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Relative abundances and palaeoecology of four suid genera in the Turkana Basin, Kenya, during the late Miocene to Pleistocene

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ABSTRACT

Most suids (Mammalia: Suidae, pigs) worldwide are omnivores living in closed environments, but the African warthog (*Phacochoerus*) has special adaptations for grazing in open environments. Similar specializations have been recorded from Plio-Pleistocene African suids. Four genera, *Nyanzachoerus*, *Notochoerus*, *Kolpochoerus,* and *Metridiochoerus,* have been discovered in late Miocene to middle Pleistocene locations around the Turkana Basin.

We analyse the relative abundances of these four suid genera compared to other mammals, from approximately 8–0.7 Ma. The dataset includes most of the mammal specimens collected from locations around the Kenyan side of the Turkana Basin. Species of genus *Nyanzachoerus* were dominant before 4 Ma, but their relative abundance decreases through time thereafter. At the same time, *Notochoerus* increases in relative abundance, followed by *Kolpochoerus,* and finally *Metridiochoerus*. Their peak relative abundances do not overlap: *Notochoerus* peaks at 3.44–2.53 Ma, *Kolpochoerus* at 2.53–1.87 Ma, and *Metridiochoerus* at 1.38–0.7 Ma.

We interpret the palaeoecology of these suids based on their relative abundances over time and on published isotope and pollen data. We find that *Nyanzachoerus* was replaced by its abrasive-diet-specialized successor *Notochoerus*, possibly in response to a rapid decrease in forest cover. *Notochoerus* adapted at first to the expanding wood- and grasslands, and then to more arid shrublands. After a period of severe aridity around 2.7–2.5 Ma, more variable environments allowed *Kolpochoerus* and *Metridiochoerus* to disperse, while *Notochoerus* disappeared, perhaps having lost its competitive edge. Further changes in the environment encouraged the expansion of grasslands over shrublands, favouring *Metridiochoerus*. *Kolpochoerus* persisted in the more closed environments near water sources.

1. Introduction

Suids (Mammalia: Suidae, pigs) are a widespread family of mainly omnivorous, non-ruminant, forest dwelling, medium sized artiodactyls. However, in Africa, warthogs (*Phacochoerus*) have special adaptations for grazing and open environments: their legs are relatively longer than those of other pigs, their orbits are placed high up on the back of the cranium (Ewer, 1958), and their third molars are hypsodont and have flat occlusal surfaces, commonly exposing over twenty tightly packed columnar cusps (Owen, 1850; Koenigswald, 2011). The extinct Asian genera *Hippohyus* and *Sivahyus* also had taller molars and more complicated enamel crenulation than most other suids (Pilgrim, 1926), but many extinct suids of Africa developed even more hypsodont teeth, and added more cusps to their third molars during the Plio-Pleistocene than suids in Europe or Asia. Here, we will examine the ecological context of their evolution. We want to know whether it is possible to identify the competitive advantages of these suids in the setting of changing shared environments.

During the late Miocene to middle Pleistocene four suid genera, *Nyanzachoerus*, *Notochoerus*, *Kolpochoerus* and *Metridiochoerus*, were abundant in the Turkana Basin of northern Kenya (Harris and White, 1979). *Nyanzachoerus* and *Notochoerus* belong to the extinct subfamily Tetraconodontinae (Van der Made, 1999). *Kolpochoerus* and *Metridiochoerus* belong to the subfamily Suinae, which includes all living suids. All of these genera have in common two traits: morphological changes in their third molars (Harris and White, 1979), and an increase in δ^{13}C-values over time (Harris and Cerling, 2002; Cerling et al., 2015). Morphological changes towards longer, flatter and more hypsodont molars are typical adaptations for an abrasive diet (Janis and Fortelius, 1988), which can mean that the diet itself is abrasive or that abrasive particles are associated with the diet (Damuth and Janis, 2011, Karme et al., 2016). Eating grass is well known to cause dental abrasion

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although whether this is caused by siliceous phytoliths (Baker et al., 1959; McNaughton et al., 1985; Epstein, 1994; Rabenold and Pearson, 2014) or harder extrinsic mineral particles (Sanson et al., 2007; Lucas et al., 2013) is still debated; evidence for a significant abrasive effect of phytoliths relative to dust was recently presented empirically by Merceron et al. (2016) and experimentally by Karme et al. (2016). In addition, more positive δ^{13}C-values indicate a diet containing C4-plants, e.g. mainly tropical grasses (Cerling et al., 2015).

The expansion of C4-grasses, which started in the Miocene, continued in the Pliocene (Retallack et al., 1990; Edwards et al., 2010), although the overall area of grasslands remained stagnant or decreased during 12–1.4 Ma in northeast Africa (Feakins et al., 2013). Levin et al. (2011) concluded from the isotopes of paleosol carbonates that there had been a steady increase in C4-plants in the floodplain environments of the Omo-Turkana Basin since 4 Ma. However, the pollen record from deep ocean cores show that shrubs were more common than grasses from 4.9 to 3 Ma in northeast Africa (Bonnefille, 2010; Liddy et al., 2016). The pollen data also suggest that an aridity shift occurred around 4.3 Ma (Liddy et al., 2016) and peaked at 2.7–2.5 Ma (Bonnefille, 2010). However, the ocean core data might not adequately represent an area as distant from the Gulf of Aden as the Turkana Basin. Open landscapes dominated by C4 biomass emerged only in the early Pleistocene (Ségalen et al., 2007). Recently, Fortelius et al. (2016) used an ecometric analysis of the dental traits of large mammals to estimate the precipitation levels of different Plio-Pleistocene localities of the Turkana Basin, and concluded that the most arid time interval in the Turkana Basin was approximately from 3 to 2 Ma.

The fossil data from the Turkana Basin and Omo Valley area have allowed researchers to understand the past animal communities of eastern Africa, and the environment where our own ancestors were living (Leakey and Leakey, 1978, Harris, 1983, Harris et al., 1988, Harris and Leakey, 2003, Leakey and Harris, 2003, Bobe et al., 2002, Bobe and Behrensmeyer, 2004, Bobe and Leakey, 2009, Werdelin and Lewis, 2013). The Turkana fossil record has also been a basis for research into the late Oligocene, Miocene (Leakey et al., 2011) and Plio-Pleistocene (Behrensmeyer et al., 1997; Werdelin and Lewis, 2005) faunal turnover and climatic change (deMenocal, 2004; Hernández Fernándes and Vrba, 2006). Isotope analyses have been used to determine the dietary adaptations of mammals, which are also used as an indicator of changing environments, especially from wooded closed habitats to open grasslands (Harris and Cerling, 2002; Bibi et al., 2013; Cerling et al., 2015).

Suid and proboscidean fossils are informative biostratigraphical indicators, because they underwent rapid species differentiation and radiation during the Plio-Pleistocene (Cooke and Maglio, 1972), and are therefore good biostratigraphic indicators. This, combined with the easy identification of suid teeth, has undoubtedly led to the extensive collection of suid specimens, which has an effect on the relative abundance of suids among other mammals in the collections. We are aware that the relative abundances of fossil taxa do not necessarily reflect the abundances of species in the living communities; suids as a group are most likely over represented. Within the suid family, however, the relative abundances of suid taxa are nevertheless likely to reveal the differences between the individual suid genera over time, and that is our focus here.

Patterson et al. (2017) analysed bovid and suid abundances from archaeological and palaeontological sites across the upper Burgi, KBS, and Okote Members (1.95–1.38 Ma) of the Koobi Fora Formation east of Lake Turkana, and Hakala (2011) measured suid abundances from the same members. Both studies reported an increase in *Metridiochoerus* and a decrease in both *Kolpochoerus* and *Notochoerus* from the upper Burgi to KBS Member. These studies are based on the same data source as our analysis, however, they do not deal with the changes before the turnover between the upper Burgi and KBS, nor with the west side of Lake Turkana. In addition, abundance analyses for bovids during the Plio-Pleistocene have been carried out to identify changes in genus-level dominance in order to reveal environmental changes (Bobe and Eck, 2001; Bobe et al., 2007). Here, we extend the comparison of the abundances of four suid genera from the late Miocene to Plio-Pleistocene, including the fossil material from both sides of Lake Turkana.

While the morphological changes and isotope records suggest that the four suid genera adapted to expanding grasslands, we want to know if their ecological niches were similar during the changing climatic and environmental conditions of the Plio-Pleistocene. Site occupancy and locality coverage have been used to understand the dynamics of ecological and palaeoecological communities (Jernvall and Fortelius, 2004; Fortelius et al., 2014). In such a small geographical area as the Turkana Basin, when dealing with such an abundant group as suids, presence/absence data shows no spatial differences, as the suids are present in almost every collection site. However, temporal separation can be seen. To obtain better temporal separation between the genera, we investigate the pattern of relative abundances over time. In the fossil record unimodality (the "hat" pattern; Liow et al., 2010) is well established for the species, genera, and higher taxa of terrestrial mammals (Jernvall and Fortelius, 2004; Quental and Marshall, 2013; Carotenuto et al., 2010), marine invertebrates (Foote et al., 2007; Tietje and Kiessling, 2013; Raia et al., 2016), and marine micro-organisms (Liow and Stenseth, 2007), highlighting a lack of recovery from decline. The pattern has been documented for occupancy, range, and diversity of species, as proxies for abundances. The prevailing interpretation for the "hat" pattern in the fossil record is that widespread and abundant species might, for multiple reasons, suffer an evolutionary slowdown, and therefore be overtaken by fast- evolving, newly arisen species with properties more closely attuned to the current conditions (Fortelius et al., 2014).

The purpose of this study is to understand how a C4-diet specialist group reacted to environmental changes during the Plio-Pleistocene in the Turkana Basin, in environments that also saw the evolution of early hominins. We compare the relative abundances of four African suid genera from the late Miocene to middle Pleistocene, and connect the changes in their abundances to published isotope and pollen records (Harris and Cerling, 2002; Braun et al., 2010; Cerling et al., 2015; Liddy et al., 2016; Bonnefille, 2010) to interpret their palaeoecology and interactions.

2. Material and methods

The data for this analysis come from the Turkana Basin Paleontology Database (http://naturalhistory.si.edu/ete/ETE_Datasets_Turkana.html), which has been complemented by other datasets for Lothagam, Kanapoi, and sites on the western side of Lake Turkana (curated by Meave Leakey), as well as datasets from both sides of Lake Turkana after 2005. A summary of the updated dataset has been published as supplementary material in Fortelius et al., 2016. Unfortunately, the dataset contains locations only in Kenya, and excludes Ethiopia, which restricts the analysis of the basin artificially by national borders.

The stratigraphic sequence can be divided into artificial bins of equal duration (for example in Bibi and Kiessling, 2015), or into primary members, which have exact dates but unequal durations (Brown and McDougall, 2011). In order to achieve consistency between the eastern and western localities, and to preserve the finest possible time resolution, we have used the primary members as our time intervals, which are dated by the interbedded tuff layers.

The Pliocene strata of the Turkana Basin in Kenya include the Kanapoi, Nachukui, and Koobi Fora Formations. The Pleistocene strata include the Nachukui and Koobi Fora Formations. The earliest data points (late Miocene) for this study are from the Lower and Upper Nawata Formations (Brown and McDougall, 2011). Volcanic ash (tuff) layers can be found throughout the strata of the Turkana Basin. Sediment units between the tuff layers have been formally defined as members (Table 1) (Brown and Feibel, 1991; Brown and McDougall, 2011). The tuff layers can be dated