0.0097**	2.28	0.0647
ANOVA *Vvv*	1.92	0.1388	0.43	0.7869	0.63	0.6421
ANOVA *Str*	1.10	0.3588	0.62	0.6507	0.35	0.8466
ANOVA *Sdr*	**4.23**	**0.0101**	1.72	0.1499	0.69	0.5975
ANOVA $HAsfc_{9}$	2.37	0.0825	**3.67**	**0.0074**	1.32	0.2650
ANOVA $HAsfc_{81}$	1.04	0.3820	**4.37**	**0.0024**	**2.71**	**0.0333**
ANOVA *Tfv*	2.17	0.1038	0.57	0.6824	1.10	0.3621

Table 3.6. Post-hoc multiple comparisons for the microwear texture data (central tendencies) between all extant and fossil suid species using non-parametric Dunn's test to mitigate violation of assumptions inherent to parametric statistics (Dunn, 1964). Abbreviations: K, Kanapoi; H, Hadar.

Comparison	*Asfc*	*epLsar*	*S5v*	*Sda*	*Sdv*	*Sv*	*Ssk*	*Vvv*	*Str*	*Sdr*	$HAsfc_{9}$	$HAsfc_{81}$	*Tfv*
Extant													
H. meinertzhageni - *Phacochoerus* sp.	-0.7	0.86	0.92	0.12	0.61	0.49	-2.68**	0.97	0.22	0.51	0.24	1.48	-0.73
H. meinertzhageni - *Po. larvatus*	-3.06**	2.33*	-0.08	-0.07	-0.18	-0.56	-1.78	-0.01	-0.44	-0.77	1.11	1.5	-0.82
H. meinertzhageni - *Po. porcus*	-3.72***	3.48***	0.73	1.55	1.37	1.04	-1.56	1.38	-0.65	-0.03	-0.82	-0.14	-0.84
Phacochoerus sp. - *Po. larvatus*	-4.6****	2.85**	-1.97*	-0.34	-1.53	-2.06*	1.86	-1.93	-1.28	-2.51*	1.68	-0.01	-0.17
Phacochoerus sp. - Po. porcus	-4.67****	4.09****	-0.13	2.18*	1.26	0.91	1.21	0.79	-1.26	-0.71	-1.54	-2.16*	-0.31
Po. larvatus - *Po. porcus*	-1.65	2.25*	1.22	2.47*	2.34*	2.35*	-0.04	2.14*	-0.42	1	-2.74**	-2.22*	-0.2
Extant - fossil													
H. meinertzhageni - *K. afarensis*	-3.75***	3.89***	2.09*	1.5	1.79	1.59	-1.94	2.19*	-0.22	1.24	-1.13	-0.12	-1.26
H. meinertzhageni - *No. euilus*	-1.07	2.19*	2.31*	1.59	1.87	1.9	-2.21*	2.46*	-0.79	1.23	1.16	2.01*	-1.43
H. meinertzhageni - *Ny. jaegeri*	-0.67	0.89	0.38	0.67	0.61	0.34	-1.54	1.06	-0.46	0.87	-1.2	0.35	-0.89
H. meinertzhageni - *Ny. pattersoni* (H)	-1.55	3.48***	1.4	0.75	0.95	0.41	-1.34	1.45	-1.13	-0.09	0.77	1.65	-1.05
H. meinertzhageni - *Ny. pattersoni* (K)	-1.83	2.89**	0.78	1.43	1.06	0.39	-0.48	0.97	-1.26	-0.55	-1.13	0.02	-0.98
K. afarensis - *Phacochoerus* sp.	6.27****	-6.22****	-2.34*	-2.85**	-2.41*	-2.23*	-1.73	-2.44*	0.91	-1.47	2.84**	3.4***	1.06
K. afarensis - *Po. larvatus*	1.41	-3.39***	-4.81****	-3.47***	-4.38****	-4.8****	0.3	-4.89****	-0.51	-4.51****	5.02****	3.66***	0.95
K. afarensis - *Po. porcus*	-0.85	0.27	-1.67	0.44	-0.25	-0.51	0.15	-0.77	-0.74	-1.72	0.23	-0.07	0.38
No. euilus - *Phacochoerus* sp.	0.73	-2.84**	-2.94**	-3.24**	-2.71**	-3.05**	-1.37	-3.17**	2.25*	-1.53	-1.99*	-1	1.47
No. euilus - *Po. larvatus*	-5.11****	0.56	-5.75****	-3.99****	-4.94****	-5.99****	0.9	-5.96****	0.82	-4.9****	-0.02	-1.1	1.39
No. euilus - *Po. porcus*	-4.69****	2.73**	-1.98*	0.37	-0.32	-0.92	0.48	-1.12	0.03	-1.74	-2.94**	-3.01**	0.59
Ny. jaegeri - *Phacochoerus sp.*	0.15	-0.27	0.53	-0.8	-0.17	0.09	-0.91	-0.37	0.87	-0.62	1.92	1.2	0.41
Ny. jaegeri - *Po. larvatus*	-2.53*	1.38	-0.61	-1.02	-1.06	-1.11	0.15	-1.5	0.15	-2.09*	2.93**	1.22	0.32
Ny. jaegeri - *Po. porcus*	-3.29**	2.76**	0.36	0.91	0.78	0.74	0.11	0.27	-0.18	-1.05	0.52	-0.56	0.13
Ny. pattersoni (H) - *Phacochoerus* sp.	1.54	-4.73****	-0.88	-1.14	-0.64	0.14	-2.3*	-0.89	2.39*	1.05	-0.96	-0.35	0.61

Ny. pattersoni (H) - *Po. larvatus*	-2.65**	-2.32*	-2.75**	-1.51	-2.09*	-1.77	-0.7	-2.73**	1.33	-1.23	0.56	-0.37	0.49
Ny. pattersoni (H) - *Po. porcus*	-3.39***	0.51	-0.76	1.28	0.75	0.98	-0.52	0.12	0.54	0.08	-2.19*	-2.34*	0.16
Ny. pattersoni (K) - *Phacochoerus* sp.	2.07*	-3.7***	0.24	-2.39*	-0.83	0.19	-3.93****	-0.03	2.67**	1.89	2.47*	2.61**	0.49
Ny. pattersoni (K) - *Po. larvatus*	-2.18*	-1.2	-1.62	-2.84**	-2.32*	-1.76	-2.39*	-1.86	1.6	-0.4	4.19****	2.74**	0.35
Ny. pattersoni (K) - *Po. porcus*	-3.06**	1.32	0.05	0.4	0.63	1.02	-1.67	0.76	0.7	0.68	0.28	-0.23	0.06
Fossil													
K. afarensis - *No. euilus*	7.62****	-4.92****	0.51	0.18	0.12	0.8	-0.66	0.66	-1.58	-0.09	6.35****	5.87****	-0.4
K. afarensis - *Ny. jaegeri*	3.31***	-3.15**	-1.84	-0.74	-1.16	-1.33	-0.01	-0.97	-0.41	-0.17	-0.45	0.63	0.16
K. afarensis - *Ny. pattersoni* (H)	4.03****	-0.41	-1.17	-1.35	-1.5	-2.2*	1	-1.25	-1.85	-2.52*	3.68***	3.51***	0.29
K. afarensis - *Ny. pattersoni* (K)	3.57***	-1.68	-2.46*	0.02	-1.33	-2.3*	2.81**	-2.27*	-2.15*	-3.51***	-0.12	0.26	0.46
No. euilus - *Ny. jaegeri*	0.23	-1.19	-2.09*	-0.83	-1.24	-1.68	0.27	-1.26	0.24	-0.14	-3.09**	-1.8	0.33
No. euilus - *Ny. pattersoni* (H)	-1.2	3.12**	-1.61	-1.57	-1.7	-2.93**	1.54	-1.81	-0.85	-2.64**	-0.66	-0.49	0.6
No. euilus - *Ny. pattersoni* (K)	-1.83	1.85	-3.02**	-0.12	-1.52	-3.06**	3.5***	-2.92**	-1.15	-3.71***	-4.84****	-4.09****	0.78
Ny. jaegeri - *Ny. pattersoni* (H)	-0.83	2.71**	1.07	-0.07	0.24	0.01	0.57	0.21	-0.66	-1.26	2.47*	1.39	0.02
Ny. jaegeri - *Ny. pattersoni* (K)	-1.15	2.04*	0.37	0.7	0.36	-0.03	1.55	-0.35	-0.81	-1.78	0.36	-0.45	0.1
Ny. pattersoni (H) - *Ny. pattersoni* (K)	-0.47	-1.06	-1.07	1.17	0.18	-0.05	1.49	-0.83	-0.22	-0.78	-3.23**	-2.78**	0.13

Table 3.7. Post-hoc multiple comparisons for the microwear texture data (variance) between all extant and fossil suid species using non-parametric Dunn's test to mitigate violation of assumptions inherent to parametric statistics (Dunn, 1964). Abbreviations: K, Kanapoi; H, Hadar.

Comparison	*Asfc*	*epLsar*	*S5v*	*Sda*	*Sdv*	*Sv*	*Ssk*	*Vvv*	*Str*	*Sdr*	*HAsfc*$_{9}$	*HAsfc*$_{81}$	*Tfv*
Extant													
H. meinertzhageni - Phacochoerus sp.	0.84	1.82	0.59	-0.34	-1.38	-0.57	0.48	0.39	1.03	-1.98*	-0.66	-0.15	1.5
H. meinertzhageni - Po. larvatus	1.87	3.6***	-0.38	-0.95	-2.06*	-1.44	1.46	-0.88	0.83	-2.97**	-1.47	-0.84	2.25*
H. meinertzhageni - Po. porcus	-0.7	2.02*	0.69	0.02	-1.07	-0.45	0.63	0.45	1.66	-0.75	-0.13	0.1	1.4
Phacochoerus sp. - *Po. larvatus*	2*	3.42***	-1.89	-1.19	-1.3	-1.69	1.9	-2.46*	-0.42	-1.87	-1.56	-1.35	1.42
Phacochoerus sp. - Po. porcus	-2.14*	0.62	0.26	0.47	0.22	0.08	0.31	0.16	1.14	1.51	0.68	0.34	0.11
Po. larvatus - Po. porcus	-3.57***	-1.72	1.56	1.3	1.11	1.24	-0.99	1.86	1.46	2.84**	1.77	1.27	-0.87
Extant - fossil													
H. meinertzhageni - K. afarensis	0.63	2.55*	0.43	-0.27	-1.63	-0.52	1.47	0.23	0.72	-2.18*	-0.98	-0.07	1.61
H. meinertzhageni - No. euilus	1.07	2.49*	0.4	-0.39	-1.7	-0.77	0.74	0.2	0.59	-2.33*	-1.93	-1.13	1.78
H. meinertzhageni - Ny. jaegeri	0.79	2.17*	1.49	0.26	-0.31	0.86	-0.51	0.91	1.04	-1.15	-2.14*	0.4	2.07*
H. meinertzhageni - Ny. pattersoni (H)	1.38	1.98*	1.33	-0.7	-1.8	-0.25	0.4	0.37	1.17	-1.18	-0.8	-0.71	1.48
H. meinertzhageni - Ny. pattersoni (K)	2.26*	3.27**	0.66	-0.62	-1.15	-0.76	0.12	0.08	0.91	-2.3*	-0.66	0.39	1.23
K. afarensis - Phacochoerus sp.	0.49	-1.37	0.38	-0.16	0.44	-0.15	-2*	0.37	0.72	0.27	0.62	-0.18	-0.13
K. afarensis - Po. larvatus	2.85**	2.51*	-1.8	-1.55	-1.04	-2.13*	0.05	-2.48*	0.3	-1.9	-1.15	-1.76	1.53
K. afarensis - Po. porcus	-1.96	-0.25	0.52	0.4	0.51	-0.02	-1	0.41	1.69	1.78	1.13	0.25	0.04
No. euilus - Phacochoerus sp.	-0.42	-1.25	0.5	0.1	0.55	0.38	-0.51	0.46	1.08	0.54	2.73**	2.15*	-0.45
No. euilus - Po. larvatus	2.11*	3.03**	-1.89	-1.43	-1.07	-1.76	1.89	-2.67**	0.65	-1.82	0.99	0.63	1.34
No. euilus - Po. porcus	-2.62**	-0.11	0.6	0.57	0.58	0.33	0.03	0.47	1.93	2*	2.46*	1.72	-0.17
Ny. jaegeri - Phacochoerus sp.	-0.15	-0.94	-1.4	-0.73	-1.13	-1.82	1.25	-0.82	-0.29	-0.65	2.22*	-0.72	-1.16
Ny. jaegeri - Po. larvatus	1.01	1.03	-2.52*	-1.43	-1.9	-2.83**	2.37*	-2.26*	-0.53	-1.75	1.36	-1.51	-0.36
Ny. jaegeri - Po. porcus	-1.69	-0.36	-1.01	-0.28	-0.81	-1.5	1.29	-0.59	0.59	0.55	2.39*	-0.37	-0.92

Ny. pattersoni (H) - *Phacochoerus* sp.	-1.01	-0.35	-1.35	0.67	0.81	-0.56	0.14	0.02	-0.29	-1.38	0.29	1.01	-0.01
Ny. pattersoni (H) - *Po. larvatus*	0.8	2.81**	-3.17**	-0.4	-0.35	-2.15*	1.9	-2.28*	-0.69	-3.18**	-1.15	-0.2	1.31
Ny. pattersoni (H) - *Po. porcus*	-2.8**	0.34	-0.74	0.94	0.8	-0.33	0.4	0.16	0.9	0.46	0.87	1.06	0.1
Ny. pattersoni (K) - *Phacochoerus* sp.	-2.6**	-2.67**	-0.14	0.54	-0.39	0.36	0.66	0.54	0.19	0.64	0.03	-0.96	0.46
Ny. pattersoni (K) - *Po. larvatus*	-0.85	0.43	-1.94	-0.57	-1.63	-1.23	2.49*	-1.77	-0.2	-1.11	-1.46	-2.29*	1.83
Ny. pattersoni (K) - *Po. porcus*	-3.97****	-1.34	0.16	0.84	-0.08	0.34	0.78	0.55	1.25	1.93	0.68	-0.37	0.44
Fossil													
No. euilus - *Ny. jaegeri*	1.19	-0.31	-0.12	-0.32	-0.1	-0.68	-2.1*	-0.09	-0.38	-0.32	-2.58**	-2.93**	0.4
No. euilus - *Ny. pattersoni* (H)	0.43	0.23	1.67	0.68	1.41	1.82	-2.41*	1.05	0.69	0.82	-1.98*	0.66	1.15
No. euilus - *Ny. pattersoni* (K)	1.58	-0.87	1.86	-0.89	-0.52	0.49	-1.99*	0.32	0.98	1.79	0.25	-1.29	-0.11
Ny. jaegeri - *Ny. pattersoni* (H)	3.39***	1.73	0.51	-0.75	0.84	-0.54	-2.62**	-0.27	0.47	-0.47	0.56	0.93	-0.64
Ny. jaegeri - *Ny. pattersoni* (K)	-0.07	0.36	1.75	0.82	1.49	2.14*	-1.6	1.11	0.87	0.97	-0.96	1.88	1.02
Ny. pattersoni (H) - *Ny. pattersoni* (K)	0.83	-0.71	2.07*	-0.72	-0.49	1.01	-0.62	0.41	1.32	2.14*	2.13*	0.74	-0.4
K. afarensis - *No. euilus*	2.77**	2.08*	0.63	-0.57	0.97	-0.09	-1.27	-0.23	0.79	-0.27	2.51*	3.16**	-0.98
K. afarensis - *Ny. jaegeri*	0.49	-0.7	-0.52	-1.13	-1.61	-1.42	1.13	-0.81	-0.1	0.24	1.98*	-1.33	-1.13
K. afarensis - *Ny. pattersoni* (H)	1.47	0.74	-1.29	-1.04	-0.87	-2.01*	0.82	-1.14	-0.4	-1.03	2.16*	-0.11	-1.43
K. afarensis - *Ny. pattersoni* (K)	1.49	2.18*	-1.16	0.14	1.14	-0.87	-0.49	-0.5	-0.45	-1.91	0.26	1.87	-0.45

Table 3.8. PCA scores pooled for extant taxa.

Variable	PC 1	PC 2	PC 3
Asfc	0.032	0.501	-0.275
epLsar	0.080	-0.347	0.512
S5v	0.412	0.071	-0.043
Sda	0.366	-0.063	0.335
Sdv	0.413	-0.027	0.172
Sv	0.438	0.030	-0.044
Ssk	-0.189	-0.091	0.222
Vvv	0.429	0.027	0.017
Str	0.015	0.056	-0.241
Sdr	0.323	-0.020	-0.421
$Asfc_{9}$	-0.045	0.532	0.356
$Asfc_{81}$	0.010	0.558	0.305
Tfv	0.015	-0.100	-0.108

4.2 Fossil suid diets

Most of the microwear variables that separate extant suid species also separate the fossil species analyzed in this work and include *Asfc*, *S5v*, *Sv*, *Ssk*, *Vvv*, $HAsfc_{9}$, and $HAsfc_{81}$ (Tables 3.4–3.5, Figure 3.2). As in the case of extant suids, the measures of complexity (*Asfc*) and anisotropy (*epLsar*) largely drive separations between taxa, but in the case of fossil species, heterogeneity ($HAsfc_{9}$ and $HAsfc_{91}$) also seems to play a big role ($p<0.0001$, Table 3.5). The median values of *Asfc* are higher in *K. afarensis* (5.79) and lowest in *Ny. jaegeri* (1.83) and *No. euilus* (1.66), while the values are intermediate in *Ny. pattersoni* (Kanapoi = 2.54; Hadar = 2.12). Conversely, *Ny. jaegeri* and *No. euilus* have the highest values of *epLsar*, 0.0040 and 0.0027, respectively, while *Ny. pattersoni*

(Kanapoi), *Ny. pattersoni* (Hadar), and *K. afarensis* have 0.020, 0.0016, and 0.0014, respectively. When considering *Asfc* and *epLsar* together (Figure 3.3), *K. afarensis* more closely resembles *Po. porcus* and *Po. larvatus*, while *Ny pattersoni* (at both Hadar and Kanapoi) is closer to *Po. larvatus*. Finally, *Ny. jaegeri* and *No. euilus* more closely resemble *Phacochoerus* (Figure 3.3). With respect to *S5v*, a measure of feature depth, *Ny. jaegeri* (1.45) and *Ny. pattersoni* (1.35 in Kanapoi and 1.25 in Hadar), have higher median values than *No. euilus* (0.91) and *K. afarensis* (0.97). *Nyanzachoerus jaegeri* and *Ny. pattersoni* (both in Hadar and Kanapoi) also have the highest median values of *Sv*, *Vvv*, *Ssk*, and *Sdr*. In the case of heterogeneity ($HAsfc_{9}$ and $HAsfc_{91}$), *Ny. jaegeri* (1.96 and 2.26), *Ny. pattersoni* from Kanapoi (1.11 and 2.84), and *K. afarensis* (1.08 and 3.45), have median values that are significantly higher than *Ny. pattersoni* from Hadar (0.29 and 0.40) and *No. euilus* (0.18 and 0.35) ($p<0.0001$, Table 3.6).

The variances of *Asfc*, *Ssk*, $HAsfc_{9}$ and $HAsfc_{81}$ are also significantly different between taxa. For *Asfc*, differences were only statistically significant between *Ny. jaegeri* and *Ny. pattersoni* from Hadar ($p<0.001$, Table 3.7), and *K. afarensis* and *No. euilus* ($p<0.01$, Table 3.7). *Nyanzachoerus jaegeri* and *Ny. pattersoni* from Hadar also differ in the variance of Ssk ($p<0.01$, Table 3.7). Finally, the differences in heterogeneity ($HAsfc_{9}$ and $HAsfc_{81}$) are different between *No. euilus* and *Ny. jaegeri*, but also between *No. euilus* and *K. afarensis* ($p<0.01$, Table 3.7).

When the differences in the microwear signal are visualized in the PCA, there is a certain degree of overlap between all the fossil suid species analyzed. However, differences are still visible, especially when looking at the distribution of values in PC2. Most *K. afarensis* and *No. euilus* values do not overlap, while all other suids occupy an intermediate area between these two species. The results are better visualized in Figure 3.4C, where each point is the median value for PC1 and PC2 in multivariate space, and the lines represent the standard deviation. *Kolpochoerus afarensis* falls very close to *Po. porcus*, while *Ny. pattersoni* from Kanapoi occupies an intermediate position between *Po. porcus* and *Po. larvatus*. *Nyanzachoerus jaegeri* and *Ny. pattersoni* from Hadar also occupy an intermediate position but are closer to *Phacochoerus*. Finally, *Notochoerus euilus* is separated from both fossil and modern species, though its values are also closer to those of *Phacochoerus*.

4.3 Geological units

The results presented above suggest that *Asfc* and *epLsar* are the two best measures to distinguish the diet of extant and fossil suids. However, when grouped by geological unit (Kanapoi and Hadar members BM, SH, DD, and KH), no differences were encountered between these two variables in the fossil taxa ($p>0.05$; Table 3.5). Hadar's KH Member has a higher median value of *Asfc* (4.22), however, compared to the DD Member (1.95), although this difference is not statistically significant given the variance (Table 3.4). Statistically significant differences were found in *S5v*, *Sv*, *Ssk, Vvv*, all of which differ significantly only between Kanapoi and Hadar DD Member. Kanapoi has higher median values of *S5v* (1.44), *Sv* (2.18), *Ssk* (-0.84), and Vvv (0.08) than Hadar DD Member: *S5v* (0.86), *Sv* (1.51), *Ssk* (-0.30), and *Vvv* (0.05). The Hadar BM Member also has significantly lower values of *Ssk* (-0.29) and *Vvv* (0.05) than Kanapoi. Finally, heterogeneity is higher at Kanapoi ($HAsfc_{9}$ = 1.22, $HAsfc_{81}$ = 2.67) than for Hadar's BM ($HAsfc_{9}$ = 0.21, $HAsfc_{81}$ = 0.36), SH ($HAsfc_{9}$ = 0.63, $HAsfc_{81}$ = 1.61), and DD (HAsfc_{9} =

0.31, $HAsfc_{81}$ = 0.47) members, but has similar median values to Hadar KH Member ($HAsfc_{9}$ = 1.20, $HAsfc_{81}$ = 4.03).

5. Discussion

5.1 Extant suid microwear texture baseline

Characterizing the diet of fossil suids is challenging because most extant suids, and presumably most of their extinct relatives, have generalized diets (Meijaard et al., 2011). Diets, however, may vary depending on the habitats they occupy and the resources available in their habitats as a result. For example, extant *Po. larvatus* individuals show seasonal variation in diet (Jones, 1984). They also live in different habitats, from dry bushland to forested habitats, and they vary their diet across these habitats accordingly (Skinner et al., 1976; Jones, 1984; Seydack, 1990). This study shows that despite a high degree of overlap in the microwear signal, preferred food differences in extant suid species are reflected in microwear variation, and in turn can be used to infer aspects of diet of fossil suids.

Differences in the diets of extant taxa are especially notable in two microwear texture variables, *Asfc* (complexity) and *epLsar* (anisotropy), which are among the most widely used features to differentiate tooth use in these type of analyses (Ungar, 2010; Ungar et al., 2010, 2017; Souron et al., 2015b). Extant suids with broad diets, *Po. porcus* and *Po. larvatus*, have high values of complexity in comparison to the grazer *Phacochoerus* and the mixed feeder *Hy. meinertzhageni*. The microwear textures of extant suids are compatible with other microwear studies and confirm that *Asfc* and *epLsar* can distinguish between classic dietary dichotomies: browser vs grazer, and hard-object vs tough-object feeding (Ungar et al., 2010, 2017; Scott, 2012a, 2012b; Souron et al., 2015b). In other mammal groups, such as primates and bovids, microwear textures featuring high complexity (*Asfc*) and low anisotropy (*epLsar*) are associated with hard object specialists or browsers (Daegling et al., 2011). In contrast, low complexity values and high anisotropy values are associated with species that graze or consume tough leaves (Scott et al., 2006; Ungar et al., 2007; Scott, 2012a, 2012b). When all variables are combined in a principal component analysis, it is possible to further distinguish between different suid feeding behaviors.

The microwear analysis of extant suid taxa serves as a reference baseline to compare fossil suid taxa. General predictions can be made about the diet of fossil suids based on dental morphology. I discuss the results of the fossil species analyzed in this work below.

5.2 Fossil Suidae from Hadar

The Pliocene deposits of Hadar are dominated by two suids from the subfamily Tetraconodontinae, *Ny. pattersoni* and *No. euilus*, and one suid from the subfamily Suinae, *K. afarensis* (Cooke, 1978a; Fessaha, 1999). Tetraconodontines were large suids (Harris and White, 1979), even larger than modern *Hylochoerus* that has a maximum male body mass of 275 kg (Meijaard et al., 2011). Tetraconodontines first appeared in Africa in the Miocene and then became extinct in the Pleistocene (Made, 1999; Pickford, 2006). The early representatives of this subfamily in Africa, *Nyanzachoerus*, are characterized by very large third and fourth premolars and bunodont to bunolophodont molars, as is the case of *Ny. kanamensis* (Harris and White, 1979; Harris, 1983; Made, 1999). *Nyanzachoerus* is believed to be ancestral to *Notochoerus*, a derived genus that shows a tendency to increase the number of pillars, length, and height of the third molars, and to reduce the number and size of the premolars and the incisors through time. There is also a tendency towards thinner enamel with increased folding (Harris and White, 1979). These changes in the masticatory complex represent a temporal morphocline in the *Nyanzachoerus-Notochoerus* lineage (Made, 1999) and have been linked to the incorporation of more C_4 grasses into the diet (Harris and Cerling, 2002; Bedaso et al., 2013; Wynn et al., 2016; Souron, 2017). *Notochoerus euilus* individuals at Hadar are among the earliest representatives of this lineage, but they already express derived characteristics of the masticatory apparatus. The third suid species present at Hadar is *K. afarensis*. Most of the Pliocene representatives of the genus *Kolpochoerus* were much smaller than the tetraconodontines and possessed similar dental adaptations to those seen in extant *Potamochoerus* or *Sus*, for example low-crowned bunodont third molars (Harris and White, 1979; Harris, 1983; Fessaha, 1999; Bishop et al., 2006; Haile-Selassie and Simpson, 2013; Souron et al., 2015a). A summary of the most important craniodental characteristics and paleoecological data on the three fossil suids from Hadar is provided below.

Nyanzachoerus pattersoni (subfamily Tetraconodontinae)

This suid exhibits a larger body size than any extant suid. Its dentition is morphologically close to *Potamochoerus* but is differentiated, among other things, in having slightly taller and more lophodont molars, as well as larger premolars. Carbon stable isotope analyses have yielded an average $\delta^{13}C$ of -2.91±1.47‰ at Kanapoi

(Geraads and Bobe, 2017), and -3.81±1.33‰ at Hadar (Wynn et al., 2016), which overall implies mostly a mixed C_3-C_4 diet. The microwear results suggest a mixed feeding diet, but with complexity (*Asfc*) and anisotropy (*epLsar*) values that are lower than any modern suid taxa analyzed in this work and indicate that *Ny. pattersoni*'s diet was likely different to that seen in any modern suid species and did not include large amounts of hard objects. The most significant differences between the Kanapoi and Hadar samples of *Ny. pattersoni* are between heterogeneity measures ($Hafsc_9$ and $Hafsc_{81}$), which are much lower at Hadar and closer to the values seen in *Phacochoerus* and *Po. larvatus*. The range of microwear values for different variables is also larger in Hadar, suggesting a broader dietary niche breadth.

Notochoerus euilus (subfamily Tetraconodontinae)

This well-represented species is the most abundant of the genus *Notochoerus*, a group of derived tetraconodonts with craniodental features that are hypothesized to represent adaptations to grazing diets (Harris and White, 1979). In many respects, their craniodental morphology is convergent with extant *Phacochoerus* (e.g., vertical and tall occipital, orbits situated high up in the cranium, hypsodont third molars, reduced premolars and incisors, flattened anterior mandibular symphysis). Throughout the Hadar sequence, there is a trend towards premolar reduction in this species, as well as larger and more hypsodont third molars (Fessaha, 1999). Carbon stable isotope analyses from Hadar suggest a grazing diet, with a $\delta^{13}C$ average of -1.75±1.43‰ (Wynn et al., 2016), which is higher than that of *Ny. pattersoni*. The microwear results are consistent with a grazing diet but the microwear signal is much broader than expected, which I speculate may be related to seasonal dietary shifts and opportunistic feeding such as those seen in extant warthogs (Cumming, 1975). In general, both carbon stable isotopes and dental microwear analyses confirm that *No. euilus* ate mostly grasses.

Kolpochoerus afarensis (subfamily Suinae)

In many respects, this species is morphologically very similar to modern *Potamochoerus* but had a larger body size, based on the overall size of the dentition and the skull (Souron, 2012). *Kolpochoerus afarensis* has bunodont and brachyodont molars, and hypsodont incisors that are used, among other things, to acquire underground resources like roots, rhizomes, and earthworms (Lazagabaster, 2013). Carbon stable isotope analysis from Hadar yielded average $\delta^{13}C$ values of -3.76±2.50‰ (Wynn et al., 2016), suggesting a mixed C_3-C_4 diet. My results, however, show that this suid was probably more omnivorous, with a microwear signal that overlaps with that of extant *Po. porcus* (though $n = 6$) whose diets incorporate hard and brittle foods such as nuts and seeds. The microwear results are compatible with what was expected for *K. afarensis* based on the craniodental features shared with modern *Potamochoerus*.

5.3 Paleohabitats at Hadar and comparison with Kanapoi

Based on ecomorphology and community structure analysis, Reed (2008) identified fluctuating paleoenvironments across the Hadar sequence timespan, ranging from intermediate cover bushland, open woodland, to shrubland habitats with varying regions of wetlands and edaphic grasslands across space. Reed (2008) characterized the Basal Member (~3.45–3.42 Ma) by woodlands, grasslands, and some riverine forest, a reconstruction that is consistent with the rich riverine pollen record in this member

(Bonnefille et al., 2004), and with data from paleosol carbonates only indicating ~ 30% C4 grass cover (Hailemichael, 2000; Aronson et al., 2008). The overlying Sidi Hakoma Member (~3.42–3.26 Ma) had the most forested and closed habitats in the SH-1 submember, with high rainfall and low seasonality, as reconstructed from the fossil mammals (Reed, 2008). This characterization is supported by pollen analyses (Bonnefille et al., 1987, 2004) and dental microwear analyses of Hadar bovids (Scott, 2012a, 2012b). The SH-3 and SH-4 submembers probably consisted of woodlands and wet grasslands (Reed, 2008). In fact, mollusk shell analyses indicate that the SH-3 had the least evaporated condition of the Hadar paleolake (Hailemichael et al., 2002), which would also indicate the presence of wetlands. The Denen Dora Member (~3.24–3.20 Ma) consisted mostly of edaphic or wetland grasslands and the DD-1 submember was still much influenced by the presence of the lake (Campisano and Feibel, 2008). The pollen record indicates a transition from woodland to wetlands, open woodlands, and grasslands (Bonnefille et al., 2004) associated with fluvial systems (Campisano and Feibel, 2008). The wetland dominated habitats in the DD member were replaced by more xeric conditions in the Kada Hadar Member (~3.20–2.95 Ma) (Reed, 2008), but the pollen record and various spatial analyses of the submembers (Campisano, 2007) suggests that a riverine forest was still present at this time.

The results in this work included a disparate array of microwear signals and suggest that fossil suid diets at Hadar were broad. On the one hand, *Nyanzachoerus pattersoni* had a mixed diet, indicated by the microwear and carbon isotope data, which included different types of dietary resources. This suid is relatively abundant in the Sidi Hakoma Member, when habitats have been reconstructed as more wooded and closed, with high rainfall and shorter dry seasons (Reed, 2008). But *Ny. pattersoni* disappears from the region in the overlying Denen Dora Member ~3.24 Ma, when the habitats get more open and grasslands spread (Bonnefille et al., 2004; Reed, 2008). The Denen Dora Member is dominated by *Notochoerus euilus* (>80% of relative suid abundance), a suid characterized by a grazing-dominated diet as indicated by both carbon stable isotope and dental microwear texture data. This is compatible with more open habitats after ~3.2 Ma. However, the overall microwear signal is quite variable and suggest that *No. euilus* had a wide dietary breadth (Figure 3.4B) and, as mentioned above, I hypothesize that some of these microwear signals may be the product of occasional or seasonal feeding on non-grass foods. Finally, *K. afarensis*, which is present across all the Hadar members, has microwear consistent with a variable diet that probably included hard objects in the diet, such as fruits or nuts, or underground resources that are more available in seasonal environments. The slight trend in this species towards lower values of complexity and higher values of anisotropy through the Hadar sequence indicates a small increase in grazing resources in the Kada Hadar Member ~3.1 Ma. *Notochoerus euilus* also has higher values of anisotropy in this member, suggesting more grazing at the end of the Hadar sequence, which is compatible with the reconstruction of Reed (2008). In general, the microwear texture evidence across Hadar species is consistent with the presence of some woody cover at Hadar but also grasslands at the site/in the region, which became more abundant especially after 3.24 Ma.

5.4 Dietary breadth expansion in the *Australopithecus anamensis—Australopithecus afarensis* lineage

One of the goals of this study is to explore possible habitat differences that would indicate a cause for the increase in dietary breadth in *A. afarensis* compared with *A. anamensis at* Kanapoi and Hadar (Kimbel et al., 2006; Sponheimer et al., 2013) through the examination of changes in suid diets. When the microwear values across suid species were pooled to compare the data between sites, there was no statistically significant differences between the two. This is probably due to the substantial overlap in the microwear texture metrics between the different species analyzed, which was a similar case for modern taxa. However, when each fossil suid species is discussed separately as in Section 4.2., a pattern emerges.

First, *Nyanzachoerus pattersoni* had a broader diet in Hadar than in Kanapoi, which probably included the exploitation of more grazing resources in Hadar. After 3.24 Ma, this suid is no longer found in the region, and this coincides with a peak in abundance of *Notochoerus euilus*, which shows a grazing-dominated diet but also variable. This grazing signal is much stronger than that observed in its putative ancestor in Kanapoi, *Ny. jaegeri*. Despite the diet overlap, these changes exemplify modifications in the feeding strategies of these two lineages towards broader diets with the inclusion of more graze, suggesting, in turn, changes in the environments between Kanapoi and Hadar, namely the expansion of grasslands in Hadar.

Kolpochoerus afarensis, which is absent at Kanapoi but present at Hadar (Cooke, 1978a; Fessaha, 1999; Geraads and Bobe, 2017), has *Asfc* values that are much higher than those seen at Kanapoi and are comparable to those of the extant species *Po. porcus*, suggesting the exploitation of hard food items, such as unripe or hard fruits, tubers, and other underground resources like rhizomes. This fact by itself suggests that there was some type of habitat filtering to limit *Kolpochoerus* species at Kanapoi, i.e. Kanapoi lacked some of the resources exploited by *Kolpochoerus*. Alternatively, Kolpochoerus could have been outcompeted in these resources and/or habitats by tetraconodontines. *Kolpochoerus* is present in other parts of the Turkana Basin at ~3.9 Ma like Allia Bay but absent from Mursi <4.0 Ma (Drapeau et al., 2014), and nevertheless it is always less well represented than it is at Hadar 500 ka later. On the other hand, tetraconodontines were very abundant both at ~4.0 Ma sites and at Hadar (Fessaha, 1999; Drapeau et al., 2014; Geraads and Bobe, 2017; Rannikko et al., 2017), which implies that habitat filtering, including climatic factors, rather than competition was responsible for the lack of *Kolpochoerus* at Kanapoi.

The combined evidence of the reconstructed habitats and the suid isotopes and microwear suggests that the habitats at Hadar were more heterogeneous and/or seasonal than at Kanapoi, though Kanapoi already shows some degree of fragmentation (Wynn, 2000; Ungar et al., 2017). This could mean that both the suids and the hominins needed to seek out different food resources due to these climatic variables that affected C_3 resources between the two localities. These results also support dietary niche partitioning among suids at Hadar, which was not evident from carbon stable isotope analyses (Harris and Cerling, 2002; Wynn et al., 2016; Manthi et al., 2017). Niche partitioning among suids further suggests there were resource differences in the habitats that forced hominins at Hadar to expand their niche breadth.

In sum, the changes in the dietary ecology of Hadar suids with respect to Kanapoi supports the idea that the increased dietary breadth in *Au. afarensis* compared to *Au. anamensis* was probably due to changes in the environment. Namely, a change in climate that caused an increase in habitat fragmentation and the reduction of C_3 resources and/or an increase in seasonality that changed the presence of these C_3 dietary resources seasonally. Both hominins and suids may have adapted to this new scenario by exploiting fall back foods or other resources when the preferred foods where not available, something that did not occur at Kanapoi. New stable isotopic data indicates that the incorporation of C_4 resources in hominin's diets may have occurred as early as 3.76 Ma, a pattern also observed in *Theropithecus* (Levin et al., 2015), suggesting that hominins were expanding the types of food resources and potentially the environments that they were able to exploit at this time. As if we argue here for Hadar, environmental changes were partly responsible of that early dietary shift observed in hominins, the analysis of suid's diets between ~4.0 and ~3.5 Ma may also shed light on this issue.

6. Conclusions

The dental microwear texture analysis presented in this work revealed that despite a high degree of overlap in the microwear signal, the suids from Hadar occupied different dietary niches, a suggestion that was not evident from analyses of stable isotopes alone. The microwear results support that *No. euilus* was a grazer, *Ny. pattersoni* was a mixed feeder, and *K. afarensis* was an omnivore. These results are compatible with what is known of the craniodental morphology of these three species. While *K. afarensis* and *Ny. pattersoni* had low-crowned bunodont molars that resemble modern *Potamochoerus* or

Sus, *No. euilus* had elongated and hypsodont third molars more comparable to modern *Phacochoerus*. The overlap in microwear signal may be explained by the fact that most suids have generalized diets and even when they have the morphology that allows specialization in a particular food resource, they still opportunistically or seasonally feed on other foods. Microwear results also suggest an increase in the overall dietary niche space occupied by suids at Hadar ~3.45–2.95 Ma in comparison with those at Kanapoi ~4.1 Ma. This is especially reflected by higher values of complexity (*Asfc*) in *K. afarensis*, a suid that is not present in Kanapoi, and by an increase in grazing diets in both *Ny. pattersoni* and in the *Ny. jaegeri–No. euilus* lineage. A turn towards more open habitats after ~3.24 Ma may explain the disappearance of *Ny. pattersoni* in the fossil record and the peak in abundance in *No. euilus*. Overall, these differences between suid diets at these two sites suggests that the habitats at Hadar were more heterogenous or fragmented and that the climate was probably more seasonal than in Kanapoi. In the face of the likely reduction of C_3 resources available in Hadar, *A. afarensis* also exploited C_4 resources but this exploitation seems to have been limited to tough parts of these plants, according to dental microwear analyses. The suid microwear texture data presented here suggests that other resources (e.g., hard objects like fruits, nuts, and underground resources such as tubers) were also available in Hadar, but hominins were not exploiting them. This raises the possibility that a true dietary breadth expansion (in terms of food physical properties) was yet to come. Currently, there is no substantial evidence to support a significant transition towards flexible dietary behaviors in the *A. anamensis-A. afarensis* lineage. Most likely, the observed increase in the breadth of carbon stable isotope values are due to a reduction of C_3 resources available in the region.

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CHAPTER 4. DIETARY ECOLOGY OF PLIOCENE SUIDAE (MAMMALIA, ARTIODACTYLA): ISOTOPIC EVIDENCE FROM WORANSO-MILLE, AFAR, ETHIOPIA

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Abstract

Wild pigs were abundant and diverse during the Pliocene in Eastern Africa, as evidenced by the great number of fossils recovered from different paleontological sites. The Woranso-Mille paleoanthropological site has provided evidence of early hominin evolution between ~3.76 Ma and ~3.2 Ma. Here, the diet of extinct suids from this time frame is explored through the analysis of carbon and oxygen stable isotope ratios from the enamel of dental remains from Woranso-Mille. The results indicate that Pliocene suids were partitioning dietary niches to a certain extent. *Kolpochoerus millensis* had a variable C_3-C_4 diet that included a certain amount of C_3 resources in the diet, which is compatible with its generalized dentition similar in morphology and size to extant omnivores of the genus *Potamochoerus* and *Sus*. The replacement of *K. millensis* ~ 3.5 Ma by its descendant *K. afarensis*, a suid of larger body size, is related to a significant increase in the amount of C_4 resources in the diet. On the other hand, the diet of *Nyanzachoerus jaegeri* and *Notochoerus euilus* were mostly based on C_4 resources, which confirms the *a priori* expectations that the derived craniodental morphology of these suids were adaptations to consume abrasive foods such as C_4 grasses. In general, the carbon and oxygen stable isotope data are compatible with mixed habitats consisting of densely vegetated areas probably associated with a river or other body of water, and open grasslands (Curran and Haile-Selassie, 2016). The increase in relative abundance of *No. euilus* in the U-WM together with the increase in C_4 resource consumption of *K. afarensis* in the upper Woranso-Mille interval (3.47–3.20 Ma) suggest changes towards more open habitats through time.

Key words: suid diet, middle Pliocene, niche partitioning, paleoecology, feeding

1. Introduction

The extinct relatives of pigs and hogs (family Suidae) were an important component of eastern African faunas during the Pliocene, as evidenced by the large number of fossils recovered from paleontological sites across Africa (Cooke and Ewer, 1972; Cooke, 1978a, 1978b, 2007; Harris and White, 1979; Harris, 1983; Cooke and Hendey, 1992; White, 1995; Bishop et al., 1999; Made, 1999; Harris et al., 2003;

Pickford, 2006; Bishop, 2010; Geraads and Bobe, 2017; Reda et al., 2017; Lazagabaster et al., 2018). Suid fossils have been intensively studied because of their value as biochronological markers (White and Harris, 1977; Cooke, 1978b, 1985; Harris and White, 1979) but they have also been used in paleohabitat reconstructions (Bishop, 1994, 1999; Cuddahee, 2008) and in other evolutionary and paleocological issues within the framework of mammalian – including hominin – evolution (White, 1995; Cooke, 2007; Souron, 2012).

The main reason that suids are so useful in these endeavors is because their dentition evolved rapidly and markedly during the Plio-Pleistocene in Africa (Harris and White, 1979), possibly in response to dietary shifts triggered by global and/or regional environmental changes (DeMenocal, 1995; Reed, 1997; Harris and Cerling, 2002; deMenocal, 2004; Maslin et al., 2014). In fact, suid evolution is a good example of the impact that the spread of grasslands had on the evolution of Eastern African biota (Harris and Cerling, 2002; Cooke, 2007). As C_4 grasslands spread (Cerling et al., 2011), suids adapted their masticatory apparatus to the consumption of foods with a higher content of abrasive particles (e.g., silica and grit associated with grasses) (Harris and White, 1979; Made, 1999; Cooke, 2007). Thus, most African suid lineages are characterized by one or more species which exhibit parallel and progressive dental evolutionary trends, including the increase in third molar length and height and the reduction of the premolars (Harris and White, 1979).

Carbon stable isotope analysis have shown, however, that the relationship between the consumption of C_4 resources (e.g., grasses) and craniodental morphology in African Suidae is not straightforward and that suids had C_4-enriched diets well before the appearance of derived anatomical features supposedly related to the consumption of those diets (Harris and Cerling, 2002). For instance, Late Miocene African suids already had an important C_4 component in their diets but their craniodental morphology did not differ significantly to that of their more primitive Asian relatives (Harris and Cerling, 2002; Harris and Leakey, 2003). It is during the Pliocene when derived craniodental adaptations (e.g., significant increase in third molar length and height) make their appearance in the suid fossil record. Yet, even during this time carbon stable isotope values are similar among suid species with very different craniodental adaptations (Wynn et al., 2016).

Our understanding of the evolution of African suid diets during the Pliocene was hampered by the limited temporal and spatial paleodietary data available. The fossil sample of Harris and Cerling's (2002) stable isotope analysis of fossil suid diets had important temporal gaps (e.g., between 4.0 Ma and 3.5 Ma) and was restricted to the Turkana Basin, in Kenya and Ethiopia, and some specimens from Laetolil, in Tanzania. Suid diets in other important fossiliferous areas, like the Afar region in Ethiopia, remained largely unexplored. This deficit in the Afar has now partially been covered by the work of Semaw et al. (2005), White et al. (2009), Bedaso (2011), Levin et al. (2015, 2008), Wynn et al. (2016), and Robinson et al. (2017). For example, Levin et al. (2015) have shown an increase in the consumption of C_4 resources by early hominins and cercopithecids ~3.76 Ma in Woranso-Mille, lower Awash Valley, Ethiopia, while Wynn et al. (2016), Robinson et al. (2017) and also myself in Chapter 2 of this dissertion, have identified a trend towards the incorporation of C_4 resources in suid diets from ~3.45 Ma to ~2.6 Ma. In addition, microwear analyses have revealed that the suids from Hadar (~ 3.45–2.95 Ma), Afar, Ethiopia, had broader diets that included more graze but also included hard objects and/or underground resources in comparison to older sites, in particular the site of Kanapoi (~ 4.1 Ma), in Kenya (Chapter 3 of this dissertation). Here, we use stable isotope analyses to investigate the diet of the Suidae from Woranso-Mille, in the lower Awash Valley, Afar, Ethiopia. With the data presented here and the increasingly available carbon stable isotopes values in the literature, it is now possible to build a continuous sequence of suid dietary change in the Afar region and broadly in Eastern Africa between ~3.8 Ma and ~2.6 Ma.

1.1 Pliocene African Suidae

The evolution of African Suidae since the Pliocene can be understood in terms of four major genera, comprising *Nyanzachoerus*, *Notochoerus*, *Kolpochoerus*, and *Metridiochoerus* (Harris and White, 1979). *Nyanzachoerus* and *Notochoerus* belong to the Tetraconodontinae, a subfamily of suids with no living counterparts. Some representatives of the genus *Nyanzachoerus* were among the earliest to migrate into Africa during the Miocene (Harris and White, 1979; Made, 1999; Bishop, 2010). The suid *Nyanzachoerus pattersoni* was described from Kanapoi ~ 4.1 Ma and Hadar ~ 3.45 – 3.2 Ma (Cooke and Ewer, 1972; Cooke, 1978a) but it was synonymized with *Ny. kanamensis* by Harris and White (1979) and other authors that followed (e.g., Geraads and Bobe, 2017). The genus *Nyanzachoerus* eventually gave rise to the genus Notochoerus during the Pliocene (Harris and White, 1979; Made, 1999; Bishop, 2010). The available fossil evidence suggests that the suid *Ny. jaegeri* is the ancestor of *No. euilus* (Cooke and Ewer, 1972; Harris and White, 1979) and both suids may have co-occurred between ~3.8 Ma and ~3.6 Ma (Reda et al., 2017). In fact, the similarity of their dental adaptations has led several authors to argue for the inclusion of *Ny. jaegeri* in *Notochoerus* (Made, 1999; Harris and Leakey, 2003; Harris et al., 2003; Bishop, 2010; Kullmer, 2008; Geraads and Bobe, 2017), a hypothesis currently not supported by cranial remains (Reda et al., 2017). *Notochoerus* species were characterized by their derived craniodental adaptations with respect to *Nyanzachoerus*, including longer and taller third molars, smaller premolars, reduced incisors, longer diastemas, mandibles with symphysis flattened anteriorly, more vertical occipitals, less concave cranial vaults, and more posteroventrally oriented zygomatic arches (Harris and White, 1979). Some, if not all, of these features may have served as adaptations to grazing diets (Made, 1999; Harris and Cerling, 2002).

Nyanzachoerus and *Notochoerus* are the most abundant suids in Africa during the Pliocene but they are gradually overturned by two genera of the subfamily Suinae, *Kolpochoerus* and *Metridiochoerus.* The earliest representatives of the genus *Kolpochoerus*, *K. deheinzelini* and *K. millensis*, were suids of small size, with low-crowned bunodont molars like those of extant *Potamochoerus* or *Sus*. The species *K. millensis* was named to accommodate specimens from Woranso-Mille and Gona between ~3.8 Ma and ~3.5 Ma (Haile-Selassie and Simpson, 2013) that seem to represent a transitional form between the older *K. deheinzelini* and the younger *K. afarensis*. According to Souron et al (2016), *K. afarensis* (~3.5–2.95 Ma) would later give rise to the lineage *K. limnetes* / *K. olduvaiensis* and the lineage *K. phillipi* / *K. majus*. The genus *Metridiochoerus* appears in East Africa ~3.4 Ma and the earliest specimens (third molars) resemble those of *Kolpochoerus*. Fossils attributed to this genus are scarce until the latest part of the Pliocene and beginning of the Pleistocene, when they radiate into a variety of forms and expand their range throughout eastern and southern Africa (Cooke, 1994; Pickford, 2013; Lazagabaster et al., 2018).

1.2 Geological context of Woranso-Mille

The Woranso-Mille paleontological study area is located in the northwestern part of the central Afar region of Ethiopia and has been under investigation by the Woranso-Mille Paleontological Research Project (WORMILPRP) since 2005 (Haile-Selassie et al., 2007; Deino et al., 2010) (Figure 3.1). The accomplishment of 13 field seasons have resulted in the collection of more than 6,000 fossils of Pliocene age, including remains of at least three hominin species, *Australopithecus afarensis*, *A. anamensis*, and the newly described taxon *A. deyiremeda*, as well as the enigmatic Burtele foot with its primitive bipedal locomotion (Haile-Selassie et al., 2010b, 2010a, 2012, 2016; Haile-Selassie and Melillo, 2015). The site has also yielded abundant fossil remains of other mammals (Geraads et al., 2009; Sanders and Haile-Selassie, 2012; Frost et al., 2014; Werdelin et al., 2014), including ~1700 specimens attributed to the family Suidae, some of which have already been described (Haile-Selassie and Simpson, 2013; Reda et al., 2017). The Woranso-Mille study area is divided into a series of localities with ages that range from ~3.82 to ~3.0 Ma, though there are localities of uncertain age that could expand this range even further (Haile-Selassie et al., 2007; Deino et al., 2010; Saylor et al., 2016). More information on the chronology of the Woranso-Mille localities can be found in Section 2.1 of this chapter.

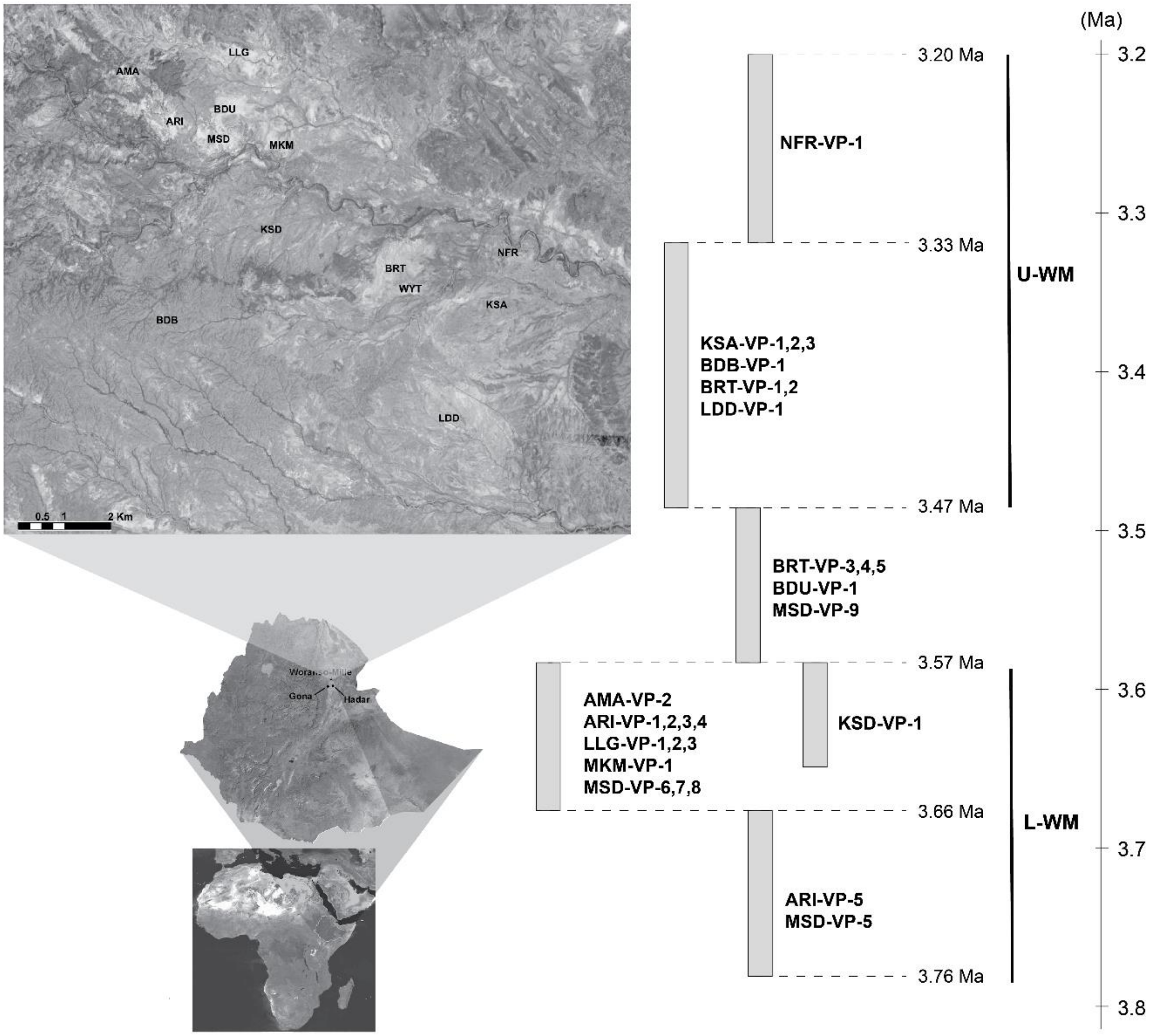

Figure 4.1. Map of Woranso-Mille paleontological research area, showing the geographical and temporal distribution of the different localities. Map provided by Y. Haile-Selassie.

1.3 Carbon and oxygen stable isotope of mammal tooth enamel as paleoecological indicators

Stable isotopes analyses of tooth enamel are widely used to infer diets of extinct mammals, providing an independent assessment of paleodietary hypotheses based on morphological data, and a mean to reconstruct past environmental conditions (Bocherens et al., 1996; Koch, 1998; MacFadden, 2000; Clementz et al., 2003; Levin et al., 2008, 2015; Cerling et al., 2011; Lazagabaster et al., 2016; Rowan et al., 2017; Lehmann et al., 2018). Carbon stable isotope values reflect the isotopic composition of the plants eaten and oxygen stable isotope values inform about drinking habits, both when the tooth crown was forming.

Carbon isotope data of plants are usually presented using δ-notation, where $\delta=(R_{sample}/R_{standard}-1)*1000$ in per mil (‰) units and R_{sample} and $R_{standard}$ are the ratios of heavy to light isotopes (in this case, ^{13}C and ^{12}C) of the sample and standard, respectively. $\delta^{13}C$ values are reported relative to Vienna Pee Dee Belemnite (VPDB) and depend on the three photosynthetic pathways through which CO_2 is fixed by plants: C_3 (Hatche-Slack cycle), C_4 (Calvine-Benson cycle), and CAM (Crassulacean Acid Metabolism) (Smith and Epstein, 1971; DeNiro and Epstein, 1978; Ambrose and DeNiro, 1986; Dawson et al., 2002). The C_3 pathway is found mainly in dicotyledonean trees and shrubs, but also high-altitude (> 000 m) and temperate grasses and have $\delta^{13}C$ values ranging from −22 ‰ to −36 ‰ in tropical Africa (mean: −27.4 ± 2.0 ‰) (Kohn, 2010). The wide range of $\delta^{13}C$ values of C_3 vegetation is due to variation in environmental factors such as solar radiation, water and nutrient availability, and temperature (Farquhar et al., 1982; Ehleringer et al., 1987; O'Leary, 1988; Van der Merwe and Medina, 1991; Ehleringer and Monson, 1993; Koch, 1998; Heaton, 1999; Diefendorf et al., 2010; Kohn, 2010). For example, in open and closed canopy forests $\delta^{13}C$ values decrease from the upper to the lower canopy because of the decrease in solar radiation (Vogel, 1980; Ehleringer et al., 1986; Van der Merwe and Medina, 1991; Heaton, 1999; Cerling et al., 2004). The C_3 biomass typically displays ^{13}C-depleted $\delta^{13}C$ values in closed canopy and mesic environments such as rainforests, and ^{13}C-enriched δ^{13}C values in open and arid environments with warm growing seasons such as woodlands (Van der Merwe and Medina, 1991; Cerling and Harris, 1999; Heaton, 1999; Cerling et al., 2004; Kohn, 2010). On the other hand, the C_4 pathway is generally employed by low elevation grasses in tropical Africa, with δ^{13}C values ranging from −14 ‰ to −11 ‰ (mean: −12.7 ± 1.2 ‰) (Heaton, 1999; Cerling et al., 2003, 2015). The CAM (Crassulacian acid metabolism) pathway is used by succulent plants and yields δ^{13}C values between those of C_3 and C_4 plants (O'Leary, 1981, 1988; Heaton, 1999). It is unlikely that succulents comprised a significant component of herbivore diets in eastern Africa during the Pliocene and therefore, their contribution to the discussion of suid's paleodiets in this work is not considered significant.

The stable oxygen isotope composition of the carbonate component of herbivore tooth enamel is affected by the δ^{18}O values of precipitation, surface and plant water, as well as animal physiology and behavior (Kohn and Cerling, 2002). Stable oxygen isotope data can be used to evaluate the drinking habits of mammals in the past, specifically whether they are non-obligate drinkers (they obtain a great amount of water from the diet) or obligate drinkers (they obtain most of the water from drinking). This information, in turn, may be used to evaluate relative aridity in terrestrial ecosystems (Levin et al., 2006). In general, higher δ^{18}O values of enamel are present in more arid environments.

2. Material and Methods

2.1 Sample and chronology

A total of 105 samples belonging to five extinct species of the family Suidae were analyzed. Two belong to the subfamily Suinae, including *Kolpochoerus millensis* (n = 37) and *K. afarensis* (n = 15), while the other three belong to the subfamily Tetraconodontinae, including *Nyanzachoerus pattersoni* (n = 21), *Ny. jaegeri* (n = 17), and *Notochoerus euilus* (n = 21). The data on *No. euilus* was already published in the work of Levin et al. (2015). Although each specimen analyzed can be placed in more tightly constrained chronologies, for the purposes of this study, fossils were placed in two different time intervals. The lower time interval (L-WM) consists of localities with an age between ~3.76 Ma and ~3.57 Ma time, including AMA-VP-1, AMA-VP-2, ARI-VP-1, ARI-VP-2, ARI-VP-3, BDU-VP-1, BDU-VP-2, KSD-VP-1, LLG-VP-1, LLG-VP-2, MKM-VP-1, MSD-VP-1, MSD-VP-2, and MSD-VP-5. The upper time interval (U-WM) consists of localities with an age between ~3.47 and ~3.2 Ma, including BDB-VP-1, BRT-VP-1, BRT-VP-2, KSA-VP-2, KSA-VP-3, LDD-VP-1, NFR-VP-1, and WYT-VP-2. Three samples of *Ny. jaegeri* from FYA, a locality with an estimated age of >4.0 Ma based on preliminary biochronological analyses, were also included. A list of the specimens analyzed can be found in Appendix B, Table SI 2.

In addition, I compiled a database of published $\delta^{13}C$ values of specimens attributed to the same suid lineages present in Woranso-Mille from other sites in East Africa (Appendix B, Table SI 3). We assigned each sample a different time interval. The L-EA is roughly contemporaneous with the L-WM while the U-EA is roughly contemporaneous with the U-WM. The time interval >3.8 Ma was assigned to samples older than the L-WM, and the time interval <3.2 Ma was assigned to samples younger than the U-WM. For the purposes of this work, we group the values in three different suid lineages with ancestor-descendant relationship, including the lineage formed by *Kolpochoerus deheinzelini* / *K. millensis* / *K. afarensis*, the lineage formed by *Nyanzachoerus jeageri* / *Notochoerus euilus*, and the lineage formed by *Ny. pattersoni*, which also includes specimens <4.1 Ma and called *Ny. kanamensis* by other authors (e.g., Harris and White, 1979; White et al., 2009).

2.2 Stable isotope analyses

All teeth were sampled in the National Museum of Ethiopian in Addis Ababa using a handheld rotary drill with a diamond bit after initial cleaning of the tooth surface using gentle abrasion. Where possible third molars were sampled. Tooth enamel powders were treated with 10‰ H_2O_2 and 0.1 M buffered acetic acid solution for 15 minutes and rinsed three times with deionized water after each treatment. After treatment, powders were dried in a 60˚C oven overnight. For isotopic analysis, approximately 400 to 700 micrograms dried powders were placed in silver capsules and digested in H_3PO_4 at 90˚C (common acid bath) and the resultant CO_2 was cryogenically purified using a custom-built automated device described by Passey et al. (2010) and modified for small samples. The $^{13}C/^{12}C$ and $^{18}O/^{16}O$ ratios of CO_2 were measured using a dual inlet system on a Thermo MAT 253 gas sourced isotope ratio mass spectrometer at Johns Hopkins University. External precision (1σ) of $\delta^{13}C$ and $\delta^{18}O$ values of tooth enamel reference materials were 0.3‰ and 0.2‰ respectively over the course of the analyses. All data are reported relative to the Vienna Pee Dee Belemnite standards. The acid fractionation factor of 1.00725 was used for determination of $\delta^{18}O$ values of the fossil enamel digested in acid at 90˚C (Passey et al. 2007). All stable isotope analyses were carried out by N. Levin.

2.3 Stable isotope dietary overlap

We calculated the stable isotope dietary overlap (%) of the L-WM and the U-WM in the bivariate space represented by $\delta^{13}C$ and $\delta^{18}O$ by dividing the area of the convex hull where at least two species overlap by the total convex hull area occupied by all suid species in each time interval. The convex hull areas were determined manually using the software ImageJ.

2.4 Relative abundance

Abundance data was calculated for all Woranso-Mille localities as the number of identified specimens (NISP) of each suid species and the minimum number of individuals (MNI). The MNI was obtained by counting the most repeated tooth attributed to a species in the same locality. The relative abundance (%) is the proportion of each suid species with respect to the total NISP or MNI.

3. Results

We provide summary statistics and the results of both parametric (ANOVA, t-test, and Tukey’s HSD multiple comparisons) and non-parametric tests (Kruskal-Wallis, Mann Whitney, and Dunn’s multiple comparisons) used to compare carbon stable isotope ($\delta^{13}C$) and oxygen stable isotope ($\delta^{18}O$) values between suid taxa within the two

Woranso-Mille time intervals, L-WM (3.76–3.57 Ma) and U-WM (3.47–3.20 Ma) and between time intervals. We also compared $\delta^{13}C$ values of the suids from the time intervals from Woranso-Mille with those at other sites in East Africa of the same or different chronology.

3.1 Carbon stable isotope ($\delta^{13}C$) results of Woranso-Mille Suidae

The $\delta^{13}C$ of the Woranso-Mille suids range from –10.18 ‰ to 2.85 ‰ (Tables 4.1–4.2, Figures 4.2–4.3) and therefore occupy most of the carbon dietary spectrum, including C_3–dominated diets ($\delta^{13}C$ = –12 to –8 ‰) mixed C_3–C_4 diets ($\delta^{13}C$ = –1 to –8 ‰), and C_4–dominated diets ($\delta^{13}C$ = –1 to 3 ‰). Statistical tests support differences in $\delta^{13}C$ between suid taxa both within the lower interval (L-WM) (ANOVA: F = 22.32; df = 3; $p<0.0001$) and within the upper interval (U-WM) (ANOVA: F = 7.72; df = 2; p = 0.0015) (Table 4.3).

In the L-WM, *Kolpochoerus millensis* has the lowest $\delta^{13}C$ of all the WM suids, with an average of –5.27 ± 2.17 ‰, and the largest sample size (n = 32) (Table 4.2). The $\delta^{13}C$ of *K. millensis* significantly differ between two of the better-sampled localities, ARI (μ = –6.28 ± 2.22 ‰, n = 16) and MSD (μ = –2.77 ± 1.86 ‰, n = 7) (Mann Whitney, p = 0.0061). In fact, the lowest $\delta^{13}C$ value of this suid is found at ARI (–10.18 ‰) and the highest at MSD (–0.79 ‰) (Table 4.1). The $\delta^{13}C$ of *K. millensis* are significantly lower than those of *Nyanzachoerus jaegeri* (Tukey's Q = 7.72, p = 0.0002) and *Notochoerus euilus* (Tukey's Q = 7.25, p = 0.0002) (Table 4.3). Nevertheless, in the L-WM *Ny. jaegeri* has $\delta^{13}C$ an average of –0.42 ± 1.87 ‰ (n = 11) and *No. euilus* has an average of –0.72 ± 1.35 ‰ (n = 7). *Nyanzachoerus pattersoni* also has significantly lower values (μ

= –4.28 ± 1.91 ‰, n = 8) than *Ny. jaegeri* (Tukey's Q = 6.15, p = 0.0004) and *No. euilus* (Tukey's Q = 5.68, p = 0.0011), though non-parametric tests do not support statistical differences between *Ny. pattersoni* and *No. euilus* (Dunn's z = 2.46, p = 0.0844) (Tables 4.2–4.3). The lowest δ^{13}C value of *Ny. jaegeri* is recorded at LLG (–4.01 ‰) and the highest at ARI (2.85 ‰) (Table 4.1), but the sample size is too low for robust statistical comparisons between these two localities. The differences between *Ny. jaegeri* and *Ny. pattersoni* are more marked in ARI, where their δ^{13}C values do not even overlap (Table 4.2). There are only two samples of *Ny. jaegeri* at ARI but the average is –1.07 ± 2.51 ‰, while the average of *Ny. pattersoni* is –5.08 ± 1.83 ‰ (n = 3) (Table 4.2). The δ^{13}C does not differ significantly in the L-WM between *K. millensis* and *Ny. pattersoni* (Tukey's Q = 1.57, p = 0.6858) on one hand between *Ny. jaegeri* and *No. euilus* on the other hand (Tables 4.2–4.3).

In the U-WM, *No. euilus* shows higher δ^{13}C (μ = –0.90 ± 1.10 ‰, *n* = 14) than *K. afarensis* (μ = –2.44 ± 2.02 ‰, n = 15) (Tukey's Q = 3.75, p = 0.0306) and *Ny. pattersoni* (μ = –3.16 ± 1.27 ‰, *n* = 14) (Tukey's Q = 5.50, p = 0.0012), though the differences between *No. euilus* and *K. afarensis* only approach significance in non-parametric tests (Dunn's z = 2.33, p = 0.0587) (Tables 2–3). There are no statistical differences between *K. afarensis* and *Ny. pattersoni* (Tukey's Q = 1.75, p = 0.4381) (Table 4.3). Both the lowest and highest δ^{13}C value of *K. afarensis* occur at BRT, –4.64 ‰ and –0.14 ‰, respectively (Table 4.1), but the average values are similar between *K. afarensis* from BRT (μ = –2.33 ± 2.52 ‰, *n* = 7) and NFR (μ = –2.83 ± 1.40 ‰, n = 7) (Table 4.2–4.3). The lowest value of *No. euilus* is registered at NFR (–3.62) and the highest at ARI (0.84)

(Table 4.1), but there are no statistical differences supported between these two sites (Mann Whitney, $p = 0.5460$).

There are significant differences in $\delta^{13}C$ between L-WM and U-WM ($t = 3.29$, $p = 0.0013$) (Table 4.4). The $\delta^{13}C$ is lower in the L-WM ($\mu = -3.79 \pm 2.88$ ‰, $n = 63$) than in the U-WM ($\mu = -1.89 \pm 1.76$ ‰, $n = 42$) (Table 4.2). When the average is corrected by abundance, these differences still hold but are less marked. The $\delta^{13}C$ average in the L-WM is –3.41 ‰ when corrected by number of identified specimens (μ NISP) and –2.68 ‰ when corrected by minimum number of individuals (μMNI). In the U-WM, the μ NISP is –1.93 ‰ and the μ MNI is –1.72 ‰ (Table 4.2). The $\delta^{13}C$ differences between L-WM and U-WM are mostly driven by the higher values of *K. afarensis* in comparison to *K. millensis* ($t = 4.34$, $p<0.0001$) (Table 4.4). With respect to the other taxa, *No. euilus* and *Ny. pattersoni* have similar $\delta^{13}C$ across the Woranso-Mille sequence, while *Ny. jaegeri* is not present in U-WM. It is worth mentioning a slight increase in *Ny. pattersoni* from an average of –4.28 ± 1.91 ‰ in L-WM to an average of –3.16 ± 1.27 ‰ in L-UM (Table 4.2), but these differences are not statistically supported ($t = -1.63$, $p = 0.1195$) (Table 4.4). *Nyanzachoerus pattersoni* is sampled in most of Woranso-Mille Pliocene localities but at the expense of low sample size in some localities. The $\delta^{13}C$ values of *Ny. pattersoni* are slightly higher in KSA ($\mu = -3.36 \pm 1.75$ ‰, $n = 4$) and LDD ($\mu = -3.21 \pm 1.38$ ‰, $n = 6$), in comparison with the comparative older localities of MKM ($\mu = -4.97 \pm 1.25$ ‰, $n = 2$), AMA ($\mu = -3.78 \pm 2.52$ ‰, $n = 2$), and ARI ($\mu = -5.08 \pm 1.83$ ‰, $n = 3$) (Table 4.1). The lowest $\delta^{13}C$ value is recorded at ARI (–6.47 ‰) and the highest at KSA (–1.34 ‰) but sample size is too low for statistical comparisons between these two localities.

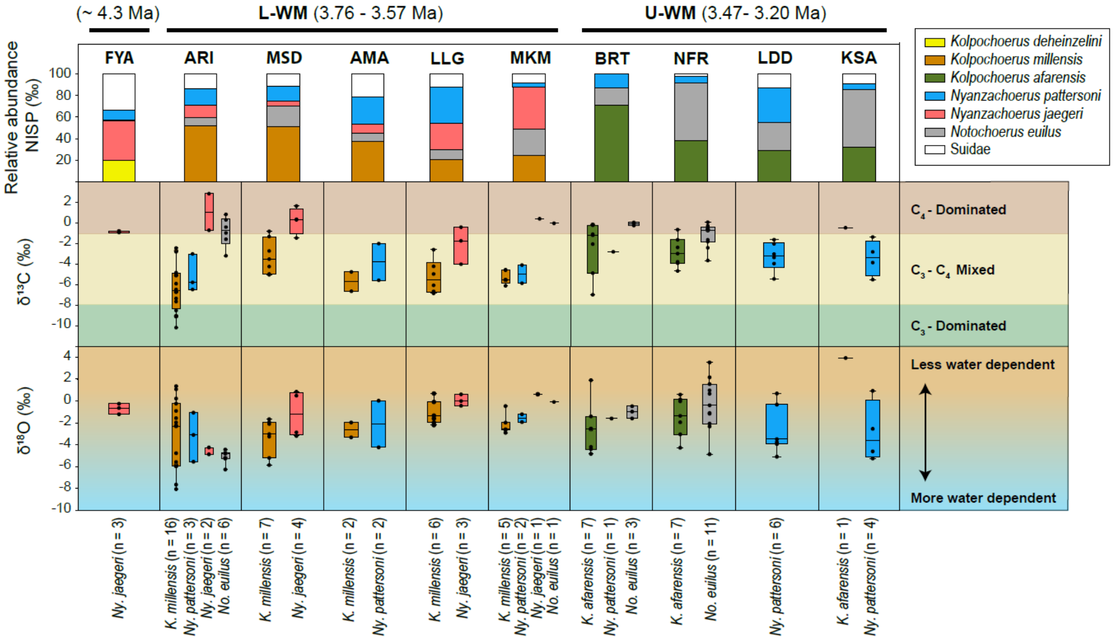

Figure 4.2. Results of carbon isotope ($\delta^{13}C$) and oxygen isotope ($\delta^{18}O$) analyses, and abundance of suid species at different Woranso-Mille localities. Localities with n < 3 were excluded from the graph, including BDU (n = 2), WYT (n =1) and BDB (n = 1) (see Table 4.1). Boxplots in the upper row of the graph show $\delta^{13}C$ data for each suid species. The background colors indicate C_3-dominated diets (green), mixed C_3-C_4 diets (yellow), and C_4-dominated diets in brown. Numbers in parenthesis indicate sample size. The bars on the upper part of the graph show relative abundance expressed as the proportion of number of identified specimens (NISP). Abbreviations: L-WM, lower Woranso-Mille time bin; U-WM, upper Woranso-Mille time bin. Boxplots in the lower row of the graph show $\delta^{18}O$ data for each suid species. The background colors indicate greater water dependence (lighter-blue) and lesser water dependence (darker-orange).

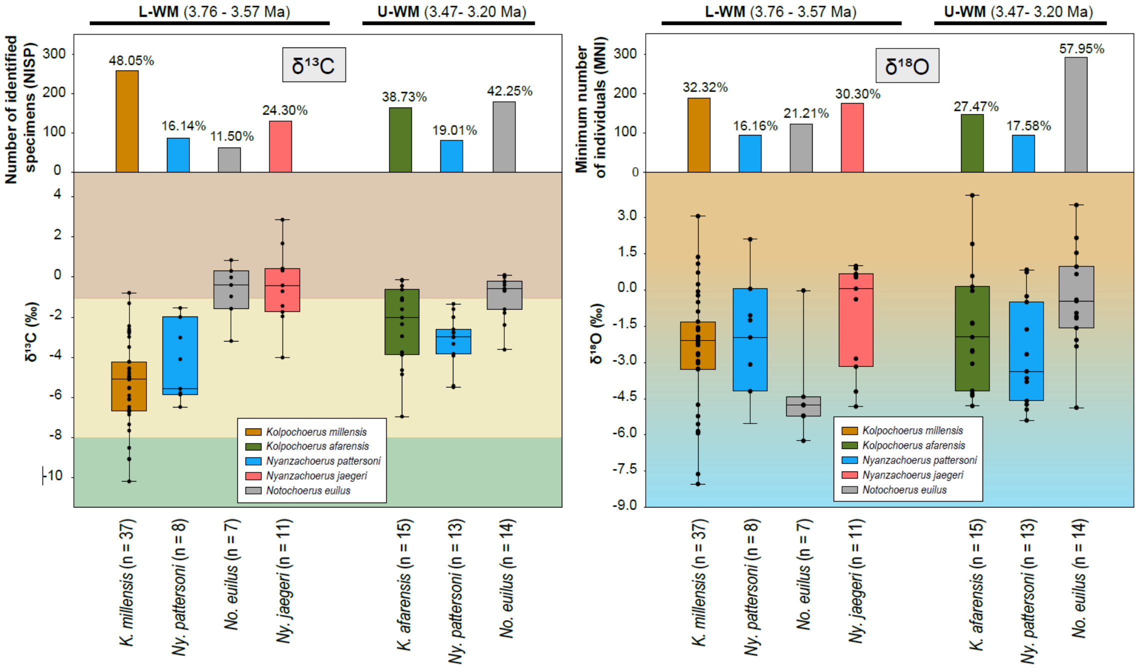

Figure 4.3. Results of carbon isotope (δ^{13}C) and oxygen isotope (δ^{18}C) analyses, and abundance of suid species at two Woranso-Mille time bins. A) Boxplots show δ^{13}C data for each suid species. The background colors indicate C_3-dominated diets (green), mixed C_3-C_4 diets (yellow), and C_4-dominated diets in brown. Numbers in parenthesis indicate sample size. The bars on the upper part of the graph show abundance expressed as number of identified specimens (NISP). The percentages over the graph indicate relative abundance. Abbreviations: L-WM, lower Woranso-Mille time bin. B) Boxplots show δ^{18}O data for each suid species. The background colors indicate greater water dependence (lighter-blue) and lesser water dependence (darker-orange). The bars on the upper part of the graph show abundance expressed as minimum number of individuals (MNI).

Table 4.1. Summary statistics of carbon isotope ratios ($\delta^{13}C$) of Woranso-Mille by locality.

Site	Taxon	n	min	max	mean	sd
MKM	*K. millensis*	5	-6.10	-4.54	-5.26	0.67
	No. euilus	1			-0.02	
	Ny. jaegeri	1			0.42	
	Ny. pattersoni	2	-5.85	-4.09	-4.97	1.25
ARI	*K. millensis*	16	-10.18	-2.44	-6.28	2.36
	No. euilus	6	-3.19	0.84	-0.83	1.44
	Ny. jaegeri	2	-0.71	2.85	1.07	2.51
	Ny. pattersoni	3	-6.47	-3.01	-5.08	1.83
LLG	*K. millensis*	6	-6.85	-2.60	-5.23	1.63
	Ny. jaegeri	3	-4.01	-0.42	-2.06	1.82
KSD	*K. millensis*	1			-2.98	
MSD	*K. millensis*	7	-5.02	-0.79	-3.21	1.69
	Ny. jaegeri	4	-1.44	1.67	0.23	1.28
AMA	*K. millensis*	2	-6.61	-4.73	-5.67	1.33
	Ny. pattersoni	2	-5.56	-1.99	-3.78	2.52
NFR	*K. afarensis*	7	-4.64	-0.63	-2.83	1.40
	No. euilus	11	-3.62	0.10	-1.14	1.11
BRT	*K. afarensis*	7	-6.95	-0.14	-2.33	2.59
	Ny. pattersoni	1			-2.77	
	No. euilus	3	-0.22	0.08	-0.05	0.15
KSA	*K. afarensis*	1			-0.44	
	Ny. pattersoni	4	-5.49	-1.34	-3.36	1.75
FYA	*Ny. jaegeri*	3	-0.92	-0.80	-0.85	0.06
BDU	*Ny. jaegeri*	1			-1.96	
	Ny. pattersoni	1			-1.54	
WYT	*Ny. pattersoni*	1			-2.98	
LDD	*Ny. pattersoni*	6	-5.42	-1.60	-3.21	1.38
BDB	*Ny. pattersoni*	1			-2.61	

Table 4.2. Summary statistics for carbon isotope ratios ($\delta^{13}C$) of Woranso-Mille by time interval. Abbreviations: L-WM, lower Woranso-Mille (3.76-3.57 Ma); U-WM, upper Woranso-Mille (3.47-3.2 Ma); *n*, total samples analyzed; min, minimum value; max, maximum value; med, median; μ, mean; sd, standard deviation; μ (NISP), mean corrected by number of identified specimens; μ (MNI), mean corrected by minimum number of individuals.

	$\delta^{13}C$							
Taxon	*n*	min	max	med	μ	sd	μ (NISP)	μ (MNI)
L-WM								
Kolpochoerus millensis	37	-10.18	-0.79	-5.07	-5.27	2.17		
Notochoerus euilus	7	-3.19	0.84	-0.4	-0.72	1.35		
Nyanzachoerus jaegeri	11	-4.01	2.85	-0.42	-0.42	1.87		
Nyanzachoerus pattersoni	8	-6.47	-1.54	-4.82	-4.28	1.91		
All	63	-10.18	2.85	-4.22	-3.79	2.88	-3.41	-2.68
U-WM								
Kolpochoerus afarensis	15	-6.95	-0.14	-2.02	-2.44	2.02		
Notochoerus euilus	14	-3.62	0.1	-0.59	-0.90	1.10		
Nyanzachoerus pattersoni	13	-5.49	-1.34	-2.98	-3.16	1.27		
All	42	-6.95	0.1	-1.89	-1.89	1.76	-1.93	-1.72

Table 4.3. Results of parametric (ANOVA and Tukey's post-hoc) and non-parametric (Kruskal-Wallis and Dunn's post-hoc with Bonferroni corrected p-values) comparisons of carbon isotope ratios ($\delta^{13}C$) of Woranso-Mille within time interval. Significant differences are bolded. Abbreviations: L-WM, lower Woranso-Mille; U-WM, upper Woranso-Mille.

$\delta^{13}C$ comparisons within member	ANOVA			Kruskal-Wallis	
	df	F	p	$\chi 2$	p
Lower Woranso- Mille (L-WM)	**3**	**22.32**	**<0.0001**	**32.37**	**<0.0001**
Upper Woranso-Mille (U-WM)	**2**	**7.72**	**0.0015**	**13.53**	**0.0011**

	Tukey's		Dunn's	
	Q	p	z	p
L-WM				
K. millensis – Ny. pattersoni	1.57	0.6858	0.81	1.0000
K. millensis – Ny. jaegeri	**7.72**	**0.0002**	**4.81**	**<0.0001**
K. millensis – No. euilus	**7.25**	**0.0002**	**3.85**	**0.0007**
Ny. pattersoni – Ny. jaegeri	**6.15**	**0.0004**	**2.87**	**0.0247**
Ny. pattersoni – No. euilus	**5.68**	**0.0011**	2.46	0.0844
Ny. jaegeri – No. euilus	0.47	0.9873	0.13	1.0000
U-WM				
K. afarensis – Ny. pattersoni	1.75	0.4381	1.40	0.4850
K. afarensis – No. euilus	**3.75**	**0.0306**	2.33	0.0587
Ny. pattersoni – No. euilus	**5.50**	**0.0012**	**3.63**	**0.0008**

Table 4.4. Results of parametric (t-test) and non-parametric (Mann-Whitney) comparisons of carbon isotope ratios ($\delta^{13}C$) of Woranso-Mille and $\delta^{18}O$ between time intervals. Abbreviations: L-WM, lower Woranso-Mille (3.76-3.57 Ma); U-WM, upper Woranso-Mille (3.47-3.2 Ma). Significant differences between taxa are bolded.

Comparisons		t-test		Mann-Whitney	
Taxa (L-WM)	Taxa (U-WM)	t	p	z	p
No. euilus	*No. euilus*	0.34	0.7337	-0.52	0.6013
No. euilus / *Ny. jaegeri*	*No. euilus*	0.72	0.4768	-0.79	0.4249
K. millensis	***K. afarensis***	**4.34**	**<0.0001**	**-3.74**	**0.0002**
Ny. pattersoni	*Ny. pattersoni*	-1.63	0.1195	-1.56	0.1195
All	**All**	**3.29**	**0.0013**	**-3.14**	**0.0017**

3.2 Oxygen isotope ($\delta^{18}O$) results of Woranso-Mille Suidae

The $\delta^{18}O$ of the Woranso-Mille suids range from –8.03 ‰ to 3.92 ‰ (Tables 4.5–4.6, Figures 4.2–4.4). Statistical tests support differences in $\delta^{18}O$ between suid taxa only within the lower interval (L-WM), though these are barely significant (ANOVA: F = 2.82; df = 3; p = 0.0468), while the statistical comparisons approach significance in the upper interval (U-WM) (ANOVA: F = 2.92; df = 2; p = 0.0660) (Table 4.7).

In the L-WM, *Notochoerus euilus* has the lowest $\delta^{18}O$ values of all the WM suids, with an average of –4.37 ± 2.01 ‰ (n = 7) (Table 4.6). The values of *No. euilus* only differ from *Nyanzachoerus jaegeri* (μ = –1.09 ± 2.23 ‰, *n* = 11) (Tukey's Q = 4.40, p = 0.0149) (Table 4.7). The low $\delta^{18}O$ of *No. euilus* in the L-WM are driven exclusively by the samples from locality ARI, which have an average of –5.10 ± 0.63 ‰ (n = 6) (Table 4.5). The other sample (only one) of *No. euilus* in the L-WM comes from MKM and is much higher (–0.02 ‰) than in ARI. It is worth to point out that *Ny. jaegeri* also has low $\delta^{18}O$ at ARI (μ = –4.54 ± 0.44 ‰, n = 2) and a higher value in MKM (0.58), but also in the other localities of the L-WM where it is present, including MSD ($\mu = -1.18 \pm 2.15$ ‰, $n = 4$) and LLG ($\mu = 0.09 \pm 0.53$ ‰, $n = 3$), and even in the older locality FYA ($\mu = -0.69 \pm 0.48$ ‰, $n = 3$) (Table 4.5). There are no other significant differences between species in the L-WM ($p>0.05$, Table 4.7).

In contrast with the L-WM, in the U-WM *No. euilus* has the highest δ^{18}O average ($\mu = -0.43 \pm 2.11$ ‰, $n = 14$), which is barely significantly different (Tukey's $Q = 3.46$, $p = 0.0485$) from the δ^{18}O of *Ny. pattersoni* ($\mu = -2.56 \pm 2.21$ ‰, $n = 13$) and not different (Tukey's $Q = 1.88$, $p = 0.3852$) from *Kolpochoerus afarensis* ($\mu = -1.59 \pm 2.52$ ‰, $n = 15$) (Tables 4.6–4.7). The locality KSA records both the lowest and highest δ^{18}O value in the U-WM, which belong to *Ny. pattersoni* (–5.35 ‰) and *K. afarensis* (3.92 ‰) (Table 4.5).

There are significant differences in δ^{18}O between L-WM and U-WM ($t = 1.77$, $p = 0.0078$), though these differences are not supported by non-parametric tests (Mann Whitney, $p = 0.1172$) (Table 4.8). These results are mostly driven by the higher δ^{18}O of *No. euilus* in the U-WM in comparison to *No. euilus* in the L-WM ($t = -4.09$, $p = 0.0006$). The δ^{18}O of *K. afarensis* does not differ significantly from *K. millensis* ($t = 1.17$, $p = 0.2447$) and *Ny. pattersoni* remains fairly similar across the Woranso-Mille sequence ($t = 0.68$, $p = 0.5050$) (Table 4.8).

Table 4.5. Summary statistics of carbon isotope ratios ($\delta^{18}O$) of Woranso-Mille by locality.

Site	Taxon	n	min	max	mean	sd
FYA	*Ny. jaegeri*	3	-1.2	-0.25	-0.69	0.48
MKM	*K. millensis*	5	-2.94	-0.5	-2.15	0.98
	No. euilus	1			-0.02	
	Ny. jaegeri	1			0.58	
	Ny. pattersoni	2	-1.96	-1.25	-1.60	0.50
ARI	*K. millensis*	16	-8.03	1.37	-3.13	3.10
	No. euilus	6	-6.24	-4.42	-5.1	0.63
	Ny. jaegeri	2	-4.85	-4.23	-4.54	0.44
	Ny. pattersoni	3	-5.53	-1.05	-3.22	2.24
LLG	*K. millensis*	6	-2.19	0.72	-1.06	1.15
	Ny. jaegeri	3	-0.41	0.64	0.09	0.53
KSD	*K. millensis*	1			3.06	
MSD	*K. millensis*	7	-5.88	-1.66	-3.30	1.65
	Ny. jaegeri	4	-3.2	0.86	-1.18	2.15
AMA	*K. millensis*	2	-3.28	-1.93	-2.60	0.95
	Ny. pattersoni	2	-4.19	0.05	-2.07	3.00
NFR	*K. afarensis*	7	-4.28	0.58	-1.42	1.80
	No. euilus	11	-4.87	3.52	-0.28	2.37
BRT	*K. afarensis*	7	-4.8	1.91	-2.55	2.32
	Ny. pattersoni	1			-1.58	
	No. euilus	3	-1.57	-0.46	-0.99	0.56
KSA	*K. afarensis*	1			3.92	
	Ny. pattersoni	4	-5.35	0.89	-2.94	2.81
BDU	*Ny. jaegeri*	1			0.97	
	Ny. pattersoni	1			2.1	
WYT	*Ny. pattersoni*	1			-0.45	
LDD	*Ny. pattersoni*	6	-4.9	0.79	-2.50	2.25
BDB	*Ny. pattersoni*	1			-4.54	

Table 4.6. Summary statistics for oxygen stable isotopes ($\delta^{18}O$) of Woranso-Mille by time interval. Abbreviations: L-WM, lower Woranso-Mille (3.76-3.57 Ma); U-WM, upper Woranso-Mille (3.47-3.2 Ma); *n*, total samples analyzed; min, minimum value; max, maximum value; med, median; μ, mean; sd, standard deviation; μ (NISP), mean corrected by number of identified specimens; μ (MNI), mean corrected by minimum number of individuals.

	$\delta^{18}O$							
Taxon	*n*	min	max	med	μ	sd	μ (NISP)	μ (MNI)
L-WM								
Kolpochoerus millensis	37	-8.03	3.06	-2.1	-2.49	2.51		
Notochoerus euilus	7	-6.24	-0.02	-4.77	-4.37	2.01		
Nyanzachoerus jaegeri	11	-4.85	0.97	0.03	-1.09	2.23		
Nyanzachoerus pattersoni	8	-5.53	2.1	-1.60	-1.86	2.41		
All	63	-8.03	3.06	-2.1	-2.38	2.51	-2.26	-2.36
U-WM								
Kolpochoerus afarensis	15	-4.8	3.92	-1.95	-1.59	2.52		
Notochoerus euilus	14	-4.87	3.52	-0.71	-0.43	2.11		
Nyanzachoerus pattersoni	13	-5.35	0.89	-3.32	-2.56	2.21		
All	42	-5.35	3.92	-1.48	-1.51	2.40	-1.28	-1.12

Table 4.7. Results of parametric (ANOVA and Tukey's post-hoc) and non-parametric (Kruskal-Wallis and Dunn's post-hoc with Bonferroni corrected p-values) comparisons of oxygen stable isotopes ($\delta^{18}O$) of Woranso-Mille within time interval. Significant differences are bolded.

Comparisons within member	ANOVA			Kruskal-Wallis	
	df	F	p	χ2	p
Lower Woranso- Mille (L-WM)	**3**	**2.82**	**0.0468**	**7.95**	**0.0469**
Upper Woranso-Mille (U-WM)	2	2.92	0.0660	5.47	0.0648

	Tukey's		Dunn's	
	Q	p	z	p
L-WM				
K. millensis – Ny. pattersoni	0.85	0.9315	0.66	1.0000
K. millensis – Ny. jaegeri	1.89	0.5451	1.69	0.5398
K. millensis – No. euilus	0.29	0.2944	1.80	0.4278
Ny. pattersoni – Ny. jaegeri	1.04	0.8832	0.70	1.0000
Ny. pattersoni – No. euilus	3.36	0.09264	1.93	0.3207
Ny. jaegeri – No. euilus	**4.40**	**0.01489**	**2.74**	**0.0366**
U-WM				
K. afarensis – Ny. pattersoni	1.58	0.5104	1.01	0.9320
K. afarensis – No. euilus	1.88	0.3852	1.37	0.5058
Ny. pattersoni – No. euilus	**3.46**	**0.0485**	2.33	0.0601

Table 4.8. Results of parametric (t-test) and non-parametric (Mann-Whitney) comparisons of oxygen stable isotopes ($\delta^{18}O$) of Woranso-Mille between time intervals. Abbreviations: L-WM, lower Woranso-Mille (3.76–3.57 Ma); U-WM, upper Woranso-Mille (3.47–3.2 Ma). Significant differences between taxa are bolded.

Comparisons		t-test		Mann-Whitney	
Taxa (L-WM)	Taxa (U-WM)	t	p	z	p
No. euilus	***No. euilus***	**-4.09**	**0.00061**	**-2.72**	**0.00647**
No. euilus / Ny. jaegeri	***No. euilus***	**-2.23**	**0.03356**	-1.71	0.08735
K. millensis	*K. afarensis*	1.17	0.24471	-0.85	0.39065
Ny. pattersoni	*Ny. pattersoni*	0.68	0.50489	-0.61	0.53817
All	All	1.77	0.007843	-1.56	0.11721

3.3 Stable isotope dietary overlap

In the L-WM, the stable isotope dietary overlap is 33.7%, while the overlap is almost double in the U-WM, 60.9 %, which constitutes an increase of 27.2 % (Figure 4.4). However, the absolute area of overlap is slightly lower in the U-WM; it decreased 5.8% with respect to the L-WM. What really changed is the absolute area occupied by all the suid taxa in the bivariate space; in this case the reduction is of 52.3 %. This shrinkage of the dietary space occupied by suids in the U-WM could be influenced by sample size. The sample size in the L-WM is 63 while in the U-WM is 42, a reduction of 33.3 %. Other important difference between the L-WM and U-WM is how the overlap is produced. in the L-WM, there is a complete separation between *No. euilus* and *Ny. pattersoni*, and two groups have almost no overlap, the one formed by *K. millensis* and *Ny. pattersoni*, and the one formed by *No. euilus* and *Ny. jaegeri*. On the other hand, in the U-WM, there is one less species and there is a larger overlap between *No. euilus* and the other two species, *K. afarensis* and *Ny. pattersoni* (Figure 4.4). In general, these results support an increase in dietary niche overlap based on stable isotopes among suids between the L-WM and the U-WM.

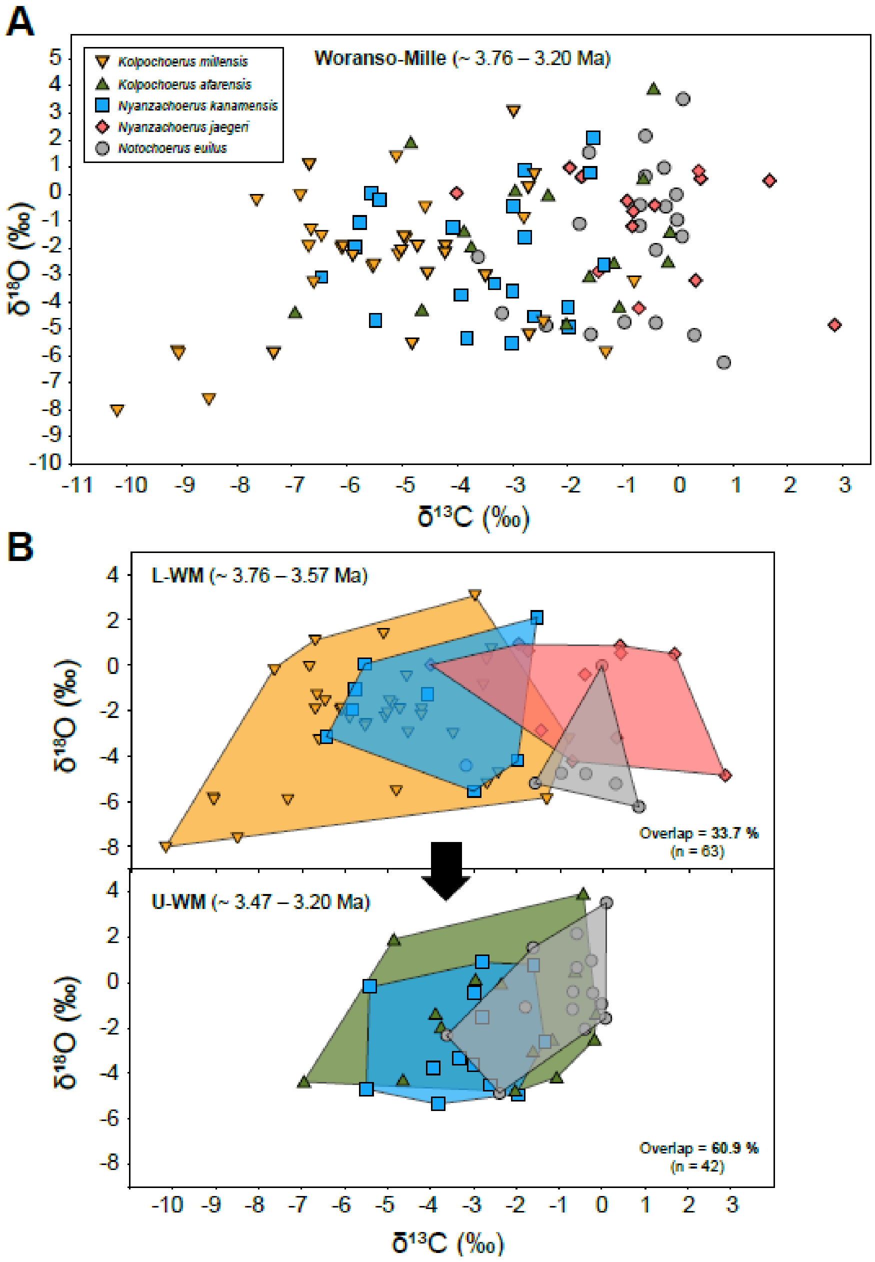

Figure 4.4. Bivariate plots of oxygen stable isotope (δ^{18}O) and carbon stable isotope (δ^{13}C) values of Woranso-Mille suids. A) All values combined from the lower interval (L-WM, ~3.76–3.57 Ma) and upper interval (U-WM, ~ 3.47–3.2 Ma). B) $\delta\ ^{18}$O and δ^{13}C values for the L-WM shown in the graph situated above and $\delta\ ^{18}$O and δ^{13}C values values for the U-WM shown below, with convex hulls drawn for each species. Overlap (%) is calculated by dividing the area of the convex hull where at least two species overlap by the total convex hull area occupied by all suid species in each time interval.

3.4 Relative abundance of Woranso-Mille Suidae

Kolpochoerus millensis is the most abundant suid in the L-WM, the NISP for this suid is 259 (48.1%) and the MNI is 32 (32.3 %) (Table 4.9, Figures 4.2–4.3). The abundance of *Kolpochoerus* decreases slightly in the U-WM; the NISP of *K. afarensis* of 165 (38.7%) and the MNI is 25 (27.5 %). *Nyanzachoerus jaegeri* is second in abundance in L-WM; the NISP is 131 (24.3%) and the MNI is 30 (30.3 %). This suid is not present in the U-WM. *Notochoerus euilus* has a low abundance in the L-WM; the NISP is 62 (11.5 %) and the MNI is 21 (21.2%). This species then becomes the most abundant suid in the U-WM; the NISP is 180 (42.3 %) and the MNI is 50 (54.9%. Finally, *Ny. pattersoni* has a similar abundance in the two Woranso-Mille time intervals; the NISP is 87 (16.1 %) and the MNI is 16 (16.2 %) in the L-WM, while in the U-WM the NISP is 81 (19.0 %) and the MNI is 16 (17.6%) (Table 4.9).

It is worth noting the differences in the two measures of relative abundance, NISP and MNI. For example, *Kolpochoerus* has higher relative abundance when the NISP is used. The relative abundance of *K. millensis* is 48.1 % when using NISP and 32.3 % when using MNI. In the case of *K. afarensis,* the relative abundance is 38.7% when using NISP and 27.5 % when using MNI. On the contrary, *Notochoerus* has higher relative abundance when the MNI is used. The relative abundance of *N. euilus* in the L-WM is 11.5 % when using NISP and 21.2% when using MNI. In the U-WM, *N. euilus* has a relative abundance of 42.3% when using NISP and 54.9% when using MNI (Table 4.9, Figures 4.2–4.3).

Table 4.9. Abundance of Woranso-Mille suids. Abbreviations: L-WM, Lower Woranso-Mille (~3.76–3.57 Ma); U-WM, Upper Woranso-Mille (~3.47–3.2 Ma); NISP, number of identified specimens; MNI, minimum number of individuals; *f*, frequency; %, percentage.

Taxon	NISP		MNI	
	f	%	*f*	%
L-WM				
Kolpochoerus millensis	259	48.1	32	32.3
Notochoerus euilus	62	11.5	21	21.2
Nyanzachoerus jaegeri	131	24.3	30	30.3
Nyanzachoerus pattersoni	87	16.1	16	16.2
All	539		99	
U-WM				
Kolpochoerus afarensis	165	38.7	25	27.5
Notochoerus euilus	180	42.3	50	54.9
Nyanzachoerus pattersoni	81	19.0	16	17.6
All	426		91	
Total	965		190	

3.5 Comparisons of suid $\delta^{13}C$ from Woranso-Mille with other sites of East Africa

The results of the comparison of the carbon isotope data ($\delta^{13}C$) of the suid species from Woranso-Mille with those of other sites in East Africa are shown in Tables 4.10–4.13 and Figure 4.5. There are only four significant differences supported by statistical analyses (Tables 4.11–4.13). Three of them occur in the lineage *Kolpochoerus deheinzelini* / *K. millensis* / *K. afarensis*, one of which is the C_4-enrichment of *K.*

afarensis in the U-WM with respect to the L-WM, as we already reported in section 3.1 of this work. In the U-WM, *Kolpochoerus* is also significantly C_4-enriched (μ = –2.44 ± 2.02 ‰, n = 15) in comparison to East African sites that are older than the L-WM (>3.8 Ma) (μ = –6.21 ± 2.33 ‰, n = 20) (Tukey's Q = 6.32, p = 0.0004). Sites in East Africa <3.2 Ma (μ = –3.51 ± 2.72 ‰, n = 17) are also C_4-enriched in comparison to sites >3.8 Ma (Tukey's Q = 4.53, p = 0.0211) (Tables 4.10–4.11). However, sites in East Africa that are contemporaneous with the U-WM (U-EA), are not significantly different than any of the time intervals in Woranso-Mille or in East Africa (p>0.05) (Table 4.11, Figure 4.5).

The other significant difference picked up by statisitical comparisons occurs in the *Nyanzachoerus jaegeri* / *Notochoerus euilus* lineage between the L-WM and contemporaneous sites of East Africa (L-EA) (Tukey's Q = 4.94, p = 0.0064) (Table 4.12). In this case again, the L-WM (μ = –0.54 ± 1.65 ‰, n = 18) is C_4-enriched in comparison to the L-EA (μ = –2.11 ± 2.01 ‰, n = 51) (Table 4.10, Figure 4.5).

No differences were picked up between any of the time intervals in the *Ny. pattersoni* lineage (p>0.05) (Table 4.13, Figure 4.5).

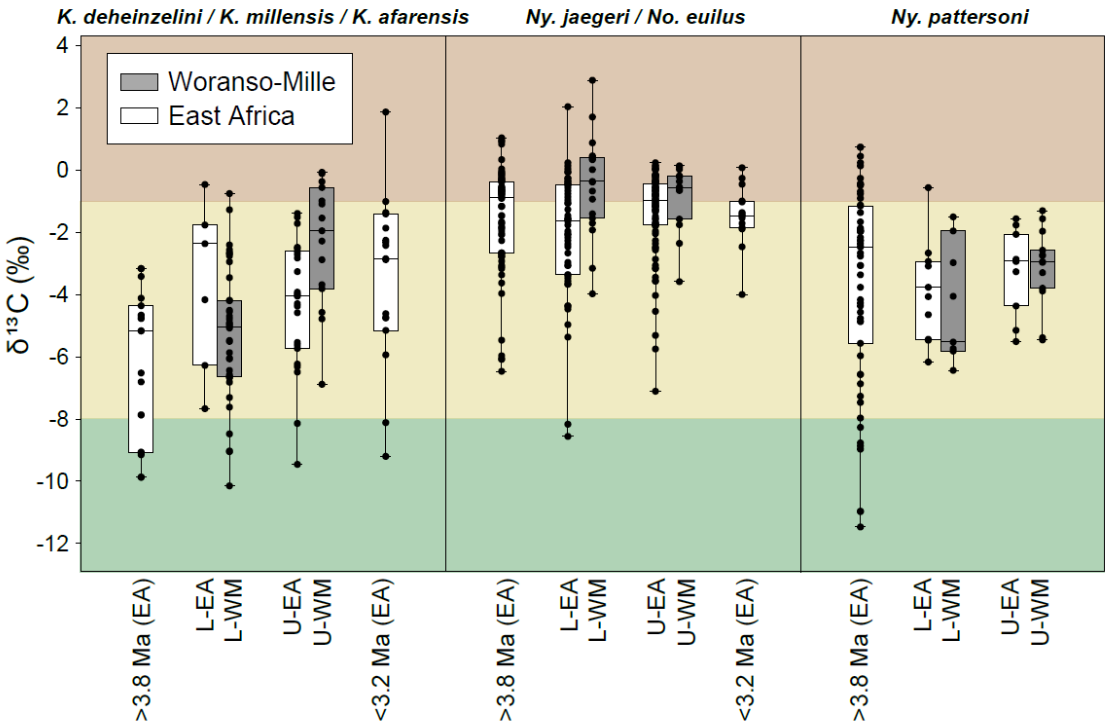

Figure 4.5. Results of carbon stable isotope ($\delta^{13}C$) comparisons of three suid Pliocene lineages between Woranso-Mille and other sites in East Africa. We considered *Kolpochoerus deheinzelini* / *K. millensis* / *K. afarensis* one lineage, *Nyanzachoerus jaegeri* / *Notochoerus euilus* another lineage, and *Ny. pattersoni* another lineage. Abbreviations: EA, East Africa; L-WM, lower Woranso-Mille time bin (~3.76–3.57 Ma); U-WM, upper Woranso-Mille time bin (3.47–3.20 Ma).

Table 4.10. Summary statistics of suid carbon isotope data ($\delta^{13}C$) from Woranso-Mille and from other sites from East Africa where the same suid species found at Woranso-Mille have been reported. Abbreviations: EA, East Africa; L-WM, lower Woranso-Mille (3.76–3.57 Ma); U-WM, upper Woranso-Mille (3.47–3.2 Ma); L-EA and U-EA, sites from East Africa with similar chronology to L-WM and U-WM, respectively; *n*, total samples analyzed; min, minimum value; max, maximum value; med, median; μ, mean; sd, standard deviation.

	n	min	max	med	μ	sd	References
Kolpochoerus deheinzelini / K. millensis / K. afarensis							
> 3.8 Ma (EA)	20	-9.90	-3.20	-5.20	-6.21	2.33	1,2,3
L-EA	6	-7.70	-0.50	-3.30	-3.82	2.78	4,5
L-WM	37	-10.18	-0.79	-5.07	-5.27	2.17	This study
U-EA	24	-9.47	-1.41	-4.06	-4.34	2.06	5,6
U-WM	15	-6.95	-0.14	-2.02	-2.44	2.02	This study
< 3.2 Ma (EA)	17	-9.23	1.83	-2.88	-3.51	2.72	6,7
Nyanzachoerus jaeageri / *Notochoerus euilus*							
> 3.8 Ma (EA)	70	-6.50	1.00	-0.93	-1.59	1.70	1,2,3,8,9,10,11,12,13,14
L-EA	51	-8.59	2.00	-1.68	-2.11	2.01	4,5,10,11,14
L-WM	18	-4.01	2.85	-0.41	-0.54	1.65	This study, 15
U-EA	75	-7.14	1.30	-1.03	-1.40	1.42	2,5,6,11,12,16,17
U-WM	14	-3.62	0.10	-0.59	-0.90	1.08	This study, 15
< 3.2 Ma (EA)	15	-4.03	0.04	-1.50	-1.49	0.97	6, 17
Nyanzachoerus pattersoni							
> 3.8 Ma (EA)	58	-11.50	0.70	-2.50	-3.62	3.18	2,3,8,11,13,14
L-EA	10	-6.20	-0.60	-3.95	-3.91	1.66	5,14,17
L-WM	8	-6.47	-1.54	-4.83	-4.29	1.91	This study
U-EA	10	-5.54	-1.60	-2.97	-3.28	1.36	5,6,11,12
U-WM	13	-5.49	-1.34	-2.98	-3.16	1.27	This study

1) Semaw et al. (2005); 2) Levin et al. (2008); 3) White et al. (2009); 4) Kingston (2011); 5) Bedaso et al. (2013); 6) Wynn et al. (2016); 7) Souron (2012); 8) Drapeau et al. (2014); 9) Cerling et al. (2003); 10) Kingston and Harrison (2007); 11) Harris and Cerling (2002); 12) Uno et al. (2011); 13) Harris et al. (2003); 14) Bedaso (2011); 15) Levin et al. (2015); 16) Mbua et al. (2016); 17) Wilson (2013).

Table 4.11. Post-hoc Tukey's HSD multiple comparisons of carbon stable isotope data ($\delta^{13}C$) of *Kolpochoerus deheinzelini*, *K. millensis*, and *K. afarensis* between Woranso-Mille and other sites from East Africa where either of the three suid species have been reported. Abbreviations: EA, East Africa; L-WM, lower Woranso-Mille (3.76-3.57 Ma); U-WM, upper Woranso-Mille (3.47-3.2 Ma); L-EA and U-EA, sites from East Africa with similar chronology to L-WM and U-WM, respectively. Significant results are bolded.

Kolpochoerus deheinzelini / K. millensis / K. afarensis						
	>3.8 Ma (EA)	L-WM	L-EA	U-WM	U-EA	<3.2 Ma (EA)
>3.8 Ma (EA)		0.8746	0.0584	**0.0004**	0.1775	**0.0211**
L-WM	1.58		0.5203	**0.0133**	0.8107	0.2987
L-EA	4.01	2.43		0.5774	0.9971	0.9991
U-WM	6.32	4.75	2.31		0.2917	0.8036
U-EA	3.34	1.77	0.67	2.98		0.9591
<3.2 Ma (EA)	4.53	2.96	0.52	1.79	1.19	

F = 6.33, df = 5, $p < 0.0001$

Table 4.12. Post-hoc Tukey's HSD multiple comparisons of carbon stable isotope data ($\delta^{13}C$) of *Nyanzachoerus jaegeri* and *Notochoerus euilus* between Woranso-Mille and other sites from East Africa where the either of the two suid species have been reported. Abbreviations: EA, East Africa; L-WM, lower Woranso-Mille (3.76-3.57 Ma); U-WM, upper Woranso-Mille (3.47-3.2 Ma); L-EA and U-EA, sites from East Africa with similar chronology to L-WM and U-WM, respectively. Significant results are bolded.

Nyanzachoerus jeageri / Notochoerus euilus						
	>3.8 Ma (EA)	L-WM	L-EA	U-WM	U-EA	<3.2 Ma (EA)
>3.8 Ma (EA)		0.1973	0.8757	0.6683	0.9982	0.9999
L-WM	3.241		**0.008648**	0.968	0.4228	0.3052
L-EA	1.576	4.817		0.09521	0.6387	0.7626
U-WM	2.113	1.128	3.689		0.8938	0.8025
U-EA	0.6011	2.64	2.177	1.511		1
<3.2 Ma (EA)	0.3191	2.922	1.895	1.793	0.2819	

Welch F = 2.89, df = 5, p = 0.0021*

* Levene's test for unequal variances: p = 0.0155

Table 4.13. Post-hoc Tukey's HSD multiple comparisons of carbon stable isotope data ($\delta^{13}C$) of *Nyanzachoerus pattersoni* between Woranso-Mille and other sites from East Africa where this suid species have been reported. Abbreviations: EA, East Africa; L-WM, lower Woranso-Mille (3.76-3.57 Ma); U-WM, upper Woranso-Mille (3.47-3.2 Ma); L-EA and U-EA, sites from East Africa with similar chronology to L-WM and U-WM, respectively. Significant results are bolded.

Nyanzachoerus pattersoni					
	>3.8 Ma (EA)	L-WM	L-EA	U-WM	U-EA
>3.8 Ma (EA)		0.9735	0.9989	0.9930	0.9978
L-WM	0.86		0.9971	0.8383	0.8853
L-EA	0.37	0.48		0.9573	0.9768
U-WM	0.60	1.46	0.98		1.0000
U-EA	0.45	1.31	0.83	0.15	

F = 0.29, df = 4, p = 0.8801

4. Discussion

4.1 Feeding ecology of Woranso-Mille suids

The carbon isotope data presented in this work indicate that most Woranso-Mille suids in the ~3.76–3.2 Ma time interval had mixed C_3-C_4 diets, but there is also evidence for dietary niche partitioning among suids. In the lower Woranso-Mille interval (L-WM) the $\delta^{13}C$ values of *Kolpochoerus millensis* are consistent with diet of greater C_3 resources. On the other hand, *Nyanzachoerus jaegeri* and *Notochoerus euilus* show $\delta^{13}C$ values that indicate a significant greater consumption of C_4 resources while *Ny. pattersoni* shows intermediate $\delta^{13}C$ values that indicate a diet limited to the mixed C_3-C_4 spectrum (Figures 4.3–4.4). In the upper Woranso-Mille interval (U-WM), *No. euilus* maintains more enriched C_4 diets than *K. afarensis* and *Ny. pattersoni*, which have a mixed C_3-C_4 signal.

These results confirm some of the a priori expectations based on the craniodental morphology of the suids analyzed. For example, the C_4-enriched diet of *No. euilus* makes sense on the light of its craniodental adaptations. This suid displays multiple craniodental features that are derived in comparison with other tetraconodontines (including N*y. pattersoni*) and most *Kolpochoerus* species (including *K. millensis* and *K. afarensis*), and that may have served as adaptations to grazing diets (Made, 1999; Harris and Cerling, 2002). Some of these craniodental adaptations are convergent with the extant grazer *Phacochoerus* (e.g., long and tall third molars, reduced premolars and incisors, symphysis flattened anteriorly, long diastemas, elevated orbits, vertical occipital). The enriched C_4 signal of *No. euilus* supports the hypothesis that its derived craniodental adaptations evolved to process and consume abrasive foods such as grasses. Other sites in East Africa that are contemporaneous with L-WM in East Africa also yielded high $\delta^{13}C$

values for *No. euilus*. For example, the combined $\delta^{13}C$ average of *No. euilus* from Dikika BBM (Ethiopia, ~3.80–3.42 Ma) and Upper Laetolil Beds (Tanzania, ~3.85–3.6 Ma) is –2.11 ± 2.02 ‰ (n = 45) (Harris and Cerling, 2002; Kingston and Harrison, 2007; Kingston, 2011; Bedaso et al., 2013), slightly higher than the average of –0.72 ± 1.35 ‰ (n = 7) of Woranso-Mille.

The other suid with enriched C_4 diets in the L-WM is *Ny. jaegeri*. There is a consensus among scholars that this suid is the ancestor of *No. euilus* (Harris and White, 1979; Made, 1999, 2014; Cooke, 2007; Kullmer et al., 2008; Bishop, 2010, 2011; Geraads and Bobe, 2017; Reda et al., 2017), a hypothesis based on the derived dental features of *Ny. jaegeri* in comparison to other species of the genus *Nyanzachoerus*, including longer and slightly taller third molars, and smaller premolars that are intermediate in size and morphology between other *Nyanzachoerus* (like *Ny. pattersoni*) and *No. euilus* (Harris and White, 1979; Made, 1999; Geraads and Bobe, 2017; Reda et al., 2017). The $\delta^{13}C$ data suggest that grazing diets could have triggered the evolutionary changes in the masticatory apparatus observed in the *Ny. jaegeri* / *No. euilus* lineage. Comparative data on *Ny. jaegeri* of L-WM chronology are only available from Galili (~ 3.76 Ma), where the $\delta^{13}C$ average is –2.05 ± 2.12 ‰ (n = 6) (Bedaso, 2011). The $\delta^{13}C$ average of *Ny. jaegeri* in sites >3.8 Ma, like the Sagantole Formation at Gona and Aramis, Galili, and Mursi, in Ethiopia, and the Apak Member of Lothagam and Kanapoi, in Kenya, is –1.61 ± 1.73 ‰ (n = 67) (Harris and Cerling, 2002; Cerling et al., 2003; Semaw et al., 2005; Levin et al., 2008; White et al., 2009; Bedaso, 2011; Uno et al., 2011), which is slightly lower than the average of –0.42 ± 1.87 ‰ (n = 11) at Woranso-Mille.

In contrast to the derived craniodental adaptations displayed by *Ny. jaegeri* and especially by *No. euilus*, *K. millensis* is a suid with more generalized craniodental features, including brachyodont (low-crowned) and bunodont (round-cusped) molars, shorter third molars, and larger and more numerous premolars (*No. euilus* usually only retains third and fourth premolars, occasionally also the second, while *K. millensis* retains all four upper and lower premolars) (Haile-Selassie and Simpson, 2013). In general, the dental characteristics of *K. millensis* are remindful of modern Potamochoerus or Sus, which are omnivore species (Meijaard et al., 2011). The carbon isotope data presented here suggest that *K. millensis* did not specialize in C_4 resources such as grasses but that it could have shared the dietary flexibility of its modern relatives and occupied the mixed feeding dietary spectrum with the inclusion of C_3 resources. The dentition of *K. millensis* is smaller and closer in size to the more primitive *K. deheinzelini* (Brunet and White, 2001). In fact, the $\delta^{13}C$ average of –5.27 ± 1.87 ‰ (n = 37) of *K. millensis* in Woranso-Mille is only slightly enriched to the $\delta^{13}C$ average of –6.21 ± 2.33 ‰ (n = 20) of *K. deheinzelini* from Aramis (~4.4 Ma) and Gona (>4.55 Ma) (Semaw et al., 2005; Levin et al., 2008; White et al., 2009a). Based on the available fossil evidence, it seems that *K. deheinzelini, K. millensis,* and *K. afarensis* form a lineage of direct ancestor-descendant relationship (Souron, 2012; Haile-Selassie and Simpson, 2013). On the absence of well–preserved cranial material, the most striking difference between these chronospecies is absolute size; as a quick comparison, the third molar mesiodistal length average of *K. deheinzelini* is 25.5 ± 2.6 mm (n = 16), whereas *K. millensis* has an average of 31.8 ± 1.2 mm (n = 16), and *K. afarensis* has an average of 37.3 ± 2.6 mm (n = 50) (Haile-Selassie and Simpson, 2013). In this work we show that there is a significant change in $\delta^{13}C$

between *K. millensis* (in the L-WM, ~3.76–3.57 Ma) and *K. afarensis* (in the U-WM, ~3.47–3.2 Ma). The diet of *K. afarensis* included a greater amount of C_4 resources in comparison with earlier *Kolpochoerus* at Woranso-Mille but also in comparison with *K. afarensis* from other eastern Africa sites that are roughly contemporaneous with the U-WM. The $\delta^{13}C$ average of *K. afarensis* at Hadar SH–DD (~3.42–3.2 Ma) and Dikika SHM-UBM (~3.60–3.24), in Ethiopia, is –4.34 ± 2.06 mm (n = 24), which is significantly lower than the $\delta^{13}C$ average of K. afarensis at Woranso-Mille, –2.44 ± 2.02 mm (n = 24).

The $\delta^{13}C$ values of *Ny. pattersoni* are more or less constant through the Pliocene both in Woranso-Mille and in other sites of East Africa (Figure 4.5). This suid maintains a mixed C_3-C_4 diet throughout the Woranso-Mille chronological sequence. In other sites of East Africa of similar chronology, the $\delta^{13}C$ of *Ny. pattersoni* (= *Ny. kanamensis*) is almost identical to that of Woranso-Mille. However, it does show both more positive and more negative values in other sites of East Africa <3.8 Ma. These results are mostly driven by C_3-enriched diets at Mursi (<4.0 Ma) and C_4-enriched diets at Aramis (~4.4 Ma), Gona (~4.55 Ma) and Galili (<4.0 Ma). All these sites are in Ethiopia, but they are geographically and environmentally different. Mursi is part of the Omo Group deposits in the lower Omo Valley and is situated in the northern part of the Turkana basin, in southwestern Ethiopia (Drapeau et al., 2014), while Aramis, Gona, and Galili form part of the Awash river valley deposits (Semaw et al., 2005; Kullmer et al., 2008; White et al., 2009b). The paleoenvironmental reconstructions suggest that the habitats at Mursi were more closed than at other sites in East Africa (Drapeau et al., 2014). Suids are not only C_3-enriched at Mursi but they also constitute almost half of the fossil specimens found at the site (44% of the mammalian fauna) (Drapeau et al., 2014). The habitats at Aramis, Gona, and Galili, were probably more open (Levin et al., 2008; White et al., 2009a; Bedaso, 2011), though there has been debate on the paleoenvironmental reconstructions at Aramis (Cerling et al., 2010; Suwa and Ambrose, 2014; White et al., 2015).

4.2 Drinking habits of Woranso-Mille suids

The oxygen stable isotope data ($\delta^{18}O$) also show a mixed signal for most suids at Woranso-Mille. *Kolpochoerus millensis* shows some $\delta^{18}O$ values that suggest a greater reliance on drinking water but other specimens of *K. millensis* also show $\delta^{18}O$ higher values that suggest less use of drinking water in the L-WM. Though there is no significant change in $\delta^{18}O$ between *K. millensis* in the L-WM and *K. afarensis* in the U-WM, *K. afarensis* does appear to have less reliance on drinking water in the U-WM. The only significant change in the drinking patterns of suids between the L-WM and the U-WM occurs in *Notochoerus euilus,* which apparently had a greater reliance on drinking water in the L-WM. These results are mostly driven by the samples analyzed in ARI. In this locality, the values of $\delta^{13}C$ of *No. euilus* are high while the values of $\delta^{18}O$ are low, which is also shown by *Ny. jaegeri* (Figure 4.2). This pattern is inverse to what is seen in other localities. This suggests that these two suids are eating a large amount of C_4 resources but still relying on drinking water to cover their physiological necessities. Through diverse techniques of paleoenvironmental reconstruction Curran and Haile-Selassie (2016) concluded that ARI (and MSD) was composed of heterogeneous habitats (mosaics), probably with a densely-vegetated paleo-river and more open regions (woodlands, grasslands) away from the river. The stable isotope values presented here suggest that suids at ARI fed mostly at the grasslands but that they recurrently accessed the river to drink. The slight trend towards less reliance on drinking water and the increase in C_4 resources consumption in the U-WM suggests a shift towards more open and drier habitats through time in Woranso-Mille.

4.3 Suid dietary evolution and environmental change in Woranso-Mille and East Africa

The results agree with Curran and Haile-Selassie (2016) in that the older Woranso-Mille time interval (~3.76–3.57 Ma) was characterized by a mosaic of habitats including at least some densely vegetated areas (maybe associated with a river or other large body of water) and more open grasslands and woodlands. The suid *Kolpochoerus millensis* may have dwelled in the more covered areas of Woranso-Mille, as suggested by its small body size, its similarity with modern *Potamochoerus* (which also inhabits moderately to densely vegetated habitats) and its variable diet that included a larger amount of C_3 resources in comparison with other suids. The larger suids *Nyanzachoerus jaegeri* and *Notochoerus euilus* incorporated a larger amount of C_4 resources like grasses more regularly found in savannas of all types; they probably had good access to drinking water. In the younger time interval (~3.46–3.20 Ma) of Woranso-Mille, the suid Kolpochoerus afarensis replaces *K. millensis*. This suid has a larger body size (more so than extant *Potamochoerus*) and despite having similar craniodental adaptations, its diet shifts towards the incorporation of more C_4 resources. This dietary change suggests that the habitats of Woranso-Mille after ~3.5 Ma had lost some of the densely vegetated areas present before. The suid *Ny. pattersoni* remains almost unaltered (both in diet, morphology, and body size) through the sequence and it is possible that this suid occupied the ecotone areas or mixed habitats present throughout Woranso-Mille. The patterns of abundance also support this trend towards more open habitats. The abundance of *No. euilus* is doubled in the U-WM in comparison to the L-WM, while there is a decrease in the abundance of *Kolpochoerus*. In other words, not only are suid diets getting more C_4-enriched but also the number of C_4-eaters is greater.

The results also support that there was an increase in dietary overlap between suids in the U-WM than in the L-WM. The three suid species present in the U-WM, *K. afarensis*, *Ny. pattersoni*, and *No. euilus* seem to occupy a similar dietary niche space. However, recent microwear analyses have shown that contemporaneous suids from Hadar (members SH and DD) were exploiting foods with variable food properties. While *No. euilus* was more focused on grasses, *K. afarensis* included at least occasional feeding on hard objects (seeds or nuts) and/or underground resources (Chapter 3 of this dissertation). Nevertheless, the stable isotope data and microwear analyses combined confirm that important dietary changes occurred in different suid lineages during the Late Pliocene that may have influenced the morphological adaptations and taxonomic composition of suid communities at this time.

5. Conclusions

The analyses presented here provide evidence that Pliocene suids were partitioning dietary niches to a certain extent. *Kolpochoerus millensis* had a variable C_3-C_4 diet that included a certain amount of C_3 resources in the diet, which is compatible with its generalized dentition similar in morphology and size to extant omnivores of the genus *Potamochoerus* and *Sus*. The replacement of *K. millensis* ~3.5 Ma by its descendant *K. afarensis*, a suid of larger body size, is related to a significant increase in the amount of C_4 resources in the diet. On the other hand, the diet of *Nyanzachoerus jaegeri* and *Notochoerus euilus* were mostly based on C_4 resources, which confirms the *a priori* expectations that the derived craniodental morphology of these suids were adapted to consume abrasive foods such as C_4 grasses. Though the drinking patterns of most of the suids remain similar throughout the Woranso-Mille stratigraphical sequence, *No. euilus* seems to be more reliant on drinking water in the lower Woranso-Mille interval (3.76–3.57 Ma).

In general, the carbon and oxygen stable isotope data are compatible with mixed habitats consisting of densely vegetated areas probably associated with a river or other body of water, and open grasslands (Curran and Haile-Selassie, 2016). The increase in relative abundance of *No. euilus* in the U-WM together with the increase in C_4 resoruce consumption of *K. afarensis* in the upper Woranso-Mille interval (3.47–3.20 Ma) suggest an environmental change towards more open habitats through time. In comparison with other sites of East Africa of similar chronology, however, the diet of Woranso-Mille suids seems to be C_4-enriched (except when comparing with Laetolil, in Tanzania), which would confirm the presence of regional environments throughout East Africa.

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CHAPTER 5. DISCUSSION AND CONCLUSIONS

1. Discussion

This chapter provides a summary of the findings presented in the three papers discussed above, but also a review of the general trends in suid taxonomy, evolution, and diet change in the lower Awash Valley (LAV), and the implications of these findings for the paleoenvironmental context of hominin evolution. Below, I summarize the answers to the questions and predictions stated in Chapter 1, Section 5.

First, I asked if there is evidence for a taxonomic turnover in Late Pliocene suids in the LAV. I predicted that if this is ture the suids in the Lee-Adoyta sub-basin <2.82 Ma would be different to those in Hadar < 2.95 Ma. In Paper I (Chapter 2) I found that after ~2.82 Ma, there is evidence for suid taxonomic turnover in the Lee Adoyta sub-basin at Ledi-Geraru, with three species that were not present prior to ~2.95 Ma, including *Notochoerus* cf. *No. capensis*, *Kolpochoerus phillipi*, and *Metridiochoerus andrewsi*. The suid diets are C_4-enriched in the Gurumaha Fault Block (~2.84–2.7 Ma) in comparison with Hadar (<2.95 Ma), which is coincident with a decrease in suid relative abundance with respect to other mammals. These findings are compatible with environmental change towards habitats with less woody cover, probably even more open and arid than before in the LAV, as proposed by DiMaggio et al. (2015), Rowan et al. (2017), Bibi et al. (2017), and Robinson et al. (2017). The environmental change and faunal turnover at this time is coincident with the first occurrence of the genus *Homo* (Villmoare et al., 2015).

In Paper II, I investigated if there is an increase in dietary breadth in terms of the food physical properties (dental microwear texture) of suid lineages between Kanapoi and Hadar. Because there is one suid genus (*Kolpochoerus*) that is not present in Kanapoi but present in Hadar, I predicted that this suid would occupy a different dietary niche than the other two genera in Hadar (*Nyanzachoerus* and *Notochoerus*). The results of dental microwear texture analyses show that Hadar suids were occupying different dietary niches. In general, the results are compatible with an increase in habitat fragmentation (heterogeneity), and seasonality between Kanapoi and Hadar. The increase in dietary breadth observed in the *Australopithecus anamensis* / *A. afarensis* lineage is likely due to the lower availability of C_3 food resources in Hadar, but there is no evidence that hominins were exploiting other types of foods that were harder, even if these were likely present in Hadar, as evidenced by the dental microwear texture of *Kolpochoerus*.

Finally, I examined how suids varied across space and time in the mid Pliocene of the LAV by analyzing carbon and oxygen stable isotopes of Woranso-Mille and comparing the results with other eastern African sites of the same chronology. I predicted that suid diets would change through the Woranso-Mille sequence (~3.76–3.2 Ma) and that suid diets would differ between Woranso-Mille and other eastern African sites of the same chronology. I found that there is a significant increase in C_4-consumption in the *K. millensis – K. afarensis* lineage between the Lower Woranso-Mille (3.76–3.57 Ma) and the Upper Woranso-Mille (3.47–3.20 Ma). Furthermore, *Kolpochoerus* and *Notochoerus* have C_4-enriched diets in the Upper Woranso-Mille than in other eastern African sites of the same chronology, including Hadar and Dikika. This suggests that C_3 resources were fewer in Woranso-Mille than in other regions of the LAV at this time and therefore, that the habitats at Woranso-Mille were likely thoe with fewer trees and shrubs. There is also an increase in the relative abundance of the grazer species *No. euilus* after ~3.5 Ma in

Woranso-Mille (and especially after ~3.24 in Hadar). These findings support an increase in grazing adaptations through time since the mid-Pliocene compatible with the reduction of C_3 resources available in the LAV.

2. Taxonomy and evolution of Pliocene Suidae in the LAV

The dominant African suids in the LAV during the Pliocene are those in the subfamily Tetraconodontinae, which migrated into Africa from Eurasia during the Late Miocene. They were large suids (Harris and White, 1979), larger than the modern giant forest hog, which has a maximum male body mass of >225 kg (D'Huart, 1993), closer to the size of modern cows. The early representatives of this subfamily, *Nyanzachoerus*, are characterized by bunodont molars and large premolars (Harris and White, 1979; Harris, 1983; Made, 1999). In the sites studied in this dissertation, there are fossils attributed to two different species. The suid *Ny. pattersoni* (also called *Ny. kanamensis*) and a derived form, *Ny. jaegeri* that has relatively smaller premolars and longer and more elaborated third molars (Harris et al., 2003; Geraads et al., 2013; Reda et al., 2017).

Nyanzachoerus pattersoni is present throughout most of the Woranso-Mille sequence, and in the Basal and Sidi Hakoma Members of Hadar (~3.45–3.24 Ma) but the species disappears from the record of the LAV ~3.24 Ma. It is no longer found in the Hadar sequence after the end Denen Dora DD-2 submember, but there are very few specimens from the latter. *Nyanzachoerus jaegeri* was present in the Woranso-Mille area at least until 3.66 Ma (Reda et al., 2017), after it supposedly gave rise to *No. euilus*. Ongoing analysis of the Woranso-Mille Suidae suggest that both *Ny. jaegeri* and *No. euilus* were present at the same localities at least between 3.76 and 3.66 Ma (Reda et al., 2017). In the view of Harris and White (1979), it is common in African suid evolution to find the parent and daughter species together after their genetic split, but it is yet unclear whether in the case of the specimens of *Ny. jaegeri* and *No. euilus* from lower Woranso-Mille; they could all just be considered as part of one or the other species. The reason is that at least from the perspective of their dental characteristics, we can consider derived *Ny. jaegeri* and primitive *No. euilus* to be almost undistinguishable. Even some specimens from the Basal Member (~3.45 Ma) and the Sidi Hakoma Member (~3.42–3.24 Ma) at Hadar have large premolars that are within the range of *Ny. jaegeri* and are larger than those from the Denen Dora and Kada Hadar members at Hadar (~3.24–2.95 Ma) (Made, 1999). This scenario is very similar to what seems to occur with *Australopithecus anamensis* and *A. afarensis*, which spurred the debate whether they should be considered a single evolving anagenetic lineage (Kimbel et al., 2006). The dentognathic remains described from Woranso-Mille have a mixture of primitive and derived characteristics that make difficult their assignation to either one of these species, but they show closer affinity with *Au. anamensis* from Allia Bay/Kanapoi (Kenya) and Asa Issie (Ethiopia) than with *Au. afarensis* from Hadar (Ethiopia) (Haile-Selassie et al., 2010b). This lends support to the hypothesis that *A. anamensis* and *A. afarensis* constitute a single evolving lineage (Kimbel et al., 2006; Haile-Selassie et al., 2010b). In the case of *Ny. jaegeri* and *No. euilus*, it would be possible to set up limits (morphological and temporal ones) between both species and consider them a single evolving lineage. This idea would favor the view of Made (1999) instead of that of Harris and White (1979).

The disappearance of *Ny. pattersoni* from the LAV (it is still present in Koobi Fora until ~3.0 Ma) is coincident with an increase in the presence of *No. euilus* (the most abundant suid in the Denen Dora Member, >80%) (Cooke, 1978a; Fessaha, 1999). The later tetraconodontines of the genus *Notochoerus* are more derived in having smaller premolars (in fact, most of them lose the second premolar) and long, elaborated, third molars (Harris and White, 1979). Though no formal explanation has been proposed to the reduction of premolar size, it may well be a side-effect of the increase in the length and complexity of the third molars that could be related to genetic-mediated constraints on the total length of the post canine tooth row, but this is a question for another dissertation. The elongation of the third molars seems to be the result of a gradual trend in the *Nyanzachoerus-Notochoeru*s lineage (Made, 1999) and it has been related to the incorporation of more C_4 grasses or grit in the diet (Harris and Cerling, 2002). For instance, later specimens of *No. euilus* in the Hadar Formation, ~3.0 Ma, are already visibly more derived (e.g. longer third molars) than the earlier specimens in the sequence ~3.4 Ma (Cooke, 1978a, 2007; Fessaha, 1999; Made, 1999). Current evidence suggests that *No. euilus* is no longer present in the LAV after 2.95 Ma. The suid dental remains from the Gurumaha and Lee Adoyta fault blocks (2.82–2.60 Ma) of Lee Adoyta sub-basin, in Ledi-Geraru, are more derived than those of *No. euilus* in Hadar (e.g., number of talon/id pillars in the third molars, thinner enamel) and are attributed in this work to *No.* cf. *No. capensis*. These specimens constitute a morphological bridge between *No. euilus* and the more derived and younger specimens of *No. scotti*.

The Suinae in the LAV during the Pliocene are represented by species of the genus *Kolpochoerus* and *Metridiochoerus*. The representatives of *Kolpochoerus* in the LAV are much smaller suids in comparison to the tetraconodontines and are more similar in craniodental and skeletal morphology to extant African bushpigs (*Potamochoerus*).

Kolpochoerus are hypothesized to be associated with forested or semi-forested areas as they display typical low-crowned bunodont dentition that is similar to that of modern wild boars and bushpigs (genus *Sus* and *Potamochoerus*) (Harris and White, 1979; Harris, 1983; Bishop et al., 2006; Souron et al., 2015). Earlier forms, *K. deheinzelini* (found in locality FYA of Woranso-Mille), *K. millensis* (only described from Woranso-Mille and Gona ~ 3.76-3.57 Ma) and *K. afarensis* (first described from Hadar ~3.5-2.95 Ma but also present in Woranso-Mille) tend to have less complex third molars and smaller body size (Cooke, 1978a; Brunet and White, 2001; Souron, 2012; Haile-Selassie and Simpson, 2013). Some dental remains of *K. afarensis* from the Burtele locality at Woranso-Mille (~3.5–3.3 Ma) and one specimen of the Basal Member of Hadar (~3.45 Ma) are intermediate in size between *K. millensis* and *K. afarensis*, which also lends support to the ancestor-descendant relationship between these two species. However, the most derived *K. afarensis* from Hadar ~3.0 Ma are larger and display slightly more elaborated and taller third molars (Cooke, 1978a; Fessaha, 1999). In Ledi-Geraru, the dental specimens <2.82 Ma are attributed in this work to the species *K. phillipi*. This taxon was named by Souron et al. (2015) based on an almost complete skull recovered from ~2.5 Ma deposits at Matabaietu, Middle Awash. According to the phylogenetic scenario proposed by these authors, *K. phillipi* is part of a lineage of "bunolophodont" suines that also include the typical African Pleistocene suid *K. majus* and the extant suid *Hylochoerus meinertzhageni*, the giant forest hog.

This lineage and the one formed by *K. limnetes* / *K. olduvaiensis* (= *K. paiceae*) are descendant of *K. afarensis* (Souron et al., 2015). If this phylogenetic scenario is true, then the remains of *K. phillipi* from the Gurumaha fault block ~2.82–2.60 Ma mark the first appearance datum (FAD) of this species in the fossil record and suggest that the split of the stem species *K. afarensis* into *K. phillipi* on the one hand and *K. limnetes* on the other hand occurred ~2.9 Ma. Ongoing analysis of the Maka'amitalu fauna, in the Busidima Formation of Hadar (~2.3–2.0 Ma) confirm the presence of *K. phillipi* in these younger deposits. It is around this time (~2.0 Ma) when early *K. majus* specimens are found in the fossil record, the best example of which are the remains from Konso (Suwa et al., 2014). Therefore, current evidence suggests that *K. phillipi* evolved from K. *afarensis* ~2.9 Ma and *K. majus* evolved from *K. phillipi* ~2.0 Ma.

Another suid genus, *Metridiochoerus*, is only represented in the Pliocene by primitive specimens of *M. andrewsi*. This group is not common during the Pliocene (White et al., 2006) but underwent a remarkable evolutionary radiation during the Pleistocene in Africa (White and Harris, 1977; Cooke, 1978b; Cooke and Wilkinson, 1978; Harris and White, 1979; Pickford, 2006; Bishop, 2010). The earliest fossils assigned to *Metridiochoerus* date to ~3.4 Ma and consist of an upper third molar from the Usno Formation (north of Turkana Basin, Ethiopia) and a mandibular fragment from the Nachukui Formation (West Turkana, Kenya) (White et al., 2006). The earliest representative of the genus, *Metridiochoerus andrewsi,* is also the type species. White and Harris (1977) suggested that this taxon constitutes a long lineage subdivided into three evolutionary stages, or forms, that trend towards more hypsodont and longer, more elaborate third molars. White et al. (2006) further suggested the formal recognition of three chronospecies, comprising *M. shawi* (stage I), *M. jacksoni* (stage II), and *M. andrewsi* (stage III). The specimens from the Lee Adoyta sub-basin in Ledi-Geraru, described in this dissertation and attributed to *M. andrewsi* are the oldest of this species in the LAV, though work in progress suggest this species may be found in the Hadar KH2 submember. Furthermore, the partial male cranium LD 149-1 from the Gurumaha fault block (~2.8 Ma) is the oldest cranium of this species in Africa. This specimen bears the typical zygomatic knobs seen in other males of this species, which are almost orthogonal with respect to the antero-posterior plane of the cranium and located antero-ventrally and very close to the orbits (Harris, 1983; Lazagabaster et al., 2018).

3. Diet of Pliocene Suidae in the LAV

The evolution and dietary changes in suids and hominins in the LAV are summarized in a chronogram in Figure 5.1.

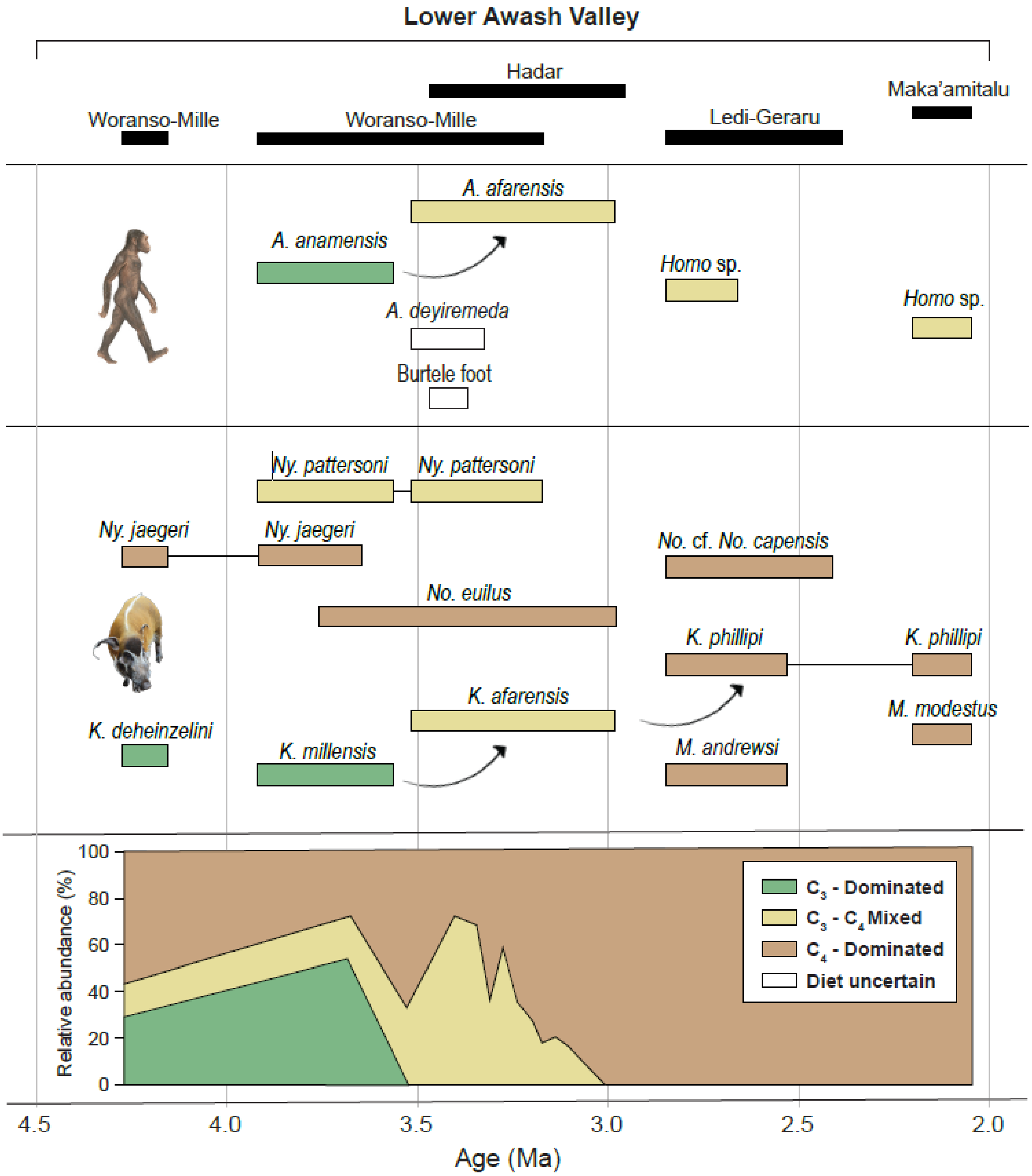

Figure 5.1. Chronogram of suid and hominin evolution in the lower Awash Valley. The colors indicate diet according to carbon stable isotope analysis. The graph in the bottom shows relative abundance based on the number of identified specimens (NISP) belonging to suid species with a specific diet.

Carbon stable isotope analyses show that, in general, Pliocene suids from the LAV had a C_3-C_4 mixed diets. However, there is also evidence for dietary niche partitioning among suids to a certain extent. In the lower time interval of Woranso-Mille (~3.76–3.57 Ma), the tetraconodontine *Nyanzachoerus jaegeri* and its descendant *Notochoerus euilus* had a diet enriched in C_4 resources in comparison to *Ny. pattersoni* and *Kolpochoerus millensis*. After ~3.47 Ma, the diet of *Ny. pattersoni* and *No. euilus* remain similar, but the diet of *K. afarensis* becomes significantly C_4-enriched in comparison to its ancestor *K. millensis*. While the overall stable isotope dietary niche (formed by both carbon and oxygen stable isotopes) is reduced in the upper time interval (~3.47–3.20 Ma) with respect to the lower time interval (~3.76–3.57 Ma) in Woranso-Mille, the three-dimensional dental microwear texture data presented in this work demonstrate that the suid diets at nearby Hadar between ~3.45 and ~2.95 Ma were, in fact, broad. For example, the dental microwear of *K. afarensis* suggests that it occasionally exploited hard objects like nuts and seeds or underground resources such as roots or tubers. This diet is compatible with its craniodental morphology. As its modern counterparts (*Sus* or *Potamochoerus*), *K. afarensis* was equipped with hypsodont incisors and powerful rostral muscles (as indicated by the deep fossae excavated for these muscles in the skull of this species) that are used to move the snout forcefully during rooting (Ewer, 1958; Cooke, 1978a). The dental microwear data on *No. euilus* also indicates that this suid had a broad diet though in general, its dental microwear is similar to that of extant *Phacochoerus*, which are mostly grazer animals, confirming that the derived craniodental features of *No. euilus* (e.g., long and tall third molars) were adaptations to eating grasses. Together, these results suggest that while suids increased their focus in C_4

resources during the Late Pliocene, different suid species targeted different elements of those C_4 resources. This may also well be the case for the suids from the Lee-Adoyta sub-basin. There is a slight trend towards the incorporation of more C_4 resources in the diet of the suids from the Gurumaha fault block (~2.8 Ma) but no significant change in comparison to those from Hadar (~3.45–2.95 Ma). As we mentioned before, there is a taxonomic turnover in suid communities at this time that is related to the appearance of more derived craniodental features. Dental microwear analyses could confirm if the diet of suids at this time changed, but unfortunately the sample size is currently too low for this type of analysis.

A summary of the diet of each Pliocene suid species mentioned in this work is presented in Table 5.1. Craniodental morphology, carbon stable isotope data, and dental microwear texture data (when available), are combined to infer the most likely diet of each species.

Table 5.1. Summary of paleodietary reconstructions of Pliocene Suidae from the lower Awash Valley.

Species	Craniodental morphology	Carbon stable isotopes	Dental microwear texture	Likely diet
Nyanzachoerus pattersoni	Mixed feeder	C_3/C_4	Mixed	Mixed feeder
Nyanzachoerus jaegeri	Mixed feeder	C_4	Mixed / Grazer	Grazer
Notochoerus euilus	Grazer	C_4	Grazer	Grazer
Notochoerus cf. *No. capensis*	Grazer	C_4	?	Grazer
Kolpochoerus deheinzelini	Omnivore	C_3/C_4, C_3	?	Omnivore
Kolpochoerus millensis	Omnivore	C_3/C_4, C_3	?	Omnivore
Kolpochoerus afarensis	Omnivore	C_3/C_4	Omnivore	Omnivore
Kolpochoerus phillipi	Omnivore	C_4	?	Grazer
Metridiochoerus andrewsi	Grazer	C_4	?	Grazer

4. Paleoenvironments in the lower Awash Valley and hominin evolution

The paleoecological data obtained in this dissertation provide a general view of the environmental sequence in the lower Awash Valley (LAV) between ~3.8 Ma and ~2.3 Ma from the perspective of suid evolution. In the time interval of ~3.8–3.6 Ma, the environment at Woranso-Mille was characterized by a mosaic of habitats that included densely vegetated areas probably associated with a river, as well as open grasslands and woodlands (Curran and Haile-Selassie, 2016). The suid *Kolpochoerus millensis* probably dwelled in the more covered areas, as suggested by its small body size and its variable diet that included a larger amount of C_3 resources in comparison with other suids. The larger suids *Nyanzachoerus jaegeri* and *Notochoerus euilus* incorporated a larger amount of C_4 resources like grasses and they probably inhabited more open areas. As mentioned before, this time interval marks the evolutionary transition between *Australopithecus anamensis* and *A. afarensis,* between *Ny. jaegeri* and *No. euilus*, and between *K. millensis* and *K. afarensis*. What seems clear from the paleoecological data presented in this work, is that the appearance of *A. afarensis, No. euilus*, and *K. afarensis*, are related to an increase in the consumption of C_4 resources and this is probably caused by the gradual and continuous spread of grasslands in the region.

On the other hand, the suid *Ny. pattersoni* remains almost unaltered (both in diet, morphology, and body size) through the lower Awash sequence and it is possible that this suid occupied the ecotone areas or mixed habitats present throughout Woranso-Mille and Hadar. This suid is relatively abundant in the Sidi Hakoma Member of Hadar (~3.42–2.24 Ma), when habitats were more wooded and closed, with higher rainfall, and shorter dry seasons in comparison to habitats <2.24 Ma in the LAV (Reed, 2008). *Nyanzachoerus pattersoni* disappears from the region ~3.2 Ma (Cooke, 1978a) and this is coincident with an increase in the abundance of *No. euilus*, a suid characterized by a grazing-dominated diet as indicated by both carbon stable isotope and dental microwear texture data. This is compatible with the environmental reconstructions of Reed (2008), who identified fluctuating paleoenvironments across the Hadar sequence timespan, ranging from intermediate cover bushland, open woodland, to shrubland habitats with varying regions of wetlands and edaphic grasslands across space. The spread of open habitats resulted in more heterogenous landscapes and this was probably related to the climate getting drier and more seasonal, a general trend observed during the Plio-Pleistocene in eastern Africa (DeMenocal, 1995, 2004; Trauth et al., 2007; Cerling et al., 2011a, 2011b; Maslin et al., 2014). A similar pattern is suggested by microwear analyses of the Hadar suids. In general, the microwear signal of the Hadar suids was broad. For example, while the microwear of *No. euilus* is like that of modern grazers *Phacochoerus,* the overall microwear signal is quite variable and this may be the product of occasional or seasonal feeding on non-grass foods. *Kolpochoerus afarensis* has microwear consistent with a variable diet that probably included hard objects in the diet, such as seeds or nuts, or underground resources that are more available in seasonal environments. The slight trend in this species towards lower values of complexity and higher values of anisotropy through the Hadar sequence indicates a small increase in grazing resources in the Kada Hadar Member ~3.1 Ma, which is supported by carbon stable isotope data (Wynn et al., 2016). *Notochoerus euilus* also has higher values of anisotropy in this member, suggesting more grazing at the end of the Hadar sequence, which is compatible with the reconstruction of Reed (2008). In general, the microwear texture evidence across Hadar species is consistent with the presence of some woody cover at Hadar but also grasslands at the site/in the region, which became more abundant especially after 3.24 Ma.

Carbon stable isotope analyses show that there was an increase in dietary overlap between suids after ~3.5 Ma with respect to suids between ~3.8 and ~3.6 Ma. The three suid species present between ~3.5 and ~3.2 Ma, *K. afarensis*, *Ny. pattersoni,* and *No. euilus* seem to occupy a similar dietary niche space. However, the microwear analyses have shown that contemporaneous suids from Hadar (members BM and SH) were exploiting foods with variable physical properties. Nevertheless, the stable isotope data and microwear analyses combined confirm that important dietary changes occurred in different suid lineages during the Late Pliocene that may have influenced the morphological adaptations and taxonomic composition of suid communities at this time.

The combined evidence of the reconstructed habitats and the suid isotopes and microwear suggests that the habitats at Hadar were more heterogeneous and/or seasonal than before (e.g., at Kanapoi ~4.1 Ma) (Wynn, 2000; Ungar et al., 2017). These results also support dietary niche partitioning among suids at Hadar, which was not evident from carbon stable isotope analyses alone (Harris and Cerling, 2002; Wynn et al., 2016; Manthi et al., 2017). Dental microwear texture analyses further suggest that there were probably resources in Hadar (e.g., hard objects such as fruits and nuts, and underground food items) that were exploited at least by the suid *Kolpochoerus* but not by *A. afarensis* (Ungar et al., 2010). Early hominins seem to have restricted their diet to the tougher parts of C_3 plants (like leaves) and C_4 plants (like the aereal part of grasses). The changes in the dietary ecology of suids supports the idea that the increased isotopic breadth in *A. afarensis* compared to *A. anamensis* was likely due to changes in the environment. Namely, a change in climate that caused an increase in habitat fragmentation and the reduction of C_3 resources and/or an increase in seasonality that changed the presence of these C_3 dietary resources seasonally. New stable isotopic data indicates that the incorporation of C_4 resources in hominin’s diets may have occurred as early as 3.76 Ma, a pattern also observed in *Theropithecus* (Levin et al., 2015). However, *A. afarensis* likely did not exploit other resources available in the environment and thus, there is no definitive evidence that a significant dietary breadth expansion (other than incorporating certain parts of C_4 plants) occurred in the hominin lineage at this time.

The analysis of the suids from the Lee-Adoyta sub-basin, Ledi-Geraru, are compatible with a shift towards more open, drier, and more seasonal habitats in the LAV during the late Pliocene, based on both the morphological and isotopic evidence from the *Kolpochoerus* and *Notochoerus* lineages, as well as the presence of *Metridiochoerus*. The fossil genus *Metridiochoerus* consists of multiple lineages of hypsodont, hyper-grazing suids that gave rise to warthogs (Phacochoerus spp.) by at least ~1.0 Ma (Harris and Cerling, 2002; Souron, 2017). Living warthogs are the most arid-adapted of all extant suids, with the desert warthog (*Phacochoerus aethiopicus*) favoring semi-desert bushland and thicket in the Horn of Africa and the common warthog (*P. africanus*) favoring mosaics of grassland and open woodlands in eastern and southern Africa savannas (Cumming, 2013; Grubb and D'Huart, 2013). Both *Phacochoerus* species have exaggerated craniodental morphologies related to specialization for the consumption of abrasive grasses and their enamel $\delta^{13}C$ values classify them as C_4 hyper-grazers (Harris and Cerling, 2002). The strong similarities in craniodental morphology and ecology inferred from stable carbon isotopes between fossil species of *Metridiochoerus* and their living descendants *Phacochoerus* (Souron, 2017) implies strong dietary and, by extension, habitat niche conservatism in this lineage since the Pliocene. I therefore propose that the migration of *Metridiochoerus* in the LAV ~2.82 Ma (and probably ~3.0 Ma) supports a marked habitat shift at this time, because it is unknown at present from the older LAV sediments, such as those of the mid-Pliocene Hadar Formation, despite having appeared in eastern Africa by at least ~3.4 Ma (White et al., 2006; Cooke, 2007) or possibly as early as ~3.8 Ma (Souron, 2012).

A change towards more open habitats has also been suggested by paleoecological studies of the bovids (Bibi et al., 2017), giraffids (Rowan et al., 2017), and mammal faunas as a whole (DiMaggio et al., 2015), as well as stable carbon isotopes ($\delta^{13}C$) of herbivore enamel (Robinson et al., 2017). Previous studies using multivariate correspondence analyses of the large mammal functional trait structure of Plio-Pleistocene LAV faunas indicated a shift to lower precipitation and higher temperature seasonality through time, with major differences between the mid-Pliocene and Hadar Formation and the late Pliocene sediments of Lee Adoyta (DiMaggio et al., 2015; Robinson et al., 2017). The Lee Adoyta mammal faunas are dominated by grazers, mostly ungulates which modern relatives that favor open and grassy habitats, which contrasts with the older Hadar Formation faunas that are characterized by C_3-C_4 mixed feeders and a taxonomically diverse mixture of terrestrial and arboreal species. For example, the only non-hominin primate species found at Lee Adoyta is the large-bodied, C_4-consuming *Theropithecus*, whereas the Hadar Formation yields a diverse monkey fauna including species of *Parapapio, Cercopithecoides*, and cf. *Rhinocolobus,* in addition to *Theropithecus* (Campisano et al., in press). The ongoing reevaluation of the suids from Maka'amitalu (~ 2.3 Ma, Budisima Formation of Hadar), confirm the presence of *K. phillipi* and *M. modestus*, the last of which is hypothesized to be the direct ancestor of *Phacochoerus*. Based on their craniodental morphology and on the available isotope evidence, Maka'amitalu seems to maintain the open and possibly dry habitats present in the region after ~3.2 Ma. Considering the entire LAV sequence from ~3.76 Ma

Woranso-Mille to the ~2.3 Ma OG Maka'amitalu, one of the most interesting paleoecological patterns concerns the trends in the relative abundance of suids. In the late Pliocene sediments of Lee Adoyta, suids comprise only 2–4% of the large mammal fauna, whereas they comprise 23–49% of those from the older sediments of Woranso-Mille and Hadar. This general decline of suid abundance could also be related to a steady increase in grassy over woody habitats through time. This grassy trend is supported by comprehensive paleosol datasets from the Awash Valley (Levin et al., 2011) and eastern Africa as a whole (Cerling et al., 2011b), as well as from community analyses of the LAV faunas (DiMaggio et al., 2015; Robinson et al., 2017). For example, although the Hadar fauna collectively indicates a mixed grassy-woody environment, multivariate analyses of the large mammal community (Reed, 2008) document a noticeable trend towards the top of the sequence towards drier environments similar to bushland-thicket, especially in the uppermost unit of the Hadar Formation (KH-2 submember). Even KH-2, however, contrasts with the reconstructed environments of Lee Adoyta, which community analyses suggest sample a relatively open grassland like those of the Serengeti Plains today (DiMaggio et al., 2015). Extant suid species, including relatively arid-adapted *Phacochoerus* spp., prefer habitats with some tree or tall grass cover, and therefore we propose that a trend towards more open habitats is a likely environmental driver behind their gradual decline in abundance through time in the LAV.

A compilation of the available carbon isotope data and relative abundance of the three main eastern African suid genera (*Nyanzachoerus, Notochoerus, Kolpochoerus*) is summarized in Figure 5.2.

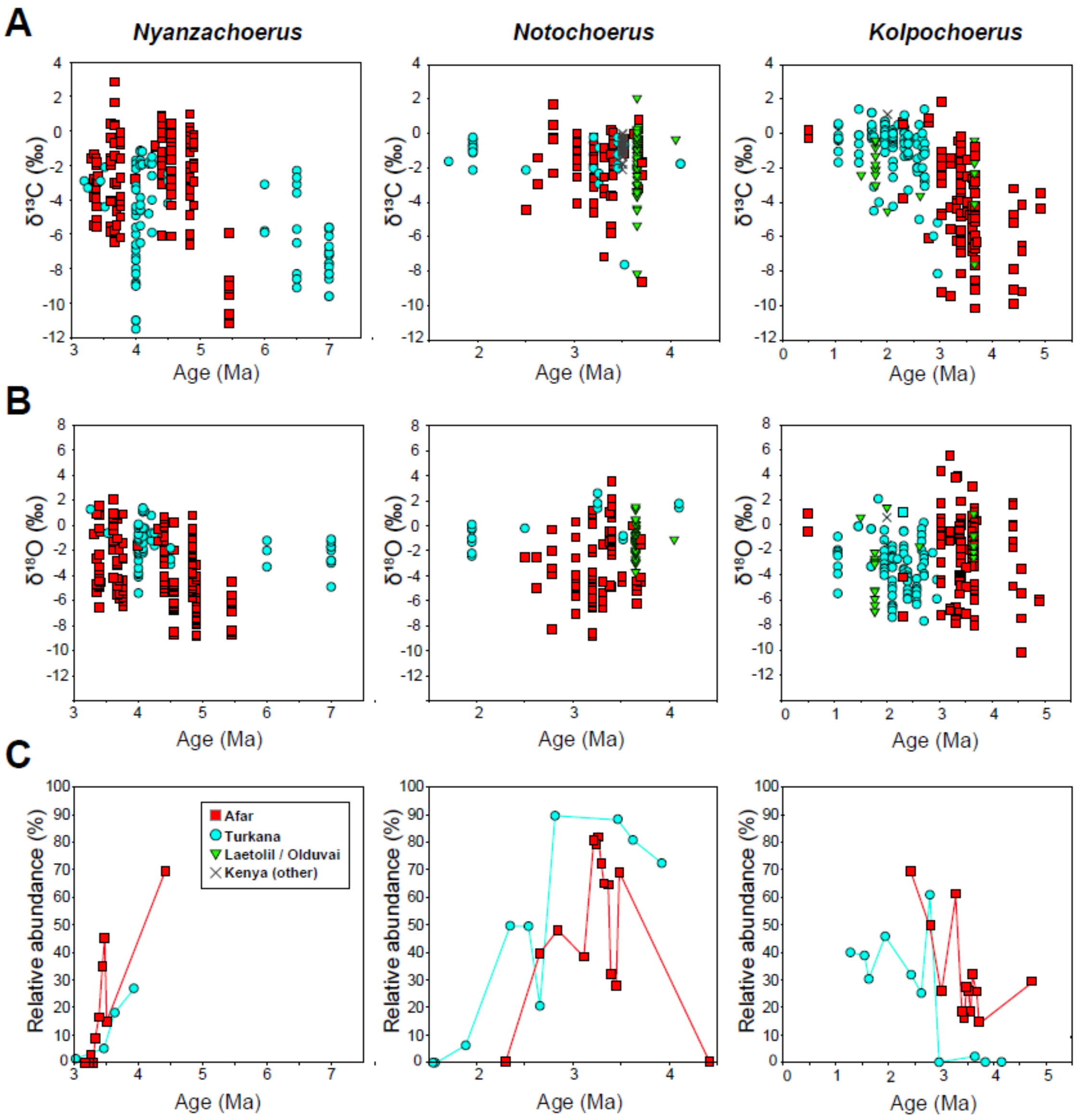

Figure 5.2. Changes in diet and relative abundance of Plio-Pleistocene Suidae in eastern Africa and colored by region. A) Carbon isotope data; B) Oxygen isotope data; C) Relative abundance. Regions: Afar, red square; Turkana, blue circle; Laetolil and Olduvai, green inverted triangles; Kenya (other than Turkana Basin), grey oblique crosses.

5. Conclusions

The study of Pliocene Suidae in the lower Awash Valley (LAV) have shown that suid evolution and diet was likely influenced by environmental changes in the region between ~3.8 and ~2.6 Ma. In the time interval between 3.76 and 3.57 Ma, four suid species inhabit Woranso-Mille in environments that likely consisted of a mix of densely vegetated areas associated with a fluvial system, and open grasslands and woodlands. Two of the Woranso-Mille suids had C_4-dominated diets, *Nyanzachoerus jaegeri* and its descendant *No. euilus* and probably fed in the open grasslands, whereas *Kolpochoerus millensis* had a C_3-enriched diet and probably occupied more wooded areas. *Nyanzachoerus pattersoni* had a mixed C_3/C_4 diet and likely occupied ecotone habitats, in the interphase of the covered areas and the more open areas. This time frame marks the transition of *Australopithecus anamensis* and *A. afarensis*.

After ~3.57 Ma, *K. millensis* is replaced by its descendant *K. afarensis,* which had a diet considerably enriched in C_4 resources. This change was likely influenced by the appearance of more open grasslands and reduction of woody cover, but especially after 3.24 Ma because at this time *Ny. pattersoni* disappears from the region and *No. euilus* becomes the most abundant suid (> 50% in Woranso-Mill after ~3.57 Ma and >80% in the DD Member of Hadar after ~3.24 Ma), even though carbon stable isotope analyses do not reveal any significant dietary change in these two suids. After ~3.57 Ma there is also a decrease in the overall suid dietary space formed by both carbon and oxygen stable isotope values but a higher dietary overlap. Dental microwear analyses of Hadar suids, however, reveal that despite the stable isotope dietary overlap, the diet of the different suid taxa was different, with *K. afarensis* occasionally exploiting hard food items such as nuts and seeds, or underground resources such as tubers. This suid is not present in Kanapoi, and there is no indication that either hominins or suids were eating hard food itmes at this older site (~4.1 Ma) situated outside of the LAV. There is also no evidence to support that *A. afarensis* was consuming these types of foods either in Kanapoi or in Hadar, even if they were likely present at least in Hadar.

After ~2.95 Ma, there is a faunal turnover in the LAV that also affected the different suid lineages, with the appearance of *Notochoerus* cf. *No. euilus, K. phillipi,* and *Metridiochoerus andrewsi*. At the time ~2.8 Ma, suid diets became slightly more C_4-enriched and suid relative abundance in the LAV marked its lowest point of the Pliocene (2–4%), likely influenced by an environmental change towards even more open and probably drier habitats. I hypothesize that these open habitats favored the evolution of early *Homo* or its migration into the region.

In general, the data presented here support that the craniodental adaptations observed in different eastern African suid lineages during the Pliocene were related to changes in diet. These changes in diet were likely triggered by environmental changes affecting all eastern Africa, but with habitat differences that could vary locally. It seems that early hominins adapted to these new environments by enhancing their dietary flexibility. An important note is that stable isotope analyses alone are not enough to determine the diet of suids in the past (and of any species with flexible dietary behaviors, such as probably early hominins). The use of alternative techniques of paleodietary reconstruction (e.g., dental microwear) are recommended as an aid to stable isotope analyses and ecomorphology.

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APPENDIX A

LIST OF FOSSIL SUID SPECIMENS FROM LEE ADOYTA

Supplementary materials for:

Fossil Suidae (Mammalia, Artiodactyla) from Lee Adoyta, Ledi-Geraru, lower Awash Valley, Ethiopia: implications for late pliocene turnover and paleoecology

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1. SI Text

This supplemental information provides a list of suid fossil specimens from the Lee-Adoyta sub-basin, including catalog number (ID and Barcode), year that each specimen was collected, stratigraphical provenience (Fault Block), generic and specific attribution, and skeletal element.

2. Tables

Table SI 1. List of suid fossil specimens from the Lee-Adoyta sub-basin, Ledi-Geraru, lower Awash Valley, Ethiopia.

ID	Barcode	Year collected	Fault Block	*Genus*	Specific epithet	Specific element	Side
LD 149-2	111048	2013	GU	*Metridiochoerus*	*andrewsi*	UM3	L
LD 338-1	111306	2013	GU	*Metridiochoerus*	*andrewsi*	M3	?
LD 149-1	110947	2013	GU	*Metridiochoerus*	*andrewsi*	CRANIUM	LR
LD 445-1	113869	2015	GU	*Metridiochoerus*	*andrewsi*	MAN (M3)	L
LD 115307	115307	2018	GU	*Metridiochoerus*	*andrewsi*	UM3	R
LD 298-1	111193	2013	GU	*Notochoerus*	cf. *No. capensis*	UM3	R
LD 107-2	113778	2015	GU	*Notochoerus*	cf. *No. capensis*	UM3	L?
LD 133-2a	113832	2015	GU	*Notochoerus*	cf. *No. capensis*	UM3	L
LD 133-2b	113831	2015	GU	*Notochoerus*	cf. *No. capensis*	UM3	L
LD 305-1	111226	2013	GU	*Kolpochoerus*	*phillipi*	MAN (dP3-M1)	R
LD 306-1	111213	2013	GU	*Kolpochoerus*	*phillipi*	frag. MAN (P4-frag. M1) + mesial frag. LP3	R
LD 327-1	111274	2013	GU	*Kolpochoerus*	*phillipi*	MAN (M2-M3) + MAN. frags. indet.	R

LD 381-2	111377	2013	GU	*Kolpochoerus*	*phillipi*	MAN (dp4 + distal frag. dp3)	R
LD 304-38	114000	2015	GU	*Kolpochoerus*	*phillipi*	LM3	R
LD 305-14	113825	2015	GU	*Kolpochoerus*	sp.	LM3	L
LD 111-1	110118	2012	GU	*Metridiochoerus*	sp.	UM3	L
LD 615-1	114405	2015	LA	*Metridiochoerus*	andrewsi	UM3	R
LD 564-1e	115185	2015	LA	*Notochoerus*	cf. *No. capensis*	MAN frag.	?
LD 564-1f	115186	2015	LA	*Notochoerus*	cf. *No. capensis*	MAN (alveolus C)	L
LD 564-1g	115187	2015	LA	*Notochoerus*	cf. *No. capensis*	MAN frag.	?
LD 564-1h	115188	2015	LA	*Notochoerus*	cf. *No. capensis*	MAN SYMPHYSIS	L
LD 564-1a	113636	2015	LA	*Notochoerus*	cf. *No. capensis*	OCCIPITAL CONDYLES	LR
LD 564-1b	115183	2015	LA	*Notochoerus*	cf. *No. capensis*	MAX (M3)	L
LD 564-1c	115184	2015	LA	*Notochoerus*	cf. *No. capensis*	MAX (M3)	R
LD 564-1d	113696	2015	LA	*Notochoerus*	cf. *No. capensis*	MAN (M3)	L
LD 115356	115356	2018	LA	*Kolpochoerus*	phillipi	MAN (M3) + P/M frags.	L
LD 586-1	114180	2015	LA	*Kolpochoerus*	phillipi	LP4	L
LD 50-1	109957	2012	OG	*Notochoerus*	cf. *No. capensis*	MAN (M3)	R
LD 709-2	114879	2015	GU	*Suidae*		ASTRAGALUS	R
LD 80-1	110082	2012	LA	*Suidae*		ASTRAGALUS	L
LD 131-3	110478	2013	LA	*Suidae*		ASTRAGALUS	R
LD 573-1	113542	2015	LA	*Suidae*		ASTRAGALUS	L
LD 568-1a	113624	2015	OG	*Notochoerus*	sp.	III METACARPAL	R
LD 568-1b	115158	2015	OG	*Notochoerus*	sp.	IV METACARPAL	R
LD 568-1c	115159	2015	OG	*Notochoerus*	sp.	V METACARPAL	R
LD 568-1d	115160	2015	OG	*Notochoerus*	sp.	NAVICULAR	R
LD 720-1	114873	2015	GU	*Kolpochoerus*	sp.	UM3	R
LD 445-2	114072	2015	GU	*Metridiochoerus*	sp.	MANDIBLE	L
LD 110-2	111199	2013	GU	*Notochoerus*	sp.	M3	?
LD 12-2	110951	2013	GU	*Notochoerus*	sp.	M3	?
LD 299-1	111190	2013	GU	*Notochoerus*	sp.	UM3	R
LD 303-4	111299	2013	GU	*Notochoerus*	sp.	M3	?
LD 304-4	111186	2013	GU	*Notochoerus*	sp.	M3	?
LD 508-4	113665	2015	GU	*Notochoerus*	sp.	UM3?	?
LD 115376	115376	2018	GU	*Notochoerus*	sp.	frag. M3	?
LD 184-1	110882	2013	GU	cf. *Notochoerus*		M3	?
LD 306-6	111217	2013	GU	cf. *Notochoerus*		frag. M1	?
LD 271-1	110985	2013	GU	cf. *Notochoerus*		LC	L
LD 348-2	111266	2013	GU	*Suidae*		LM1 or LM2	R
LD 508-3	113669	2015	GU	*Suidae*		M	?
LD 537-2	113629	2015	LA	*Notochoerus*	sp.	M3	?
LD 216-1	111067	2013	LA	*Kolpochoerus*	sp.	LP4	L

LD 115974	115974	2018	LA	*Kolpochoerus*	sp.	UC	R
LD 44-1	109955	2012	LA	*Notochoerus*	sp.	UM3	?
LD 115803	115803	2018	LA	*Notochoerus*	sp.	M3 frags.	?
LD 115969	115969	2018	LA	*cf. Kolpochoerus*		M frag.	?
LD 354-1	111207	2013	LA	*Suidae*		CRANIUM	LR
LD 314-4	111292	2013	GU	*Suidae*		TIBIA	L
LD 314-27	115130	2015	GU	*Suidae*		frag. METAPODIAL	?
LD 115881	115881	2018	GU	*Suidae*		frag. METAPODIAL	?
LD 60-7	110774	2012	LA	*Suidae*		frag. PELVIS	R
LD 115734	115734	2018	LA	*Suidae*		frag. METAPODIAL + PHALANX 2	?
LD 115673	115673	2018	LA	*Suidae*		TIBIA	L
LD 176-1	111003	2013		*Phacochoerus*	sp.	M3	?

APPENDIX B

SUID CARBON AND OXYGEN STABLE ISOTOPE DATA FROM WORANSO-MILLE

Supplementary materials for:

Dietary ecology of Pliocene Suidae (Mammalia, Artiodactyla): isotopic evidence from Woranso-Mille, Afar, Ethiopia

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1. SI Text

This supplemental information provides a list of carbon (δ13C) and oxygen (δ18O) stable isotope values and chronological information on the dental suid specimens sampled. It also provides a compilation of carbon stable isotope vales of the same suid lineages present in Woranso-Mille from other sites in eastern African of the same and different chronology. Stable isotope data was provided by Naomi Levin and Yohannes Haile-Selassie.

2. Tables

Table SI 2. List of specimens analyzed and stable isotope of carbon and oxygen data.

Species	Specimen	$\delta^{13}C$	$\delta^{18}O$	Tooth	Age	Member
Kolpochoerus afarensis	BRT-VP-1/105	-2.02	-4.80	R. UM3	3.469-3.33	U-WM
Kolpochoerus afarensis	BRT-VP-1/29	-1.06	-4.17	L. UM2	3.469-3.33	U-WM
Kolpochoerus afarensis	BRT-VP-1/54	-4.85	1.91	R. LM2	3.469-3.33	U-WM
Kolpochoerus afarensis	BRT-VP-1/82	-6.95	-4.37	L. LM3	3.469-3.33	U-WM
Kolpochoerus afarensis	BRT-VP-2/22	-0.14	-1.39	R. LM3	3.469-3.33	U-WM
Kolpochoerus afarensis	BRT-VP-2/39	-1.16	-2.55	L. LM3	3.469-3.33	U-WM
Kolpochoerus afarensis	BRT-VP-2/40	-0.18	-2.50	R. UM3	3.469-3.33	U-WM
Kolpochoerus afarensis	KSA-VP-2/116	-0.44	3.92	L. LM3	3.4-3.3	U-WM
Kolpochoerus afarensis	NFR-VP-1/13	-3.75	-1.95	L. LM3	3.469-3.33	U-WM
Kolpochoerus afarensis	NFR-VP-1/15	-0.63	0.58	R. UM3	3.469-3.33	U-WM
Kolpochoerus afarensis	NFR-VP-1/179	-1.61	-3.05	R. UM3	3.469-3.33	U-WM
Kolpochoerus afarensis	NFR-VP-1/286	-2.95	0.14	R. UM3	3.469-3.33	U-WM
Kolpochoerus afarensis	NFR-VP-1/288	-2.35	-0.03	L. LM2	3.469-3.33	U-WM
Kolpochoerus afarensis	NFR-VP-1/290	-3.88	-1.36	L. LM3	3.469-3.33	U-WM
Kolpochoerus afarensis	NFR-VP-1/60	-4.64	-4.28	R. UM3	3.469-3.33	U-WM

Kolpochoerus millensis	AMA-VP-2/22	-6.61	-3.28	L. UM3	3.66-3.57	L-WM
Kolpochoerus millensis	AMA-VP-2/58	-4.73	-1.93	L. LM3	3.66-3.57	L-WM
Kolpochoerus millensis	ARI-VP-1/275	-5.07	-2.25	L. UM3	3.66-3.57	L-WM
Kolpochoerus millensis	ARI-VP-1/293	-8.51	-7.62	R. UM3	3.66-3.57	L-WM
Kolpochoerus millensis	ARI-VP-1/54	-5.11	1.37	R. UM3	3.66-3.57	L-WM
Kolpochoerus millensis	ARI-VP-1/548h	-4.82	-5.55	L. UM1	3.66-3.57	L-WM
Kolpochoerus millensis	ARI-VP-1/548i	-7.34	-5.90	R. LM3	3.66-3.57	L-WM
Kolpochoerus millensis	ARI-VP-1/55	-7.65	-0.22	L. LM3	3.66-3.57	L-WM
Kolpochoerus millensis	ARI-VP-1/56	-9.06	-5.93	L. LM2	3.66-3.57	L-WM
Kolpochoerus millensis	ARI-VP-1/582	-6.69	1.09	R. UM3	3.66-3.57	L-WM
Kolpochoerus millensis	ARI-VP-1/591	-10.18	-8.03	R. LM3	3.66-3.57	L-WM
Kolpochoerus millensis	ARI-VP-2/20	-6.70	-1.94	L. LM3	3.66-3.57	L-WM
Kolpochoerus millensis	ARI-VP-2/60	-5.90	-2.28	R. LM3	3.66-3.57	L-WM
Kolpochoerus millensis	ARI-VP-2/65	-2.71	0.24	R. LM3	3.66-3.57	L-WM
Kolpochoerus millensis	ARI-VP-2/76	-6.47	-1.55	L. LM3	3.66-3.57	L-WM
Kolpochoerus millensis	ARI-VP-2/96	-2.79	-0.89	L. LM3	3.66-3.57	L-WM
Kolpochoerus millensis	ARI-VP-3/262	-2.44	-4.75	L. LM3	3.66-3.57	L-WM
Kolpochoerus millensis	ARI-VP-3/39	-9.08	-5.84	L. LM3	3.66-3.57	L-WM
Kolpochoerus millensis	KSD-VP-1/2	-2.98	3.06	R. LM3	~ 3.6	L-WM
Kolpochoerus millensis	LLG-VP-1/16	-6.85	-0.06	L. LM2	3.66-3.57	L-WM
Kolpochoerus millensis	LLG-VP-1/29	-4.97	-1.58	L. UM3	3.66-3.57	L-WM
Kolpochoerus millensis	LLG-VP-1/4	-6.08	-1.95	L. LM3	3.66-3.57	L-WM
Kolpochoerus millensis	LLG-VP-1/8	-4.23	-2.19	R. LM3	3.66-3.57	L-WM
Kolpochoerus millensis	LLG-VP-2/40	-6.66	-1.31	L. LM3	3.66-3.57	L-WM
Kolpochoerus millensis	LLG-VP-2/63	-2.60	0.72	R. UM3	3.66-3.57	L-WM
Kolpochoerus millensis	MKM-VP-1/136	-5.54	-2.69	L. LM3	3.66-3.57	L-WM
Kolpochoerus millensis	MKM-VP-1/138	-6.10	-2.01	L. UM2	3.66-3.57	L-WM
Kolpochoerus millensis	MKM-VP-1/191	-5.51	-2.62	R. LM3	3.66-3.57	L-WM
Kolpochoerus millensis	MKM-VP-1/345	-4.54	-2.94	L. LM3	3.66-3.57	L-WM
Kolpochoerus millensis	MKM-VP-1/8	-4.58	-0.50	L. UM2	3.66-3.57	L-WM
Kolpochoerus millensis	MSD-VP-1/116	-1.31	-5.88	L. UM3	3.76-3.57	L-WM
Kolpochoerus millensis	MSD-VP-1/26	-5.02	-2.10	R. LM3	3.76-3.57	L-WM
Kolpochoerus millensis	MSD-VP-1/57	-0.79	-3.26	L. UM3	3.76-3.57	L-WM
Kolpochoerus millensis	MSD-VP-2/212	-2.70	-5.22	L. UM3	3.76-3.57	L-WM
Kolpochoerus millensis	MSD-VP-2/243	-3.49	-3.03	R. LM3	3.76-3.57	L-WM
Kolpochoerus millensis	MSD-VP-2/82	-4.22	-1.94	L. UM3	3.76-3.57	L-WM
Kolpochoerus millensis	MSD-VP-3/41	-4.94	-1.66	L. LM3	3.76-3.57	L-WM
Notochoerus euilus	ARI-VP-1/548a*	0.30	-5.22	M	3.66-3.57	L-WM
Notochoerus euilus	ARI-VP-1/548c*	-0.97	-4.75	M3	3.66-3.57	L-WM
Notochoerus euilus	ARI-VP-1/548e*	-0.40	-4.77	M3	3.66-3.57	L-WM
Notochoerus euilus	ARI-VP-1/548g*	0.84	-6.24	M	3.66-3.57	L-WM
Notochoerus euilus	ARI-VP-1/548j*	-1.58	-5.20	R. UI2	3.66-3.57	L-WM
Notochoerus euilus	ARI-VP-1/548k*	-3.19	-4.42	L. LM2	3.66-3.57	L-WM
Notochoerus euilus	BRT-VP-1/132*	0.08	-1.57	R. UM3	3.469-3.33	U-WM
Notochoerus euilus	BRT-VP-2/93*	-0.22	-0.46	UM3	3.469-3.33	U-WM
Notochoerus euilus	BRT-VP-2/94*	-0.01	-0.95	R. UM3	3.469-3.33	U-WM
Notochoerus euilus	MKM-VP-1/55*	-0.02	-0.02	R. UM3	3.66-3.57	L-WM
Notochoerus euilus	NFR-VP-1/1*	-1.79	-1.10	R. UM3	3.469-3.33	U-WM
Notochoerus euilus	NFR-VP-1/14*	-0.59	0.66	R. LM3	3.469-3.33	U-WM
Notochoerus euilus	NFR-VP-1/16*	-0.59	2.16	L. UM3	3.469-3.33	U-WM
Notochoerus euilus	NFR-VP-1/190*	-1.61	1.54	L. LM3	3.469-3.33	U-WM
Notochoerus euilus	NFR-VP-1/197*	-3.62	-2.33	L. LM3	3.469-3.33	U-WM
Notochoerus euilus	NFR-VP-1/20*	0.10	3.52	R. UM3	3.469-3.33	U-WM
Notochoerus euilus	NFR-VP-1/227*	-0.40	-2.07	L. UM3	3.469-3.33	U-WM
Notochoerus euilus	NFR-VP-1/24*	-0.25	0.97	L. UM3	3.469-3.33	U-WM

Notochoerus euilus	NFR-VP-1/34*	-0.69	-1.17	R. UM3	3.469-3.33	U-WM
Notochoerus euilus	NFR-VP-1/50*	-2.39	-4.87	R. UM3	3.469-3.33	U-WM
Notochoerus euilus	NFR-VP-1/7A*	-0.68	-0.40	R. UM3	3.469-3.33	U-WM
Nyanzachoerus jaegeri	ARI-VP-1/299	2.85	-4.85	R. UM3	3.66-3.57	L-WM
Nyanzachoerus jaegeri	ARI-VP-1/548b	-0.71	-4.23	M3	3.66-3.57	L-WM
Nyanzachoerus jaegeri	BDU-VP-1/14	-1.96	0.97	L. UM3	3.66-3.57	L-WM
Nyanzachoerus jaegeri	FYA-VP-1/10	-0.82	-1.20	R. LM3	~ 4.3?	
Nyanzachoerus jaegeri	FYA-VP-1/11	-0.80	-0.64	R. LM2	~ 4.3?	
Nyanzachoerus jaegeri	FYA-VP-1/13	-0.92	-0.25	R. LM3	~ 4.3?	
Nyanzachoerus jaegeri	LLG-VP-1/13	-1.74	0.64	L. LM3	3.66-3.57	L-WM
Nyanzachoerus jaegeri	LLG-VP-2/36	-0.42	-0.41	R. UM3	3.66-3.57	L-WM
Nyanzachoerus jaegeri	LLG-VP-2/67	-4.01	0.03	R. UM3	3.66-3.57	L-WM
Nyanzachoerus jaegeri	MKM-VP-1/179	0.42	0.58	R. LM3	3.66-3.57	L-WM
Nyanzachoerus jaegeri	MSD-VP-1/10	0.38	0.86	R. UM3	3.76-3.57	L-WM
Nyanzachoerus jaegeri	MSD-VP-1/7	-1.44	-2.87	L. LM3	3.76-3.57	L-WM
Nyanzachoerus jaegeri	MSD-VP-2/177	0.32	-3.20	R. LM3	3.76-3.57	L-WM
Nyanzachoerus jaegeri	MSD-VP-5/54	1.67	0.50	R. UM3	3.76-3.57	L-WM
Nyanzachoerus kanamensis	AMA-VP-1/3	-1.99	-4.19	L. LM3	3.66-3.57	L-WM
Nyanzachoerus kanamensis	AMA-VP-2/1	-5.56	0.05	L. LM3	3.66-3.57	L-WM
Nyanzachoerus kanamensis	ARI-VP-1/548d	-6.47	-3.08	R. UM2	3.66-3.57	L-WM
Nyanzachoerus kanamensis	ARI-VP-1/548f	-3.01	-5.53	R. UP4	3.66-3.57	L-WM
Nyanzachoerus kanamensis	ARI-VP-2/125	-5.77	-1.05	R. UM3	3.66-3.57	L-WM
Nyanzachoerus kanamensis	BDB-VP-1/2	-2.61	-4.54	L. LM2	~ 3.4	U-WM
Nyanzachoerus kanamensis	BDU-VP-2/1	-1.54	2.10	R. UM3	3.66-3.57	L-WM
Nyanzachoerus kanamensis	BRT-VP-2/47	-2.77	-1.58	R. LM3	3.469-3.33	U-WM
Nyanzachoerus kanamensis	KSA-VP-2/86	-2.78	0.89	R. LM3	3.4-3.3	U-WM
Nyanzachoerus kanamensis	KSA-VP-3/17	-1.34	-2.61	L. UM2	3.4-3.3	U-WM
Nyanzachoerus kanamensis	KSA-VP-3/24	-3.83	-5.35	R. UM3	3.4-3.3	U-WM
Nyanzachoerus kanamensis	KSA-VP-3/31	-5.49	-4.69	L. UM2	3.4-3.3	U-WM
Nyanzachoerus kanamensis	LDD-VP-1/256	-1.60	0.79	L. LM3	3.5-3.3	U-WM
Nyanzachoerus kanamensis	LDD-VP-1/280	-2.00	-4.90	L. UM3	3.5-3.3	U-WM
Nyanzachoerus kanamensis	LDD-VP-1/348	-3.00	-3.60	L. UM3	3.5-3.3	U-WM
Nyanzachoerus kanamensis	LDD-VP-1/550	-5.42	-0.21	L. LM3	3.5-3.3	U-WM
Nyanzachoerus kanamensis	LDD-VP-1/90	-3.33	-3.32	R. LM3	3.5-3.3	U-WM
Nyanzachoerus kanamensis	LDD-VP-1/92	-3.92	-3.75	L. UM3	3.5-3.3	U-WM
Nyanzachoerus kanamensis	MKM-VP-1/181	-4.09	-1.25	L. LM3	3.66-3.57	L-WM
Nyanzachoerus kanamensis	MKM-VP-1/185	-5.85	-1.96	R. LM3	3.66-3.57	L-WM
Nyanzachoerus kanamensis	WYT-VP-2/3	-2.98	-0.45	L. UM3	3.469-3.33	U-WM

* From Levin et al (2015).

Table SI 3. Compilation of eastern African suid carbon stable isotope values, both contemporaneous with L-WM ~3.76–3.57 Ma (L-EA) and U-WM ~3.47–3.20 Ma (U-EA), as well as >3.8 Ma <3.2 Ma. Only suid lineages present in Woranso-Mille are included.

Taxon	Sample ID	Geological unit	Age (Ma)	Time unit	$\delta^{13}C$	Publication
Kolpochoerus afarensis	ZK-EN 358	Dikika_BBM	3.7	L-EA	-6.31	Bedaso et al (2013)
Kolpochoerus afarensis	LT152S	Laetoli_U	3.65	L-EA	-1.80	Kingston (2011)
Kolpochoerus afarensis	LT153S	Laetoli_U	3.65	L-EA	-7.70	Kingston (2011)
Kolpochoerus afarensis	LT154S	Laetoli_U	3.65	L-EA	-0.50	Kingston (2011)
Kolpochoerus afarensis	LT155S	Laetoli_U	3.65	L-EA	-2.40	Kingston (2011)
Kolpochoerus afarensis	LT35S	Laetoli_U	3.65	L-EA	-4.20	Kingston (2011)
Kolpochoerus afarensis	ZK-EN-D15	Dikika_UBM	3.51	U-EA	-3.99	Bedaso et al (2013)
Kolpochoerus afarensis	ZK-EN-D22	Dikika_UBM	3.51	U-EA	-4.60	Bedaso et al (2013)
Kolpochoerus afarensis	ZK-EN-D23	Dikika_UBM	3.51	U-EA	-1.53	Bedaso et al (2013)
Kolpochoerus afarensis	ZK-EN-D24	Dikika_UBM	3.51	U-EA	-2.50	Bedaso et al (2013)
Kolpochoerus afarensis	A.L. 1522-1	Hadar_SH1	3.385	U-EA	-6.33	Wynn et al (2016)
Kolpochoerus afarensis	A.L. 129-49	Hadar_SH1	3.385	U-EA	-2.53	Wynn et al (2016)
Kolpochoerus afarensis	A.L. 145-34	Hadar_SH1	3.385	U-EA	-5.75	Wynn et al (2016)
Kolpochoerus afarensis	A.L. 1582-6	Hadar_SH1	3.385	U-EA	-5.64	Wynn et al (2016)
Kolpochoerus afarensis	A.L. 199-2	Hadar_SH1	3.385	U-EA	-2.84	Wynn et al (2016)
Kolpochoerus afarensis	A.L. 199-7	Hadar_SH1	3.385	U-EA	-3.28	Wynn et al (2016)
Kolpochoerus afarensis	A.L. 200-13	Hadar_SH1	3.385	U-EA	-8.16	Wynn et al (2016)
Kolpochoerus afarensis	A.L. 224-3	Hadar_SH1	3.385	U-EA	-6.51	Wynn et al (2016)
Kolpochoerus afarensis	A.L. 229-3	Hadar_SH1	3.385	U-EA	-2.63	Wynn et al (2016)
Kolpochoerus afarensis	A.L. 237-10	Hadar_SH1	3.385	U-EA	-2.73	Wynn et al (2016)
Kolpochoerus afarensis	DIK 1-8	Dikika_SHM	3.31	U-EA	-3.94	Bedaso et al (2013)
Kolpochoerus afarensis	ZK-EN-D258	Dikika_SHM	3.31	U-EA	-6.25	Bedaso et al (2013)
Kolpochoerus afarensis	ZK-EN-D261	Dikika_SHM	3.31	U-EA	-4.39	Bedaso et al (2013)
Kolpochoerus afarensis	ZK-EN-D263	Dikika_SHM	3.31	U-EA	-4.07	Bedaso et al (2013)
Kolpochoerus afarensis	ZK-EN-D91	Dikika_SHM	3.31	U-EA	-4.04	Bedaso et al (2013)
Kolpochoerus afarensis	A.L. 1323-1	Hadar_DD2	3.2	U-EA	-1.73	Wynn et al (2016)
Kolpochoerus afarensis	A.L. 182-48	Hadar_DD2	3.2	U-EA	-4.31	Wynn et al (2016)
Kolpochoerus afarensis	A.L. 183-44	Hadar_DD2	3.2	U-EA	-5.55	Wynn et al (2016)
Kolpochoerus afarensis	A.L. 321-10a	Hadar_DD2	3.2	U-EA	-9.47	Wynn et al (2016)
Kolpochoerus afarensis	A.L. 321-8	Hadar_DD2	3.2	U-EA	-1.41	Wynn et al (2016)
Kolpochoerus afarensis	A.L. 1012-1a	Hadar_KH2	3.03	<3.2	-4.77	Wynn et al (2016)

Kolpochoerus afarensis	A.L. 1012-1b	Hadar_KH2	3.03	<3.2	-2.91	Wynn et al (2016)
Kolpochoerus afarensis	A.L. 1012-1c	Hadar_KH2	3.03	<3.2	-1.45	Wynn et al (2016)
Kolpochoerus afarensis	A.L. 1012-1c	Hadar_KH2	3.03	<3.2	-1.40	Wynn et al (2016)
Kolpochoerus afarensis	A.L. 1019-1	Hadar_KH2	3.03	<3.2	-1.90	Wynn et al (2016)
Kolpochoerus afarensis	A.L. 455-1a	Hadar_KH2	3.03	<3.2	-9.23	Wynn et al (2016)
Kolpochoerus afarensis	A.L. 516-2	Hadar_KH2	3.03	<3.2	-2.36	Wynn et al (2016)
Kolpochoerus afarensis	A.L. 516-2	Hadar_KH2	3.03	<3.2	-2.29	Wynn et al (2016)
Kolpochoerus afarensis	A.L. 518-2	Hadar_KH2	3.03	<3.2	-2.88	Wynn et al (2016)
Kolpochoerus afarensis	A.L. 727-1a	Hadar_KH2	3.03	<3.2	-2.46	Wynn et al (2016)
Kolpochoerus afarensis	A.L. 727-1c	Hadar_KH2	3.03	<3.2	-1.05	Wynn et al (2016)
Kolpochoerus afarensis	A.L. 809-1a	Hadar_KH2	3.03	<3.2	1.83	Wynn et al (2016)
Kolpochoerus afarensis	A.L. 920-1b	Hadar_KH2	3.03	<3.2	-4.65	Wynn et al (2016)
Kolpochoerus afarensis	A.L. 920-1c	Hadar_KH2	3.03	<3.2	-4.79	Wynn et al (2016)
Kolpochoerus afarensis	OMO 112/1-10002	Omo_B10	2.95	<3.2	-5.19	Souron (2012)
Kolpochoerus afarensis	OMO 211-10012	Omo_B10	2.95	<3.2	-8.15	Souron (2012)
Kolpochoerus afarensis	L 367-2	Omo_B12	2.87	<3.2	-5.97	Souron (2012)
Kolpochoerus afarensis	TC7500	Chad_Koro-Toro	3.25	U-EA	-1.20	Zazzo et al (2000)
Kolpochoerus deheinzelini	GONBULK-091	Gona_As-Duma	4.9	>3.8	-4.39	Semaw et al (2005)
Kolpochoerus deheinzelini	GONBULK-113	Gona_As-Duma	4.9	>3.8	-3.45	Semaw et al (2005)
Kolpochoerus deheinzelini	WM10W.P33	Gona_Sagantole	4.55	>3.8	-6.84	Levin et al (2008)
Kolpochoerus deheinzelini	WM10W.P80	Gona_Sagantole	4.55	>3.8	-9.18	Levin et al (2008)
Kolpochoerus deheinzelini	WM31.P21	Gona_Sagantole	4.55	>3.8	-4.15	Levin et al (2008)
Kolpochoerus deheinzelini	GONBULK-121	Gona_Sagantole	4.55	>3.8	-6.55	Semaw et al (2005)
Kolpochoerus deheinzelini	ARA. VP. 1/1250	Aramis	4.4	>3.8	-5.20	White et al (2009)
Kolpochoerus deheinzelini	ARA. VP. 1/1476c	Aramis	4.4	>3.8	-9.90	White et al (2009)
Kolpochoerus deheinzelini	ARA. VP. 1/1706	Aramis	4.4	>3.8	-4.70	White et al (2009)
Kolpochoerus deheinzelini	ARA. VP. 1/2611	Aramis	4.4	>3.8	-4.80	White et al (2009)
Kolpochoerus deheinzelini	ARA. VP. 1/645	Aramis	4.4	>3.8	-3.20	White et al (2009)
Kolpochoerus deheinzelini	ARA. VP. 1/806	Aramis	4.4	>3.8	-9.10	White et al (2009)
Kolpochoerus deheinzelini	ARA. VP. 1/986	Aramis	4.4	>3.8	-7.90	White et al (2009)
Kolpochoerus deheinzelini	645	Aramis	4.4	>3.8	-3.20	White et al (2009)
Kolpochoerus deheinzelini	806	Aramis	4.4	>3.8	-9.10	White et al (2009)

Kolpochoerus deheinzelini	986	Aramis	4.4	>3.8	-7.90	White et al (2009)
Kolpochoerus deheinzelini	1250	Aramis	4.4	>3.8	-5.20	White et al (2009)
Kolpochoerus deheinzelini	1706	Aramis	4.4	>3.8	-4.70	White et al (2009)
Kolpochoerus deheinzelini	2611	Aramis	4.4	>3.8	-4.80	White et al (2009)
Kolpochoerus deheinzelini	1476c	Aramis	4.4	>3.8	-9.90	White et al (2009)
Notochoerus euilus	HCRP498-01	Malawi_Chiwondo	?	Uncertain	-4.80	Lüdecke et al (2016)
Notochoerus euilus	HCRP654-01	Malawi_Chiwondo	?	Uncertain	-5.50	Lüdecke et al (2016)
Notochoerus euilus	160	Laetoli_L	4.05	>3.8	-0.40	Kingston and Harrison (2007)
Notochoerus euilus	ZK-EN 360	Dikika_BBM	3.7	L-EA	-2.41	Bedaso et al (2013)
Notochoerus euilus	ZK-EN 366	Dikika_BBM	3.7	L-EA	-8.59	Bedaso et al (2013)
Notochoerus euilus	ZK-EN-D239	Dikika_BBM	3.7	L-EA	-1.68	Bedaso et al (2013)
Notochoerus euilus	ZK-EN-D239-1	Dikika_BBM	3.7	L-EA	-1.62	Bedaso et al (2013)
Notochoerus euilus	Lit 59 349	Laetoli_U	3.65	L-EA	-0.50	Harris and Cerling (2002)
Notochoerus euilus	48	Laetoli_U	3.65	L-EA	-3.10	Kingston (2011)
Notochoerus euilus	93	Laetoli_U	3.65	L-EA	-1.50	Kingston (2011)
Notochoerus euilus	LT104S	Laetoli_U	3.65	L-EA	-3.10	Kingston (2011)
Notochoerus euilus	LT105S	Laetoli_U	3.65	L-EA	-4.40	Kingston (2011)
Notochoerus euilus	LT117S	Laetoli_U	3.65	L-EA	-3.00	Kingston (2011)
Notochoerus euilus	LT121S	Laetoli_U	3.65	L-EA	-0.30	Kingston (2011)
Notochoerus euilus	LT122S	Laetoli_U	3.65	L-EA	0.10	Kingston (2011)
Notochoerus euilus	LT123S	Laetoli_U	3.65	L-EA	-0.40	Kingston (2011)
Notochoerus euilus	LT36S	Laetoli_U	3.65	L-EA	-1.60	Kingston (2011)
Notochoerus euilus	LT49S	Laetoli_U	3.65	L-EA	-0.60	Kingston (2011)
Notochoerus euilus	LT50S	Laetoli_U	3.65	L-EA	-2.00	Kingston (2011)
Notochoerus euilus	LT56S	Laetoli_U	3.65	L-EA	0.20	Kingston (2011)
Notochoerus euilus	LT57S	Laetoli_U	3.65	L-EA	-2.30	Kingston (2011)
Notochoerus euilus	LT79S	Laetoli_U	3.65	L-EA	-3.40	Kingston (2011)
Notochoerus euilus	LT92S	Laetoli_U	3.65	L-EA	-0.70	Kingston (2011)
Notochoerus euilus	LT94S	Laetoli_U	3.65	L-EA	-3.70	Kingston (2011)
Notochoerus euilus	LT95S	Laetoli_U	3.65	L-EA	-1.80	Kingston (2011)
Notochoerus euilus	159	Laetoli_U	3.65	L-EA	-0.50	Kingston and Harrison (2007)
Notochoerus euilus	154	Laetoli_U	3.65	L-EA	-0.50	Kingston and Harrison (2007)
Notochoerus euilus	163	Laetoli_U	3.65	L-EA	-5.40	Kingston and Harrison (2007)
Notochoerus euilus	162	Laetoli_U	3.65	L-EA	-0.30	Kingston and Harrison (2007)
Notochoerus euilus	166	Laetoli_U	3.65	L-EA	-2.50	Kingston and Harrison (2007)

Notochoerus euilus	167	Laetoli_U	3.65	L-EA	-1.30	Kingston and Harrison (2007)
Notochoerus euilus	54	Laetoli_U	3.65	L-EA	-1.00	Kingston and Harrison (2007)
Notochoerus euilus	55	Laetoli_U	3.65	L-EA	-2.10	Kingston and Harrison (2007)
Notochoerus euilus	168	Laetoli_U	3.65	L-EA	2.00	Kingston and Harrison (2007)
Notochoerus euilus	165	Laetoli_U	3.65	L-EA	-2.10	Kingston and Harrison (2007)
Notochoerus euilus	158	Laetoli_U	3.65	L-EA	-3.60	Kingston and Harrison (2007)
Notochoerus euilus	22	Laetoli_U	3.65	L-EA	-1.10	Kingston and Harrison (2007)
Notochoerus euilus	53	Laetoli_U	3.65	L-EA	-1.10	Kingston and Harrison (2007)
Notochoerus euilus	10	Laetoli_U	3.65	L-EA	-8.20	Kingston and Harrison (2007)
Notochoerus euilus	157	Laetoli_U	3.65	L-EA	-0.90	Kingston and Harrison (2007)
Notochoerus euilus	7	Laetoli_U	3.65	L-EA	-2.70	Kingston and Harrison (2007)
Notochoerus euilus	8	Laetoli_U	3.65	L-EA	-3.50	Kingston and Harrison (2007)
Notochoerus euilus	155	Laetoli_U	3.65	L-EA	-3.40	Kingston and Harrison (2007)
Notochoerus euilus	3	Laetoli_U	3.65	L-EA	-3.70	Kingston and Harrison (2007)
Notochoerus euilus	5	Laetoli_U	3.65	L-EA	-2.20	Kingston and Harrison (2007)
Notochoerus euilus	18	Laetoli_U	3.65	L-EA	-0.10	Kingston and Harrison (2007)
Notochoerus euilus	156	Laetoli_U	3.65	L-EA	-4.50	Kingston and Harrison (2007)
Notochoerus euilus	164	Laetoli_U	3.65	L-EA	0.00	Kingston and Harrison (2007)
Notochoerus euilus	ER 225	ET_Lokochot	3.52	U-EA	-0.60	Harris and Cerling (2002)
Notochoerus euilus	ER 3686	ET_Lokochot	3.52	U-EA	-0.70	Harris and Cerling (2002)
Notochoerus euilus	ZK-EN-D16	Dikika_UBM	3.51	U-EA	-0.28	Bedaso et al (2013)
Notochoerus euilus	ZK-EN-D42	Dikika_UBM	3.51	U-EA	-1.11	Bedaso et al (2013)
Notochoerus euilus	KNM-RK 48744	Kantis	3.5	U-EA	-1.12	Mbua et al (2016)
Notochoerus euilus	KNM-RK 48749	Kantis	3.5	U-EA	-0.77	Mbua et al (2016)
Notochoerus euilus	KNM-RK 50051	Kantis	3.5	U-EA	-0.84	Mbua et al (2016)
Notochoerus euilus	KNM-RK 50069	Kantis	3.5	U-EA	-0.45	Mbua et al (2016)
Notochoerus euilus	KNM-RK 50494	Kantis	3.5	U-EA	-0.99	Mbua et al (2016)

Notochoerus euilus	KNM-RK 50539	Kantis	3.5	U-EA	-0.23	Mbua et al (2016)
Notochoerus euilus	KNM-RK 50621	Kantis	3.5	U-EA	-1.78	Mbua et al (2016)
Notochoerus euilus	KNM-RK 52994	Kantis	3.5	U-EA	-0.94	Mbua et al (2016)
Notochoerus euilus	KNM-RK 54220	Kantis	3.5	U-EA	-1.34	Mbua et al (2016)
Notochoerus euilus	KNM-RK 54221	Kantis	3.5	U-EA	-2.08	Mbua et al (2016)
Notochoerus euilus	KNM-RK 54222	Kantis	3.5	U-EA	0.02	Mbua et al (2016)
Notochoerus euilus	KNM-RK 54223	Kantis	3.5	U-EA	-0.98	Mbua et al (2016)
Notochoerus euilus	KNM-RK 54224	Kantis	3.5	U-EA	-1.71	Mbua et al (2016)
Notochoerus euilus	KNM-RK 54226	Kantis	3.5	U-EA	-0.39	Mbua et al (2016)
Notochoerus euilus	KNM-RK 55266	Kantis	3.5	U-EA	-1.03	Mbua et al (2016)
Notochoerus euilus	KNM-RK 55435	Kantis	3.5	U-EA	-1.05	Mbua et al (2016)
Notochoerus euilus	KNM-RK 55637	Kantis	3.5	U-EA	-0.03	Mbua et al (2016)
Notochoerus euilus	KNM-RK 55641	Kantis	3.5	U-EA	-0.40	Mbua et al (2016)
Notochoerus euilus	KNM-RK 55642	Kantis	3.5	U-EA	-1.30	Mbua et al (2016)
Notochoerus euilus	KNM-RK 55648	Kantis	3.5	U-EA	-0.30	Mbua et al (2016)
Notochoerus euilus	KNM-RK 55650	Kantis	3.5	U-EA	-0.59	Mbua et al (2016)
Notochoerus euilus	KNM-RK 55684	Kantis	3.5	U-EA	-0.69	Mbua et al (2016)
Notochoerus euilus	JN-EN-D14	Dikika_SH	3.385	U-EA	-1.20	Wilson (2013)
Notochoerus euilus	A.L. 198-12	Hadar_SH1	3.385	U-EA	-1.19	Wynn et al (2016)
Notochoerus euilus	A.L. 199-5	Hadar_SH1	3.385	U-EA	-5.78	Wynn et al (2016)
Notochoerus euilus	A.L. 237-13	Hadar_SH1	3.385	U-EA	-5.35	Wynn et al (2016)
Notochoerus euilus	A.L. 248-1a	Hadar_SH1	3.385	U-EA	-3.60	Wynn et al (2016)
Notochoerus euilus	A.L. 883-1	Hadar_SH1	3.385	U-EA	0.20	Wynn et al (2016)
Notochoerus euilus	ARI-VP-1/548c	WM_U	3.3345	U-EA	-1.00	Levin et al (2008)
Notochoerus euilus	ARI-VP-1/548e	WM_U	3.3345	U-EA	-0.40	Levin et al (2008)
Notochoerus euilus	ARI-VP-1/548j	WM_U	3.3345	U-EA	-1.60	Levin et al (2008)
Notochoerus euilus	ARI-VP-1/548k	WM_U	3.3345	U-EA	-3.20	Levin et al (2008)
Notochoerus euilus	BRT-VP-1/132	WM_U	3.3345	U-EA	0.10	Levin et al (2008)
Notochoerus euilus	BRT-VP-2/93	WM_U	3.3345	U-EA	-0.20	Levin et al (2008)

Notochoerus euilus	BRT-VP-2/94	WM_U	3.3345	U-EA	0.00	Levin et al (2008)
Notochoerus euilus	MKM-VP-1/55	WM_U	3.3345	U-EA	0.00	Levin et al (2008)
Notochoerus euilus	NFR-VP-1/1	WM_U	3.3345	U-EA	-1.80	Levin et al (2008)
Notochoerus euilus	NFR-VP-1/14	WM_U	3.3345	U-EA	-0.60	Levin et al (2008)
Notochoerus euilus	NFR-VP-1/16	WM_U	3.3345	U-EA	-0.60	Levin et al (2008)
Notochoerus euilus	NFR-VP-1/190	WM_U	3.3345	U-EA	-1.60	Levin et al (2008)
Notochoerus euilus	NFR-VP-1/197	WM_U	3.3345	U-EA	-3.60	Levin et al (2008)
Notochoerus euilus	NFR-VP-1/20	WM_U	3.3345	U-EA	0.10	Levin et al (2008)
Notochoerus euilus	NFR-VP-1/227	WM_U	3.3345	U-EA	-0.40	Levin et al (2008)
Notochoerus euilus	NFR-VP-1/24	WM_U	3.3345	U-EA	-0.20	Levin et al (2008)
Notochoerus euilus	NFR-VP-1/34	WM_U	3.3345	U-EA	-0.70	Levin et al (2008)
Notochoerus euilus	NFR-VP-1/50	WM_U	3.3345	U-EA	-2.40	Levin et al (2008)
Notochoerus euilus	NFR-VP-1/7A	WM_U	3.3345	U-EA	-0.70	Levin et al (2008)
Notochoerus euilus	ZK-EN-257	Dikika_SHM	3.31	U-EA	-7.14	Bedaso et al (2013)
Notochoerus euilus	ZK-EN-260	Dikika_SHM	3.31	U-EA	-0.87	Bedaso et al (2013)
Notochoerus euilus	ZK-EN-282	Dikika_SHM	3.31	U-EA	-3.19	Bedaso et al (2013)
Notochoerus euilus	ZK-EN-D10	Dikika_SHM	3.31	U-EA	-0.83	Bedaso et al (2013)
Notochoerus euilus	ZK-EN-D11	Dikika_SHM	3.31	U-EA	-3.48	Bedaso et al (2013)
Notochoerus euilus	ZK-EN-D12	Dikika_SHM	3.31	U-EA	-0.89	Bedaso et al (2013)
Notochoerus euilus	ZK-EN-D14	Dikika_SHM	3.31	U-EA	-1.19	Bedaso et al (2013)
Notochoerus euilus	ZK-EN-D255	Dikika_SHM	3.31	U-EA	-1.33	Bedaso et al (2013)
Notochoerus euilus	ZK-EN-D41	Dikika_SHM	3.31	U-EA	-2.52	Bedaso et al (2013)
Notochoerus euilus	ER 2782	ET_Tulu-Bor	3.255	U-EA	-0.80	Harris and Cerling (2002)
Notochoerus euilus	ER 2877	ET_Tulu-Bor	3.255	U-EA	-2.30	Harris and Cerling (2002)
Notochoerus euilus	ER 3334	ET_Tulu-Bor	3.255	U-EA	-2.90	Harris and Cerling (2002)
Notochoerus euilus	KNM-LT 23767	WT_Kaiyumung	3.2	U-EA	-1.80	Uno et al (2011)
Notochoerus euilus	KNM-LT 24050	WT_Kaiyumung	3.2	U-EA	-0.50	Uno et al (2011)
Notochoerus euilus	KNM-LT 26074	WT_Kaiyumung	3.2	U-EA	-1.20	Uno et al (2011)
Notochoerus euilus	KNM-LT 26596	WT_Kaiyumung	3.2	U-EA	-0.20	Uno et al (2011)
Notochoerus euilus	KNM-LT 289	WT_Kaiyumung	3.2	U-EA	-2.00	Uno et al (2011)
Notochoerus euilus	A.L. 133-11	Hadar_DD2	3.2	U-EA	-2.53	Wynn et al (2016)
Notochoerus euilus	A.L. 133-18	Hadar_DD2	3.2	U-EA	-1.79	Wynn et al (2016)
Notochoerus euilus	A.L. 133-34	Hadar_DD2	3.2	U-EA	-1.83	Wynn et al (2016)
Notochoerus euilus	A.L. 133-44	Hadar_DD2	3.2	U-EA	-1.74	Wynn et al (2016)

Notochoerus euilus	A.L. 167-24	Hadar_DD2	3.2	U-EA	-1.30	Wynn et al (2016)
Notochoerus euilus	A.L. 182-49	Hadar_DD2	3.2	U-EA	-0.44	Wynn et al (2016)
Notochoerus euilus	A.L. 182-50	Hadar_DD2	3.2	U-EA	-0.58	Wynn et al (2016)
Notochoerus euilus	A.L. 182-53	Hadar_DD2	3.2	U-EA	-0.47	Wynn et al (2016)
Notochoerus euilus	A.L. 182-78	Hadar_DD2	3.2	U-EA	-1.11	Wynn et al (2016)
Notochoerus euilus	A.L. 182-82	Hadar_DD2	3.2	U-EA	-1.37	Wynn et al (2016)
Notochoerus euilus	A.L. 207-2	Hadar_DD2	3.2	U-EA	-3.10	Wynn et al (2016)
Notochoerus euilus	A.L. 207-3	Hadar_DD2	3.2	U-EA	-0.18	Wynn et al (2016)
Notochoerus euilus	A.L. 243-2	Hadar_DD2	3.2	U-EA	-0.37	Wynn et al (2016)
Notochoerus euilus	A.L. 285-3	Hadar_DD2	3.2	U-EA	-1.52	Wynn et al (2016)
Notochoerus euilus	A.L. 318-9	Hadar_DD2	3.2	U-EA	-2.60	Wynn et al (2016)
Notochoerus euilus	A.L. 321-9	Hadar_DD2	3.2	U-EA	-0.84	Wynn et al (2016)
Notochoerus euilus	A.L. 342-17an	Hadar_DD2	3.2	U-EA	-1.22	Wynn et al (2016)
Notochoerus euilus	A.L. 342-17an	Hadar_DD2	3.2	U-EA	-0.68	Wynn et al (2016)
Notochoerus euilus	A.L. 342-7	Hadar_DD2	3.2	U-EA	-4.57	Wynn et al (2016)
Notochoerus euilus	A.L. 342-9b	Hadar_DD2	3.2	U-EA	-0.81	Wynn et al (2016)
Notochoerus euilus	A.L. 58-3	Hadar_DD2	3.2	U-EA	-4.06	Wynn et al (2016)
Notochoerus euilus	EW-EN-35	Dikika_KH2	3.03	<3.2	-1.50	Wilson (2013)
Notochoerus euilus	EW-EN-38	Dikika_KH2	3.03	<3.2	-1.40	Wilson (2013)
Notochoerus euilus	A.L. 361-6	Hadar_KH2	3.03	<3.2	-1.57	Wynn et al (2016)
Notochoerus euilus	A.L. 361-8	Hadar_KH2	3.03	<3.2	0.04	Wynn et al (2016)
Notochoerus euilus	A.L. 452-13a	Hadar_KH2	3.03	<3.2	-0.49	Wynn et al (2016)
Notochoerus euilus	A.L. 452-13b	Hadar_KH2	3.03	<3.2	-1.06	Wynn et al (2016)
Notochoerus euilus	A.L. 475-2	Hadar_KH2	3.03	<3.2	-1.89	Wynn et al (2016)
Notochoerus euilus	A.L. 478-1	Hadar_KH2	3.03	<3.2	-1.03	Wynn et al (2016)
Notochoerus euilus	A.L. 667-2	Hadar_KH2	3.03	<3.2	-1.75	Wynn et al (2016)
Notochoerus euilus	A.L. 685-3	Hadar_KH2	3.03	<3.2	-1.93	Wynn et al (2016)
Notochoerus euilus	A.L. 685-4	Hadar_KH2	3.03	<3.2	-1.50	Wynn et al (2016)
Notochoerus euilus	A.L. 689-1	Hadar_KH2	3.03	<3.2	-2.50	Wynn et al (2016)
Notochoerus euilus	A.L. 694-1	Hadar_KH2	3.03	<3.2	-4.03	Wynn et al (2016)
Notochoerus euilus	A.L. 694-1	Hadar_KH2	3.03	<3.2	-1.42	Wynn et al (2016)
Notochoerus euilus	A.L. 795-1b	Hadar_KH2	3.03	<3.2	-0.30	Wynn et al (2016)
Notochoerus euilus	TC7300	Chad_Koro-Toro	3.25	U-EA	0.90	Zazzo et al (2000)
Notochoerus euilus	TC7600	Chad_Koro-Toro	3.25	U-EA	1.30	Zazzo et al (2000)
Nyanzachoerus jaegeri	KNM-LT 26092	WT_Lothagam	?	Uncertain	-2.60	Cerling et al (2003)
Nyanzachoerus jaegeri	KNM-LT 308	WT_Lothagam	?	Uncertain	-1.80	Cerling et al (2003)
Nyanzachoerus jaegeri	HCRP457-01	Malawi_Chiwondo	?	Uncertain	-9.50	Lüdecke et al (2016)

Nyanzachoerus jaegeri	HCRP546-01	Malawi_Chiwondo	?	Uncertain	-10.60	Lüdecke et al (2016)
Nyanzachoerus jaegeri	HCRP546-02	Malawi_Chiwondo	?	Uncertain	-13.10	Lüdecke et al (2016)
Nyanzachoerus jaegeri	WM27.P2	Gona_As-Duma	4.9	>3.8	-2.96	Levin et al (2008)
Nyanzachoerus jaegeri	GONBULK-062	Gona_As-Duma	4.9	>3.8	-1.90	Levin et al (2008)
Nyanzachoerus jaegeri	GONBULK-069	Gona_As-Duma	4.9	>3.8	-2.10	Levin et al (2008)
Nyanzachoerus jaegeri	GONBULK-077	Gona_As-Duma	4.9	>3.8	-0.80	Levin et al (2008)
Nyanzachoerus jaegeri	GONBULK-079	Gona_As-Duma	4.9	>3.8	-0.60	Levin et al (2008)
Nyanzachoerus jaegeri	GONBULK-081	Gona_As-Duma	4.9	>3.8	-0.80	Levin et al (2008)
Nyanzachoerus jaegeri	GONBULK-085	Gona_As-Duma	4.9	>3.8	-0.70	Levin et al (2008)
Nyanzachoerus jaegeri	GONBULK-096	Gona_As-Duma	4.9	>3.8	-0.90	Levin et al (2008)
Nyanzachoerus jaegeri	GONBULK-102	Gona_As-Duma	4.9	>3.8	-0.60	Levin et al (2008)
Nyanzachoerus jaegeri	GONBULK-103	Gona_As-Duma	4.9	>3.8	-0.70	Levin et al (2008)
Nyanzachoerus jaegeri	GONBULK-122	Gona_As-Duma	4.9	>3.8	-0.30	Levin et al (2008)
Nyanzachoerus jaegeri	WM1.P21	Gona_As-Duma	4.9	>3.8	-0.56	Levin et al (2008)
Nyanzachoerus jaegeri	WM1s.P109	Gona_As-Duma	4.9	>3.8	-0.21	Levin et al (2008)
Nyanzachoerus jaegeri	WM5M.P183	Gona_As-Duma	4.9	>3.8	-0.40	Levin et al (2008)
Nyanzachoerus jaegeri	WM5M.P64	Gona_As-Duma	4.9	>3.8	-0.95	Levin et al (2008)
Nyanzachoerus jaegeri	GONBULK-096	Gona_As-Duma	4.9	>3.8	-0.92	Semaw et al (2005)
Nyanzachoerus jaegeri	GONBULK-103	Gona_As-Duma	4.9	>3.8	-0.75	Semaw et al (2005)
Nyanzachoerus jaegeri	GONBULK-062	Gona_As-Duma	4.9	>3.8	-1.85	Semaw et al (2005)
Nyanzachoerus jaegeri	GONBULK-069	Gona_As-Duma	4.9	>3.8	-2.11	Semaw et al (2005)
Nyanzachoerus jaegeri	GONBULK-077	Gona_As-Duma	4.9	>3.8	-0.82	Semaw et al (2005)
Nyanzachoerus jaegeri	GONBULK-079	Gona_As-Duma	4.9	>3.8	-0.62	Semaw et al (2005)
Nyanzachoerus jaegeri	GONBULK-081	Gona_As-Duma	4.9	>3.8	-0.81	Semaw et al (2005)
Nyanzachoerus jaegeri	GONBULK-085	Gona_As-Duma	4.9	>3.8	-0.71	Semaw et al (2005)
Nyanzachoerus jaegeri	GONBULK-102	Gona_As-Duma	4.9	>3.8	-0.63	Semaw et al (2005)

Nyanzachoerus jaegeri	GONBULK-122	Gona_As-Duma	4.9	>3.8	-0.33	Semaw et al (2005)
Nyanzachoerus jaegeri	GLL 0926	Galili	4.838	>3.8	-1.20	Bedaso (2011)
Nyanzachoerus jaegeri	GLL 1039b	Galili	4.838	>3.8	-0.30	Bedaso (2011)
Nyanzachoerus jaegeri	GLL 1623	Galili	4.838	>3.8	-3.40	Bedaso (2011)
Nyanzachoerus jaegeri	GLL 1850	Galili	4.838	>3.8	-2.80	Bedaso (2011)
Nyanzachoerus jaegeri	GLL 1941	Galili	4.838	>3.8	-6.00	Bedaso (2011)
Nyanzachoerus jaegeri	GLL 1308	Galili	4.838	>3.8	-0.70	Bedaso (2011)
Nyanzachoerus jaegeri	SKW 093	Galili	4.838	>3.8	0.00	Bedaso (2011)
Nyanzachoerus jaegeri	SKW 161	Galili	4.838	>3.8	-0.70	Bedaso (2011)
Nyanzachoerus jaegeri	SKW 226	Galili	4.838	>3.8	1.00	Bedaso (2011)
Nyanzachoerus jaegeri	SKW 229	Galili	4.838	>3.8	-2.80	Bedaso (2011)
Nyanzachoerus jaegeri	WM10.P45	Gona_Sagantole	4.55	>3.8	-3.66	Levin et al (2008)
Nyanzachoerus jaegeri	WM46.P1	Gona_Sagantole	4.55	>3.8	-2.82	Levin et al (2008)
Nyanzachoerus jaegeri	WMS7.P1	Gona_Sagantole	4.55	>3.8	-2.30	Levin et al (2008)
Nyanzachoerus jaegeri	WM3.P4	Gona_Sagantole	4.55	>3.8	-3.14	Levin et al (2008)
Nyanzachoerus jaegeri	GONBULK-149	Gona_Sagantole	4.55	>3.8	-0.15	Semaw et al (2005)
Nyanzachoerus jaegeri	GONBULK-141	Gona_Sagantole	4.55	>3.8	-6.12	Semaw et al (2005)
Nyanzachoerus jaegeri	GONBULK-145	Gona_Sagantole	4.55	>3.8	-0.37	Semaw et al (2005)
Nyanzachoerus jaegeri	GONBULK-149	Gona	4.4	>3.8	-0.20	Levin et al (2008)
Nyanzachoerus jaegeri	GONBULK-141	Gona	4.4	>3.8	-6.10	Levin et al (2008)
Nyanzachoerus jaegeri	GONBULK-145	Gona	4.4	>3.8	-0.40	Levin et al (2008)
Nyanzachoerus jaegeri	ARA. VP. 1/1476b	Aramis	4.4	>3.8	-1.50	White et al (2009)
Nyanzachoerus jaegeri	ARA. VP. 1/2410	Aramis	4.4	>3.8	0.90	White et al (2009)
Nyanzachoerus jaegeri	ARA. VP. 1/2650	Aramis	4.4	>3.8	-0.10	White et al (2009)
Nyanzachoerus jaegeri	ARA. VP.1/1476d	Aramis	4.4	>3.8	-2.70	White et al (2009)
Nyanzachoerus jaegeri	SAG. VP. 7/122	Aramis	4.4	>3.8	-2.70	White et al (2009)
Nyanzachoerus jaegeri	SAG. VP. 7/3	Aramis	4.4	>3.8	0.30	White et al (2009)
Nyanzachoerus jaegeri	SAG. VP. 7/47	Aramis	4.4	>3.8	0.80	White et al (2009)
Nyanzachoerus jaegeri	2410	Aramis	4.4	>3.8	0.90	White et al (2009)
Nyanzachoerus jaegeri	2650	Aramis	4.4	>3.8	-0.10	White et al (2009)
Nyanzachoerus jaegeri	1476b	Aramis	4.4	>3.8	-1.50	White et al (2009)

Nyanzachoerus jaegeri	1476d	Aramis	4.4	>3.8	-2.70	White et al (2009)
Nyanzachoerus jaegeri	3	Aramis	4.4	>3.8	-1.20	White et al (2009)
Nyanzachoerus jaegeri	47	Aramis	4.4	>3.8	-3.10	White et al (2009)
Nyanzachoerus jaegeri	122	Aramis	4.4	>3.8	-2.70	White et al (2009)
Nyanzachoerus jaegeri	KNM-LT 311	WT_Apak	4.25	>3.8	-4.00	Uno et al (2011)
Nyanzachoerus jaegeri	KP 3348	WT_Kanapoi	4.1	>3.8	-1.74	Harris et al
Nyanzachoerus jaegeri	KP 3227	WT_Kanapoi	4.1	>3.8	-1.74	Harris et al
Nyanzachoerus jaegeri	KNM-KP 205	WT_Kanapoi	4.07	>3.8	-6.50	Cerling et al (2003)
Nyanzachoerus jaegeri	KNM-KP 241	WT_Kanapoi	4.07	>3.8	-2.00	Cerling et al (2003)
Nyanzachoerus jaegeri	KNM-KP 265	WT_Kanapoi	4.07	>3.8	-5.50	Cerling et al (2003)
Nyanzachoerus jaegeri	KP 3348 B	WT_Kanapoi	4.07	>3.8	-1.70	Harris and Cerling (2002)
Nyanzachoerus jaegeri	KP-X10	WT_Kanapoi	4.07	>3.8	-1.20	Harris and Cerling (2002)
Nyanzachoerus jaegeri	WT 3222	WT_Kanapoi	4.07	>3.8	-1.90	Harris and Cerling (2002)
Nyanzachoerus jaegeri	Y4-46	Mursi	4	>3.8	-3.20	Drapeau et al (2014)
Nyanzachoerus jaegeri	GLL 0297	Galili	3.76	L-EA	-0.10	Bedaso (2011)
Nyanzachoerus jaegeri	GLL 0303	Galili	3.76	L-EA	-0.80	Bedaso (2011)
Nyanzachoerus jaegeri	GLL 0351	Galili	3.76	L-EA	-1.60	Bedaso (2011)
Nyanzachoerus jaegeri	GLL 0760	Galili	3.76	L-EA	-0.40	Bedaso (2011)
Nyanzachoerus jaegeri	GLL 1075	Galili	3.76	L-EA	-4.40	Bedaso (2011)
Nyanzachoerus jaegeri	GLL 1076 -a-b	Galili	3.76	L-EA	-5.00	Bedaso (2011)
Nyanzachoerus jaegeri	TC8000	Chad_Kolle	3.5	U-EA	-0.60	Zazzo et al (2000)
Nyanzachoerus jaegeri	TC8100	Chad_Kolle	3.5	U-EA	-0.70	Zazzo et al (2000)
Nyanzachoerus jaegeri	TC8200	Chad_Kolle	3.5	U-EA	-0.80	Zazzo et al (2000)
Nyanzachoerus pattersoni / kanamensis	KNM-ER 3177	ET_KF	?	Uncertain	-2.06	Cerling et al (2003)
Nyanzachoerus pattersoni / kanamensis	WM18.P1	Gona_Sagantole	?	Uncertain	-3.41	Levin et al (2008)
Nyanzachoerus pattersoni / kanamensis	TC8600	Chad_Kossom	5.5	>3.8	-6.80	Zazzo et al (2000)
Nyanzachoerus pattersoni / kanamensis	WM5SW.P43	Gona_As-Duma	4.9	>3.8	-4.31	Levin et al (2008)
Nyanzachoerus pattersoni / kanamensis	GLL 0843	Galili	4.838	>3.8	-2.80	Bedaso (2011)
Nyanzachoerus pattersoni / kanamensis	GLL 0865	Galili	4.838	>3.8	-4.90	Bedaso (2011)
Nyanzachoerus pattersoni / kanamensis	GLL 0880	Galili	4.838	>3.8	-0.30	Bedaso (2011)
Nyanzachoerus pattersoni / kanamensis	GLL 0886	Galili	4.838	>3.8	-2.70	Bedaso (2011)
Nyanzachoerus pattersoni / kanamensis	GLL 1068	Galili	4.838	>3.8	-6.60	Bedaso (2011)
Nyanzachoerus pattersoni / kanamensis	GLL 1302	Galili	4.838	>3.8	-0.80	Bedaso (2011)

Nyanzachoerus pattersoni / kanamensis	GLL 1590	Galili	4.838	>3.8	-0.50	Bedaso (2011)
Nyanzachoerus pattersoni / kanamensis	SKW 110	Galili	4.838	>3.8	-3.80	Bedaso (2011)
Nyanzachoerus pattersoni / kanamensis	SKW 140	Galili	4.838	>3.8	-0.50	Bedaso (2011)
Nyanzachoerus pattersoni / kanamensis	SKW 152	Galili	4.838	>3.8	-2.40	Bedaso (2011)
Nyanzachoerus pattersoni / kanamensis	SKW 178	Galili	4.838	>3.8	-2.00	Bedaso (2011)
Nyanzachoerus pattersoni / kanamensis	SKW 186	Galili	4.838	>3.8	0.20	Bedaso (2011)
Nyanzachoerus pattersoni / kanamensis	WM10.P21	Gona_Sagantole	4.55	>3.8	-0.47	Levin et al (2008)
Nyanzachoerus pattersoni / kanamensis	WMS3.P3	Gona_Sagantole	4.55	>3.8	-0.53	Levin et al (2008)
Nyanzachoerus pattersoni / kanamensis	WMS6.P23	Gona_Sagantole	4.55	>3.8	-0.72	Levin et al (2008)
Nyanzachoerus pattersoni / kanamensis	WMS7.P14	Gona_Sagantole	4.55	>3.8	0.41	Levin et al (2008)
Nyanzachoerus pattersoni / kanamensis	WMS7.P72	Gona_Sagantole	4.55	>3.8	-0.94	Levin et al (2008)
Nyanzachoerus pattersoni / kanamensis	WM30.P22	Gona_Sagantole	4.55	>3.8	-1.16	Levin et al (2008)
Nyanzachoerus pattersoni / kanamensis	LOTH-114	WT_Apak	4.5	>3.8	-4.20	Harris and Cerling (2002)
Nyanzachoerus pattersoni / kanamensis	ARA VP. 1/1476a	Aramis	4.4	>3.8	-2.30	White et al (2009)
Nyanzachoerus pattersoni / kanamensis	ARA VP. 1/184	Aramis	4.4	>3.8	-2.00	White et al (2009)
Nyanzachoerus pattersoni / kanamensis	ARA VP. 1/302	Aramis	4.4	>3.8	-2.00	White et al (2009)
Nyanzachoerus pattersoni / kanamensis	ARA VP. 1/304	Aramis	4.4	>3.8	0.70	White et al (2009)
Nyanzachoerus pattersoni / kanamensis	ARA VP. 1/988	Aramis	4.4	>3.8	-3.10	White et al (2009)
Nyanzachoerus pattersoni / kanamensis	ARA VP. 1/996	Aramis	4.4	>3.8	-2.50	White et al (2009)
Nyanzachoerus pattersoni / kanamensis	184	Aramis	4.4	>3.8	-2.00	White et al (2009)
Nyanzachoerus pattersoni / kanamensis	302	Aramis	4.4	>3.8	-2.00	White et al (2009)
Nyanzachoerus pattersoni / kanamensis	304	Aramis	4.4	>3.8	0.70	White et al (2009)
Nyanzachoerus pattersoni / kanamensis	988	Aramis	4.4	>3.8	-3.10	White et al (2009)
Nyanzachoerus pattersoni / kanamensis	996	Aramis	4.4	>3.8	-2.50	White et al (2009)
Nyanzachoerus pattersoni / kanamensis	2393	Aramis	4.4	>3.8	0.10	White et al (2009)
Nyanzachoerus pattersoni / kanamensis	2821	Aramis	4.4	>3.8	-1.40	White et al (2009)

Nyanzachoerus pattersoni / kanamensis	1476a	Aramis	4.4	>3.8	-2.30	White et al (2009)
Nyanzachoerus pattersoni / kanamensis	LOTH-105	WT_Apak-U	4.2	>3.8	-4.80	Harris and Cerling (2002)
Nyanzachoerus pattersoni / kanamensis	KP-X10	WT_Kanapoi	4.1	>3.8	-1.19	Harris et al
Nyanzachoerus pattersoni / kanamensis	WT 3222 (lwr M3)	WT_Kanapoi	4.1	>3.8	-1.94	Harris et al
Nyanzachoerus pattersoni / kanamensis	Y3-3	Mursi	4	>3.8	-6.90	Drapeau et al (2014)
Nyanzachoerus pattersoni / kanamensis	Y4-18	Mursi	4	>3.8	-2.20	Drapeau et al (2014)
Nyanzachoerus pattersoni / kanamensis	Y4-19	Mursi	4	>3.8	-11.00	Drapeau et al (2014)
Nyanzachoerus pattersoni / kanamensis	Y4-23	Mursi	4	>3.8	-8.80	Drapeau et al (2014)
Nyanzachoerus pattersoni / kanamensis	Y4-29	Mursi	4	>3.8	-3.40	Drapeau et al (2014)
Nyanzachoerus pattersoni / kanamensis	Y4-30	Mursi	4	>3.8	-8.00	Drapeau et al (2014)
Nyanzachoerus pattersoni / kanamensis	Y4-34	Mursi	4	>3.8	-5.60	Drapeau et al (2014)
Nyanzachoerus pattersoni / kanamensis	Y4-60	Mursi	4	>3.8	-9.00	Drapeau et al (2014)
Nyanzachoerus pattersoni / kanamensis	Y4-75	Mursi	4	>3.8	-4.60	Drapeau et al (2014)
Nyanzachoerus pattersoni / kanamensis	Y4-76	Mursi	4	>3.8	-7.50	Drapeau et al (2014)
Nyanzachoerus pattersoni / kanamensis	Y4-85	Mursi	4	>3.8	-4.40	Drapeau et al (2014)
Nyanzachoerus pattersoni / kanamensis	Y91	Mursi	4	>3.8	-7.30	Drapeau et al (2014)
Nyanzachoerus pattersoni / kanamensis	Y9-2	Mursi	4	>3.8	-11.50	Drapeau et al (2014)
Nyanzachoerus pattersoni / kanamensis	Y9-3	Mursi	4	>3.8	-1.90	Drapeau et al (2014)
Nyanzachoerus pattersoni / kanamensis	Y98	Mursi	4	>3.8	-6.60	Drapeau et al (2014)
Nyanzachoerus pattersoni / kanamensis	YS3500	Mursi	4	>3.8	-4.90	Drapeau et al (2014)
Nyanzachoerus pattersoni / kanamensis	YS3501	Mursi	4	>3.8	-1.70	Drapeau et al (2014)
Nyanzachoerus pattersoni / kanamensis	YS3502	Mursi	4	>3.8	-11.00	Drapeau et al (2014)
Nyanzachoerus pattersoni / kanamensis	YS3503	Mursi	4	>3.8	-8.90	Drapeau et al (2014)
Nyanzachoerus pattersoni / kanamensis	YS3504	Mursi	4	>3.8	-8.30	Drapeau et al (2014)
Nyanzachoerus pattersoni / kanamensis	YS3505	Mursi	4	>3.8	-6.00	Drapeau et al (2014)
Nyanzachoerus pattersoni / kanamensis	GLL 0328	Galili	3.76	L-EA	-3.80	Bedaso (2011)

Nyanzachoerus pattersoni / kanamensis	GLL 0430	Galili	3.76	L-EA	-2.70	Bedaso (2011)
Nyanzachoerus pattersoni / kanamensis	GLL 0477	Galili	3.76	L-EA	-6.20	Bedaso (2011)
Nyanzachoerus pattersoni / kanamensis	GLL 1240	Galili	3.76	L-EA	-0.60	Bedaso (2011)
Nyanzachoerus pattersoni / kanamensis	GLL 1798	Galili	3.76	L-EA	-4.10	Bedaso (2011)
Nyanzachoerus pattersoni / kanamensis	ZK-EN 359	Dikika_BBM	3.7	L-EA	-5.47	Bedaso et al (2013)
Nyanzachoerus pattersoni / kanamensis	ZK-EN-D203	Dikika_BBM	3.7	L-EA	-4.68	Bedaso et al (2013)
Nyanzachoerus pattersoni / kanamensis	ZK-EN-D205	Dikika_BBM	3.7	L-EA	-3.12	Bedaso et al (2013)
Nyanzachoerus pattersoni / kanamensis	ZK-EN-D259	Dikika_BBM	3.7	L-EA	-2.97	Bedaso et al (2013)
Nyanzachoerus pattersoni / kanamensis	JN-EN-D359	BBM	3.7	L-EA	-5.50	Wilson (2013)
Nyanzachoerus pattersoni / kanamensis	ER 3177	ET_Lokochot	3.52	U-EA	-2.10	Harris and Cerling (2002)
Nyanzachoerus pattersoni / kanamensis	A.L. 129-19	Hadar_SH1	3.385	U-EA	-2.97	Wynn et al (2016)
Nyanzachoerus pattersoni / kanamensis	A.L. 129-6	Hadar_SH1	3.385	U-EA	-2.96	Wynn et al (2016)
Nyanzachoerus pattersoni / kanamensis	A.L. 145-26	Hadar_SH1	3.385	U-EA	-5.54	Wynn et al (2016)
Nyanzachoerus pattersoni / kanamensis	A.L. 145-26	Hadar_SH1	3.385	U-EA	-5.18	Wynn et al (2016)
Nyanzachoerus pattersoni / kanamensis	A.L. 1592-1	Hadar_SH1	3.385	U-EA	-1.80	Wynn et al (2016)
Nyanzachoerus pattersoni / kanamensis	A.L. 223-26	Hadar_SH1	3.385	U-EA	-4.40	Wynn et al (2016)
Nyanzachoerus pattersoni / kanamensis	ZK-EN-256	Dikika_SHM	3.31	U-EA	-1.60	Bedaso et al (2013)
Nyanzachoerus pattersoni / kanamensis	ER 2881	ET_Tulu-Bor	3.255	U-EA	-3.30	Harris and Cerling (2002)
Nyanzachoerus pattersoni / kanamensis	KNM-LT 26137	WT_Kaiyumung	3.2	U-EA	-2.90	Uno et al (2011)