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**Abstract:** The newly described partial skeleton of *Paranthropus boisei* KNM-ER 47000 as well as the FwJj14E Ileret footprints provide new evidence on the paleobiology and diversity of hominins from the Okote Member of the Koobi Fora Formation at East Turkana about 1.5 Ma (million years ago). To better understand the ecological context of the Okote hominins, it is necessary to broaden the geographical focus of the analysis to include the entire Omo-Turkana ecosystem, and the temporal focus to encompass the early Pleistocene. Previous work has shown that important changes in the regional vegetation occurred after 2 Ma, and that there was a peak in mammalian turnover and diversity close to 1.8 Ma. This peak in diversity included the Hominini, with the species *Paranthropus boisei*, *Homo habilis*, *Homo rudolfensis*, and *Homo erectus* co-occurring at around 1.8 Ma. There is considerable debate about whether *H. habilis* and *H. rudolfensis* indeed constitute separate species, but even if we consider them both as *Homo habilis sensu lato*, the co-occurrence of three hominin species at any one time and place is rather unusually high diversity for hominin standards (even if not so for other mammalian groups such as suids, bovids, or cercopithecids). Here we use mammalian faunal abundance data to place confidence intervals on first and last appearances of hominin species in the early Pleistocene of the Omo-Turkana Basin, and use these estimates to discuss hominin diversity in the Okote Member. We suggest that in the early Pleistocene a wide range of depositional environments and vegetation types, along with a high frequency of volcanism, likely maintained high levels of environmental variability both in time and space across the Omo-Turkana region, and provided ecological opportunities for the coexistence of at least three hominin species alongside a diverse mammalian fauna.

## Hominin diversity and high environmental variability in the Okote Member, Koobi Fora Formation, Kenya

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### Abstract

The newly described partial skeleton of *Paranthropus boisei* KNM-ER 47000 as well as the FwJj14E Ileret footprints provide new evidence on the paleobiology and diversity of hominins from the Okote Member of the Koobi Fora Formation at East Turkana about 1.5 Ma (million years ago). To better understand the ecological context of the Okote hominins, it is necessary to broaden the geographical focus of the analysis to include the entire Omo-Turkana ecosystem, and the temporal focus to encompass the early Pleistocene. Previous work has shown that important changes in the regional vegetation occurred after 2 Ma, and that there was a peak in mammalian turnover and diversity close to 1.8 Ma. This peak in diversity included the Hominini, with the species *Paranthropus boisei*, *Homo habilis*, *Homo rudolfensis*, and *Homo erectus* co-occurring at around 1.8 Ma. There is considerable debate about whether *H. habilis* and *H. rudolfensis* indeed constitute separate species, but even if we consider them both as *Homo habilis sensu lato*, the co-occurrence of three hominin species at any one time and place is rather unusually high diversity for hominin standards (even if not so for other mammalian groups such as suids, bovids, or cercopithecids). Here we use mammalian faunal abundance data to place confidence intervals on first and last appearances of hominin species in the early Pleistocene of the Omo-Turkana Basin, and use these estimates to discuss hominin diversity in the Okote Member. We suggest that in the early Pleistocene a wide range of depositional environments and vegetation types,

along with a high frequency of volcanism, likely maintained high levels of environmental variability both in time and space across the Omo-Turkana region, and provided ecological opportunities for the coexistence of at least three hominin species alongside a diverse mammalian fauna.

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## Introduction

New fossils from the Okote Member of the Koobi Fora Formation at East Turkana (Fig. 1), Kenya, bring into focus the question of hominin diversity in the early Pleistocene of eastern Africa. The Okote Member, dating from 1.56 to 1.38 Ma (Figure 2A), has produced key fossils that contribute to our understanding of hominin evolution and diversity around 1.5 Ma (Leakey and Leakey, 1978; Wood, 1991). Some of the most noteworthy specimens from the Okote include KNM-ER 992 (the holotype of *Homo ergaster*), KNM-ER 3883 (*H. erectus* calvaria), and KNM-ER 42703 (a fragment of maxilla that constitutes the last appearance record of *H. habilis*) (Leakey et al., 2012). To these, we can add the hominin fossil footprints from Ileret (Bennett et al., 2009; Hatala et al., 2016; Roach et al., 2016) and the *Paranthropus boisei* upper limb KNM-ER 47000 described in this volume (Green et al., 2018; Lague et al., 2018; Richmond et al., 2018), both from the site FwJj14E (Fig. 1B). The hominin footprints are attributed to *Homo erectus* based mostly on their morphology, but also in part on the lack of other possible hominins in the Turkana Basin during the Okote Member times (Hatala et al., 2016). Similarly, the upper limb KNM-ER 47000 is attributed to *Paranthropus boisei* largely based on the anatomy of the fossil, but also in part based on the lack of other plausible taxonomic candidates (Richmond et al., 2018). To understand hominin diversity and ecology in the Okote Member, it is necessary to broaden our focus both temporally and geographically, and here we ask two main questions. How many hominin species occurred at East Turkana 1.5 Ma? What was their ecological context?

The Okote is one of eight geological members in the Koobi Fora Formation, and the Koobi Fora Formation is one of the five fossiliferous formations that make up the Omo Group deposits exposed in the lower Omo Valley and the Lake Turkana Basin, here referred to as the Omo-Turkana Basin (Fig. 1A, Fig. 2B). The sedimentary environments and chronological framework of the basin have been well studied for the past fifty years (de Heinzelin, 1983; Brown and Feibel, 1991; Brown, 1994; Brown and McDougall, 2011; Feibel, 2011). The Pliocene and Pleistocene Omo Group includes the Mursi, Usno, and Shungura formations in Ethiopia, and the Koobi Fora and Nachukui formations in Kenya, with relatively continuous deposition from nearly 4.4 Ma to 1 Ma. After about 0.7 Ma, deposition in the basin became more intermittent. Most of the Omo Group deposits were laid down by a major fluvial system, the paleo-Omo river, but there were also a few intervals of significant lacustrine deposition when a major lake occupied large areas of the basin (Fig. 2B).

Previous research has shown that the time between about 2 Ma and 1.4 Ma was one of high turnover and high diversity among different groups of mammals, including hominins, in the Omo-Turkana Basin (Bobe et al., 2007; Bibi and Kiessling, 2015; Fortelius et al., 2016). The question of early hominin diversity has featured prominently in the research history of the region (Walker and Leakey, 1978; Leakey et al., 2001, 2012; White, 2003, 2013; Spoor et al., 2007, 2010 ). The concept of diversity encompasses both species richness (the number of species) and the relative abundance of these species (evenness). Given the wealth of new data from the Okote Member featured in this Special Issue, here we focus on the diversity and the environments of hominins in the early Pleistocene of the Omo-Turkana Basin.

## **The environmental context**

### *Depositional environments*

The Okote Member is defined as the sedimentary sequence between the base of the Okote Tuff, which is part of the Okote Tuff Complex, and the base of the Chari Tuff (Brown and Feibel, 1986). The Okote Tuff is estimated to have an age of 1.56 Ma, while the Chari Tuff is dated to 1.38 Ma (Brown and McDougall, 2011); thus this member spans 180,000 years (Fig. 2A). The type section in Area 131 measures 21.6 m, and overall the Okote sediments are interpreted as complex fluvial deposits with an interval of lacustrine deposition best expressed in the Ileret sub-region (Feibel, 1988; Behrensmeyer and Isaac, 1997). This lacustrine phase is an expression of the Lorenyang Lake, which occupied the center of the basin from about 2 Ma to about 1.6 Ma (Fig. 2B); in the upper part of the Okote Member there is a transition to fluvial environments (Feibel, 2011). The Okote Member is widely exposed, outcropping in 26 of the collecting areas formally defined at East Turkana (Brown and Feibel, 1991). In the Karari Escarpment, there are tuffaceous mudstones in the lower part of the sequence, and small fluvial channels with basalt conglomerates in the upper part. In the Ileret area, there is evidence of lacustrine deposition in the lower sequence and of fluvial channels in the upper Okote Member that are rich in mammalian fossils (Brown and Feibel, 1986). In areas 101 to 103, channel sands and mudstones overlie the Koobi Fora Tuff Complex, a thick tuffaceous sequence (Brown and Feibel, 1986). Thus, the main sedimentary environments of the Okote Member differ across areas of East Turkana. It is likely that an expanding and contracting Lorenyang Lake and the rivers that flowed into it played an important role in the shifting depositional settings and in maintaining high environmental variability during this time (Feibel, 2011). This variation in sedimentary environments likely produced variation in the ecology of the basin during the early Pleistocene.

### *Volcanism*

The Omo-Turkana Basin has a rich record of volcanic eruptions, with tuffs that serve for regional correlations and radiometric dating (Fig. 2). Some of these tuffs were massive (e.g., Chari Tuff) and deposited over large areas of eastern Africa, and some intervals of time show smaller-scale but frequent tuff deposition, with multiple fluvially reworked tuffs (Feibel, 1999, 2011). McDougall and colleagues report 360 distinct tuffs from the Omo Group deposits during the last 4 Ma or so (McDougall and Brown, 2006; McDougall and Brown, 2008; McDougall et al., 2012). From these data, Figure 3 shows a high frequency of tuffs in the interval from about 1.6 to 1.4 Ma, which largely encompasses the Okote Member. Figure 4 depicts an 8.5 m section of FwJj14E with three of these tephtras in an interval spanning less than 20,000 years, which includes the Ileret hominin fossil footprints and the *Paranthropus boisei* upper limb KNM-ER 47000. The effects of these volcanic episodes on the environments and the ecology of the Omo-Turkana region remain to be fully explored, but it is likely that they played a role in modifying the basin's vegetation and landscapes at different scales and different time frames, and contributed to environmental variability both in time and space. In turn, high environmental variability in the basin may have provided ecological opportunities for a diverse mammalian fauna, including hominins.

#### *Paleosols and vegetation*

Stable isotopes of fossil soils provide important information about the vegetation of the Omo-Turkana Basin from more than 4 Ma to about 1 Ma (Wynn, 2004; Quinn et al., 2007; Levin et al., 2011). The data depicted in Figure 5 show that a mix of woodlands and wooded grasslands dominated the basin prior to 2 Ma, but with C<sub>3</sub> vegetation being more prevalent in the Omo (Shungura Formation) than elsewhere in the basin. These woodlands and wooded grasslands continued to exist in the basin after 2 Ma, but C<sub>4</sub> grasslands became more prevalent than before, and the C<sub>3</sub> woodlands in the Omo gave way to wooded grasslands with a mix of C<sub>3</sub> and C<sub>4</sub> vegetation (Cerling et al., 2011; Levin et al., 2011). These results parallel an increase in the abundance of grazing mammals in the Omo-Turkana Basin after 2 Ma (Bobe, 2011; Patterson et al., 2017). The high environmental variability in the basin both in time and space is highlighted by the fact that the range of  $\delta^{13}\text{C}$  values is highest in the interval from 2 Ma to 1.4 Ma than during earlier times. It should be emphasized that the increasingly prominent C<sub>4</sub> grasslands occurred in a context of persistent woody vegetation (Bamford, 2011, 2018) and well-watered conditions in the basin (Joordens et al., 2011). The range of environments from C<sub>3</sub> woodlands to C<sub>4</sub> grasslands undoubtedly contributed to the habitat heterogeneity and to the diversity of the mammalian fauna in the basin during the early Pleistocene.

To assess hominin diversity during this time, it is critical to have an understanding of the abundance and time range of different species. For example, if there are four hominin species in the KBS Member, but in the Okote Member there are only three species, does this constitute a real drop in species richness? Could the absence of one of these species be an artifact of sampling? It is important to place confidence intervals on the first and last appearances of fossil species in assessing diversity patterns. This is particularly

relevant for rare species, as these typically require large numbers of fossils to be sampled.

## **Materials and methods**

Data for Koobi Fora were taken from the PaleoTurkana Database (PTD). The database was originally compiled from the fossil collections at the National Museums of Kenya (NMK) by the first author in collaboration with A.K. Behrensmeyer of the Smithsonian Institution and Meave Leakey from NMK (Bobe, 2011; Bobe et al., 2011). It was augmented with data on the fossil mammals from Area 1A at Ileret as well as other exposures of the Koobi Fora Formation collected by the authors, in collaboration with the Koobi Fora Field School, through fieldwork at East Turkana during the 2007–2014 field seasons. The PTD is a specimen-based database wherein each fossil specimen constitutes a single record with relevant taxonomic, geographic, stratigraphic, and taphonomic information, deriving from the Koobi Fora, Nachukui, Kanapoi, and Nawata formations at East Turkana, West Turkana, Kanapoi, and Lothagam respectively. Currently the PTD has 17,680 records, and over 1,100 fossil vertebrates from the Okote Member. Many of these specimens have been published in some detail (Harris, 1983, 1991; Black and Krishtalka, 1986; Harris et al., 1988; Wood, 1991; Walker and Leakey, 1993; Harris and Leakey, 2003; Leakey and Harris, 2003; Jablonski and Leakey, 2008; Geraads et al., 2013; Werdelin and Lewis, 2013), but many specimens remain unpublished. A public version of the database has been available to the scientific community and the public since 2004 through the Smithsonian Institution (National Museum of Natural History, Evolution of Terrestrial Ecosystems Program) and the National Museums of Kenya (Department of Earth Sciences) (see Bobe et al., 2011). Both the Evolution of Terrestrial Ecosystems Program and the National Museums of Kenya hold current version of the database. The Turkana Basin Institute also maintains an updated version of the database (Fortelius et al., 2016).

In this study we also use the Omo Paleontology Database, which is similar in structure to the PTD and includes fossil vertebrates from the Mursi, Usno, and Shungura formations in the lower Omo Valley of southern Ethiopia. The Omo data derive from the work of the International Omo Research Expedition of the 1960s and 1970s, and have been the subject of numerous publications (Alemseged, 2003; Alemseged et al., 2007; Bobe and Eck, 2001; Cooke, 2007; Drapeau et al., 2014; Eck, 2007; Eck et al., 1987; Gentry, 1985; Geraads, 2014; Howell and Coppens, 1974; Howell et al., 1987; Negash et al., 2015; Souron et al., 2012; Suwa, 1990; Suwa et al., 1996; White et al., 2006; White and Suwa, 2004). We have updated this database through further fieldwork (in the Omo Mursi Formation), study of primary fossil collections at the National Museum of Ethiopia in Addis Ababa, and incorporation of all recently published references to the Omo fossils (e.g., Drapeau et al., 2014; Geraads, 2014).

Some individual fossil animals may be recorded in the PaleoTurkana and Omo databases more than once, and these occurrences are noted in the database following contextual

and taphonomic field and laboratory observations. Thus, for example, the *Paranthropus boisei* individual KNM-ER 47000 is represented by nine records in the PaleoTurkana Database, one record for each fossil skeletal element or fragment thereof (such as the scapular fragment KNM-ER 47000A, the distal humerus KNM-ER 47000B, and the shaft of the ulna KNM-ER 47000C). The database allows for a simple search so that only one record per individual is considered. Thus, in deriving mammal species abundances in Tables 1–5, only one record per individual is counted. Thus in Table 1, KNM-ER 47000 counts as one specimen of *Paranthropus boisei*. In sum, we use a modified form of NISP (number of identified specimens) in which each individual represented in the database by two or more skeletal elements or fragments is counted as one.

In this contribution, we use mammalian abundances to place confidence limits on the first appearance datum (FAD) and last appearance datum (LAD) of each of the hominin species that occurs in the Omo-Turkana Basin between 2 Ma and 1.4 Ma. The first appearance datum of a species (or higher taxon) is defined as the earliest fossil record of that species, and the last appearance datum is the latest fossil record of the species (Fig. 6). These records do not necessarily correspond to origination or extinction events; in fact they almost never do. In Figure 6, this problem is illustrated as the difference between  $t_1$  (origination) and  $t_2$  (FAD), and between  $t_3$  (LAD) and  $t_4$  (extinction). In this context, origination may refer to a speciation event or to a migration event of the species into the area of interest. Likewise, extinction may be local or global, depending on the geographic focus and the questions of the study. In principle, if there are large samples preceding the earliest record of a species, and this species is relatively abundant once it appears in the fossil record, we can have fairly high confidence that the FAD ( $t_2$ ) may be close in time to an actual origination event ( $t_1$ ). Conversely, if the earliest appearance of a species is preceded by small samples, and the species is rare once it appears, we will have low confidence that this FAD ( $t_2$ ) is close in time to an actual origination event ( $t_1$ ). The same principles apply to the last appearance of a species. If the fossil record of a species is relatively abundant up to the time of its last appearance ( $t_3$ ), and this LAD is followed by large fossil samples of other species, then we can be confident that the LAD is close in time to an actual extinction event ( $t_4$ ). But if the species is rare up to its LAD, and this record is followed by small samples, then we will have low confidence that the LAD corresponds to an actual extinction event. The absence of a species from a fossil sample may be because the species of interest was not present in the original landscape, or because of taphonomic and sampling issues, including small sample size. Paleobiologists have developed multiple approaches to deal quantitatively with FADs and LADs (Koch, 1987; Strauss and Sadler, 1989; Marshall, 1990; Holland, 2003; Marshall, 2010), and here we use one such method based on the abundance of the species under study and the abundance of the fossil record before and after their first and last occurrences, respectively (Barry et al., 2002; Bobe and Leakey, 2009). If the abundance (number of identified specimens [NISP] or minimum number of individuals [MNI]) of a species is  $n$ , and the total faunal abundance during its range is  $m$ , the relative abundance of the species is  $n/m$ . The size of the faunal samples preceding the FAD or following the LAD is given by  $r$ . Thus we estimate the probability of

finding the taxon of interest in a sample as  $P_i = 1 - (1 - n/m)^f$ . Here we use a critical value of 0.8 for  $P_i$  in estimating the 95% confidence interval for each origination and extinction event. If the sample size adjacent to the FAD or LAD of the species in question is not large enough for a  $P_i$  value greater than 0.8, then we must add samples from the next time interval successively until the critical value of 0.8 is reached. Table 5 provides the details of the calculations.

In this study, the faunal abundance data exclude micromammals (such as rodents and lagomorphs) because they typically have different taphonomic modes of preservation than those of the larger mammals that include hominins. It is important to note that, because of taphonomic processes, faunal abundance as measured by the proportion of fossils of a given species in relation to the total faunal sample under consideration does not translate directly into faunal abundances in the original paleocommunities. But in this analysis it is the relative abundance of the fossils attributed to a species that is most important. By placing confidence limits, we can assess whether the absence of a species from a given interval is likely to be a real absence or an artifact of sampling. This problem is particularly relevant for rare taxa, and Plio-Pleistocene hominin fossils are usually rare (Bobe and Leakey, 2009). In general, large samples are needed to assess the presence or absence of rare species because rare taxa are not likely to be detected in small samples (Buzas, 1990; Hayek and Buzas, 1997; Marshall, 2010). These assessments are important for our understanding of species diversity in fossil assemblages.

## Results and preliminary discussion

### *Faunal context*

The fossil hominins described from the site FwJ14E are from Area 1A (Richmond et al., 2018), the smallest of all the formally defined collecting areas in the Koobi Fora Formation (Fig. 1B). Area 1A extends for less than 1 km<sup>2</sup> (0.93 km<sup>2</sup>), but has the largest sample of fossil mammals from the Okote Member, with 189 catalogued fossil mammals (modified NISP) (Table 1). In Area 1A the Okote Member extends from its base at 1.53 Ma to about 1.45 Ma; thus it is relatively well constrained temporally and geographically. The most abundant species from the Okote Member in Area 1A are *Kobus kob*, *Kolpochoerus limnetes*, *Metridiochoerus compactus*, *Theropithecus oswaldi*, *Kobus sigmoidalis*, and *Pelorovis oldowayensis*, in that order. The fact that these species all have a diet composed primarily of C<sub>4</sub> resources (Patterson et al., 2017) indicates that grasslands were a major component of the environments associated with the FwJ14 hominin footprints and the KNM-ER 47000 *Paranthropus* upper limb. The abundance of *Kobus* in this sample is indicative of edaphic grasslands. Nevertheless, *Giraffa* and *Tragelaphus*, taxa that relied on woodlands and C<sub>3</sub> resources, are not uncommon, and there is also evidence of arboreal monkeys (*Lophocebus*) in Area 1A (Fig. 7). Thus, the Okote ecosystem likely had a mix of C<sub>4</sub> grasslands and C<sub>3</sub> woodlands near a major lake fed by rivers from the Ethiopian highlands (the paleo-Omo river) as well as rivers from the east of the basin (Brown and Feibel, 1991; Behrensmeyer and Isaac, 1997). These



heterogeneous environments may have provided ample ecological opportunities for the co-existence of closely related species. Among suids, for example, in Area 1A alone in the time from 1.53 to 1.45 Ma there were three species of *Metridiochoerus* (*M. andrewsi*, *M. compactus*, *M. hopwoodi*) and one of *Kolpochoerus*, all of them with a predominantly C<sub>4</sub> diet (Patterson et al., 2017).

Suids overall constitute about 15% of the Okote fossil mammals. By the time of the Okote Member, the earlier radiation of tetraconodontine suids had come to an end. The last surviving species of the *Nyanzachoerus-Notochoerus* radiation were *Notochoerus clarki* and *Notochoerus scotti*. The last appearance datum of *N. clarki* is in Member H of the Shungura Formation, about 1.8 Ma, about the same time as the last appearance of *N. scotti* in the KBS Member of the Koobi Fora Formation. The extinction of the last remaining species of Tetraconodontinae in eastern Africa at about 1.8 Ma is broadly coincident with the diversification of the *Metridiochoerus* group, well illustrated in the Turkana Basin fossil record (White and Suwa, 2004). Thus, there were at least six species of suids in the Omo-Turkana Basin between 2 Ma and 1.4 Ma, and four of these species coexisted in the Okote Member. All these species had a diet of predominantly C<sub>4</sub> vegetation. Thus, environmental variability produced by different sedimentary environments and shifting paleogeographic conditions, frequent volcanic eruptions, and shifting patterns of heterogeneous vegetation had an impact at different scales, from local habitats measured in meters to larger scales of tens of kilometers throughout the basin. Hominins, as relatively large mammals and as hominoids with high levels of behavioral flexibility, likely responded to this range of variability from shifting local resources (such as water, fruiting trees, open spaces, and other fauna) to larger scale ecological patterns in the entire basin.

### *The fossil hominins*

In the Okote Member there are 51 hominin fossils distributed among three species: *P. boisei*, *H. erectus*, and *H. habilis* (Table 2). If we expand our time window back in time to 2 Ma to include the Upper Burgi and KBS members (Figure 2), then the species *H. rudolfensis* is added to the list of hominin taxa at East Turkana (Table 2). In the hominin fossil record, three or four species at any one time and place is considered a high level of taxonomic diversity (Wood and Boyle, 2016). There is considerable debate about whether *H. habilis* and *H. rudolfensis* indeed constitute separate species (Lieberman et al., 1996; Wood and Baker, 2011; Leakey et al., 2012; Lordkipanidze et al., 2013; White, 2013; Antón et al., 2014), but even if we consider them both as *H. habilis sensu lato*, the co-occurrence of three hominin species at any one time and place is rather unusually high diversity for hominin standards, even if not so for other mammalian groups like suids, bovids, or cercopithecids. Here we consider the chronological ranges of these hominin species in the context of the Omo-Turkana Basin to better understand the pattern of hominin diversity at East Turkana.

The lineage *Paranthropus aethiopicus* – *P. boisei* is found in all three of the major regions of the Omo-Turkana Basin: East Turkana (Table 2), West Turkana (Table 3), and the Omo (Table 4). The earliest appearance of *Paranthropus* is in Shungura Member C, about 2.7 Ma (Fig. 8), with specimens L62-17 and L55-33 deriving from Shungura units C-5 and C-6, respectively. This FAD of *Paranthropus* represents both the earliest record of the genus in the Omo-Turkana Basin (regional FAD) and the earliest record in Africa (global FAD) (Table 5). Specimens of *Paranthropus* between 2.7 and 2.3 Ma are typically attributed to the species *Paranthropus aethiopicus* Arambourg and Coppens, 1968, the best-known representative of which is KNM-WT 17000 from the Lokalalei Member of the Nachukui Formation, dated to 2.5 Ma. The only place outside the Omo-Turkana Basin where *P. aethiopicus* has been reported is in the Upper Ndolanya Beds at Laetoli, where two specimens attributed this species date to 2.66 Ma (Harrison, 2011), about the same age as the earliest *P. aethiopicus* from the Omo. *Paranthropus aethiopicus* was relatively rare in the Omo in the time range from 2.7 to 2.3 Ma, never exceeding 0.5% of the fossil mammals in Shungura members C through F (Table 4). The species was more abundant in the upper Lomekwi and Lokalalei members of the Nachukui Formation (Table 3), but the samples from West Turkana are significantly smaller than those from the Omo. Overall, there are 51 specimens ( $n$ ) of *P. aethiopicus* in the Shungura and Nachukui formations, in a total sample of 18,355 fossil mammals ( $m$ ) (Table 5). Thus, the relative abundance ( $n/m$ ) of *P. aethiopicus* in the region is 0.003, or about 0.3% of the mammalian fauna. In the time interval preceding the FAD of *P. aethiopicus* there are 446 fossil mammals between 2.7 Ma and 3.0 Ma (Table 5). Given the low relative abundance of *Paranthropus*, the probability of finding this taxon in a sample of 446 fossils is not high. Further back in time, Shungura upper Member B has a sample of 2754 mammals dating to just over 3.07 Ma (the age of Tuff C), a sample large enough to indicate that *Paranthropus* was probably not present in the region prior to 3.07 Ma. However, it should be noted that the sample from Member B consists primarily of isolated teeth, and it may be difficult to distinguish isolated teeth of the earliest *Paranthropus* from those of *Australopithecus*.

The evolving chronospecies *P. aethiopicus* – *P. boisei* is typically divided into the earlier *P. aethiopicus* and the later *P. boisei* at about 2.3 Ma (Suwa et al., 1996). In the Omo, *P. boisei* was rare (0.08% of the fossil mammals). This lineage is most abundant at East Turkana in the KBS and Okote members, and at West Turkana in the Kaitio Member, which is equivalent in age to the KBS Member, where *P. boisei* constitutes about 2% of the fossil mammals. The last appearance datum of *P. boisei* in the Omo-Turkana Basin is at 1.4 Ma in upper Member K, about the same age as the *Paranthropus* skull from Konso (Suwa et al. 1997), but there is a younger specimen from Olduvai Gorge in Tanzania at 1.34 Ma (Domínguez-Rodrigo et al., 2013). The fossil record at East Turkana essentially dwindles above the Okote; there are few fossil specimens from the Chari Member (1.38–0.75 Ma), and at West Turkana there are only 87 specimens from the Nariokotome Member (1.38–0.75 Ma). In the Omo, there are more than 700 fossil specimens from Member L (1.38–1.1 Ma), and the absence of *Paranthropus* from this sample potentially indicates a regional extinction event (Table 5, Fig. 8).

Defining the genus *Homo* continues to be an important problem in paleoanthropology (Wood and Collard, 1999; Wood, 2009; Villmoare, 2018). Nevertheless, current evidence indicates that the earliest specimen of *Homo* is the LD 350-1 mandible from Ledi-Geraru in the Afar of Ethiopia dated to nearly 2.8 Ma (DiMaggio et al., 2015), but a specimen from the lower Tulu Bor Member of the Koobi Fora Formation (KNM-ER 5431) could be at least as old as the Ledi-Geraru mandible (Wood, 1991; Villmoare et al., 2015) (Fig. 8). After this first appearance, there is a gap of 400,000 years before specimens attributed to *Homo* appear in the Afar region (Kimbel et al., 1996), the Omo-Turkana Basin (Prat et al., 2005; Suwa et al., 1996), the Lake Baringo Basin (Hill et al., 1992), and the Malawi Rift (Schrenk et al., 1993). In the Maka'amitalu Basin of Hadar, specimen A.L. 666-1 from the Busidima Formation dates to nearly 2.4 Ma and is attributed to *Homo* aff. *H. habilis* (Kimbel et al., 1997). At about the same time, in the Omo Shungura Formation members E and F there are 17 specimens attributed to aff. *Homo* sp. (Table 4) (Suwa et al., 1996; Wood and Leakey, 2011), while in the Baringo Basin there is a temporal bone fragment, specimen KNM-BC 1 from the Chemeron Formation dated to 2.4 Ma, considered to belong to the genus *Homo* (Hill et al., 1992). Thus, the genus *Homo* may have first appeared at about the same time as *Paranthropus*, but the earliest record of *Homo* is extremely sparse (Fig. 8).

The earliest secure records of *H. habilis* in the Omo-Turkana Basin are from Upper Member G of the Shungura Formation and the Upper Burgi Member of the Koobi Fora Formation (Tables 2 and 4). Both the Shungura L894-1 and KNM-ER 1813 (Fig. 9) specimens date to nearly 1.9 Ma. KNM-ER 1813 is perhaps the iconic *H. habilis* specimen, which has been used to establish the "1813" morph (Antón et al., 2014). There are only a few other specimens at Koobi Fora referred to *H. habilis*: KNM-ER 3735 (assigned to the taxon tentatively) also from the Upper Burgi Member, KNM-ER 1805 from the KBS Member, and KNM-ER 42703 from the Okote Member. This specimen from the Okote is the LAD of *H. habilis*, not only in the Omo-Turkana Basin but globally. There are of course several specimens of *H. habilis* from Olduvai Gorge that are contemporaneous with those from East Turkana and the Omo: OH 7, OH 13, OH 24, OH 62, and OH 65 among others (Susman, 2008; Clarke, 2012). With five specimens from the entire Omo-Turkana Basin, *H. habilis* is a rare species, making up 0.06% of the mammals from Upper Member G in the Omo, and 0.09% of all mammals in the time range from the Upper Burgi to the Okote members. Although we consider the FAD of *H. habilis* to be 1.9 Ma, there are several older specimens identified as to *H. aff. H. habilis* or *H. cf. H. habilis* (e.g., A.L. 666-1) that precede this FAD. Thus, an assessment of the origins of *H. habilis* awaits a detailed study of these fossils. The LAD of *H. habilis* at about 1.4 Ma is followed by sparse fossil samples in the Omo-Turkana Basin and elsewhere in Africa. Thus, for a species as rare as *H. habilis*, the LAD is very poorly constrained (Fig. 8).

Only five specimens from the Omo-Turkana Basin are attributed to *H. rudolfensis*, and they are all from the Koobi Fora Formation. KNM-ER 1470 (Fig. 9), KNM-ER 1482, KNM-

ER 62000, and KNM-ER 62003 are from the Upper Burgi Member and date to nearly 2 Ma, while KNM-ER 60000 is from the KBS Member and dates to 1.85 Ma (Fig. 8). Thus this species is rare in the Omo-Turkana Basin, constituting about 0.15% of all mammals during its time range in the Upper Burgi and KBS members, and 0.07% in the basin as a whole (Tables 2 and 5). The *Kenyanthropus platyops* cranium KNM-WT 40000 has been linked to the ancestry of *H. rudolfensis* (Leakey et al., 2001), but it is also possible that specimens in the Omo attributed to aff. *Homo* or *Homo* sp. could represent populations ancestral to *H. rudolfensis*, although there is no direct morphological link between them. Elsewhere in Africa, the OH 65 maxilla from Olduvai Bed I (Blumenshine et al., 2003) and the Malawi mandible UR 501 (Schrenk et al., 1995) have been attributed to this species. In this case, the Malawi mandible UR 501 would constitute the FAD of *H. rudolfensis*. Is the LAD of *H. rudolfensis* in the KBS Member likely to represent an extinction event? Given the rarity of *H. rudolfensis*, the faunal samples from the Okote Member, the Natoo Member, and Member K are not large enough to confidently exclude the possibility that this species was present in the Omo-Turkana Basin during the Okote Member times (Table 5). This of course does not mean that *H. rudolfensis* must have been present during the Okote Member times, but simply that its absence could be due to sample size rather than a real extinction event.

The earliest specimens of *H. erectus* in Africa (here we consider *H. ergaster* a junior synonym of *H. erectus*) are KNM-ER 2598 and KNM-ER 3228 from the Upper Burgi Member at East Turkana dating to 1.9 Ma (Figure 8). KNM-ER 1812 and 1481 could also belong to this species. Thus, the FAD of *H. erectus* consists of four Upper Burgi specimens, with a relative abundance of 0.3% of fossil mammals (Table 2). Prior to this FAD, the Koobi Fora Formation has a significant gap in the fossil and sedimentological record of about half a million years, so that if this species was present at East Turkana we would not be able to sample it. At West Turkana there is no such hiatus, but fossil samples are not large: 188 fossil mammals from the Kalocho Member (2.33 Ma – 1.87 Ma) and 72 from the Lokalalei Member (2.53 Ma – 2.33 Ma). However, in the Omo there is a very large sample from Lower Member G (2.27 Ma – 2.15 Ma) with more than 15000 fossil mammals. This large sample constrains the first appearance of this species in the basin. The last record of *H. erectus* in the Omo-Turkana Basin is KNM-WT 19700 tentatively assigned to this species and dated to about 1 Ma (Brown et al., 2001). Around this time there are other *H. erectus* specimens from elsewhere in Africa (OH 9, OH 12, KNM-OL 4550, BOU-VP-2/66, UA 31) (Abbate et al., 1998; Asfaw et al., 2002; Potts et al., 2004), and it is likely that this species gave rise to later hominins such as *Homo heidelbergensis* or *Homo rhodesiensis*. Thus, we do not place a confidence interval on this LAD.

## Discussion

### *Hominin diversity and environmental variability*

Early Pleistocene hominin diversity needs to be understood in ecological context, i.e., in terms of spatial heterogeneity and temporal dynamics. Here we have sought to view Okote hominin diversity in the context of spatially heterogeneous, complex, and rapidly changing habitats at East Turkana, and more broadly in the Omo-Turkana Basin (Figs. 3-5). But assessments of diversity are also influenced by sample size and species abundances. Small samples are likely to capture only the most abundant species in an ecosystem, or the most abundant fossil taxa in a stratigraphic sequence. Hominin fossils are rare. There are, for example, only five specimens attributed to *Homo rudolfensis* among nearly 7000 fossil mammals in the basin between 2 Ma and 1.6 Ma (Tables 2-4). Thus, the relative abundance of *H. rudolfensis* is ~0.07% of the fossil mammals during this time. The absence of this hominin species from the Okote Member could well be an artifact of sampling. By assessing the abundance of fossils in the Omo-Turkana Basin, we have placed confidence intervals on the first and last appearance data of hominin species, and thus gained a better understanding of the uncertainties associated with the chronological range of these species (Figs. 6, 8). In turn, this understanding is necessary to evaluate patterns of speciation, extinction, and species richness in the fossil record.

The Okote Member of the Koobi Fora Formation provides evidence of at least two hominin species co-occurring in Area 1A during the time interval from 1.56 Ma to 1.45 Ma. In addition to the hominins, there are at least 29 other mammalian species among 25 genera represented in the fossil record of just one relatively small area (Area 1A) (Table 1, Fig. 7). Some of the most abundant mammals, e.g., *Kobus*, *Metridiochoerus*, *Kolpochoerus*, and *Theropithecus*, were predominantly C<sub>4</sub> grazers (Patterson et al., 2017), but other common mammals were either mixed feeders, e.g. *Tragelaphus*, or C<sub>3</sub> browsers, e.g. *Giraffa*. *Homo* was among the mixed feeders, while *Paranthropus* relied primarily on C<sub>4</sub> dietary resources (Patterson et al., 2017). The abundance of *Kobus* is indicative of edaphic grasslands. Sedimentary environments, stable isotopes from paleosols (Figure 5), and fossil wood point to a heterogeneous environment with extensive C<sub>4</sub> grasslands, but also with significant woody vegetation under relatively mesic conditions near a river flowing into a lake (Bamford, 2017; Feibel, 2011; Levin et al., 2011). Volcanic ashes deposited over the landscape frequently disrupted this heterogeneous environment, increasing the levels of environmental variability (Figure 3). At the site FwJ14E alone there are three tephras in an interval of less than 20,000 years (Figure 2, Figure 4). The environmental variability that characterized Area 1A of Okote Member was a feature of the Omo-Turkana Basin at least from 2 Ma to 1.4 Ma, when the environments in the basin seem to have been reorganized in relation to earlier time intervals (Figure 5). In this broader geographic and chronologic scale (Omo-Turkana Basin from 2 to 1.4 Ma) there is evidence of significant turnover of mammal species and of high mammalian diversity (Bobe et al., 2007; Bibi and Kiessling, 2015; Fortelius et al., 2016). Hominins seem to have been part of this high mammalian diversity, with possibly four species between 2.0 and 1.8 Ma (Fig. 9). One of these species (*Homo rudolfensis*) has not been found in the Okote Member, but its absence could well be due to the rarity of the species rather than to a real extinction event (Table 5, Fig. 8). The mechanisms whereby three or four hominin species may have co-

existed remain to be fully explored, but there is some indication that character displacement played a role, as it does in modern African apes (Berthaume and Schroer, 2017). We suggest that the high degree of environmental variability in the Omo-Turkana Basin at different geographic and temporal scales between 2 Ma and 1.4 Ma played a fundamental role in creating ecological opportunities for high species diversity, as seen in hominins and other mammals.

Of the four hominin species considered here, only *Paranthropus boisei* and *Homo erectus* occur in all three regions of the Omo-Turkana Basin (lower Omo Valley, East Turkana, West Turkana). Are their fossils more abundant because these species had larger population sizes in the early Pleistocene? Were *P. boisei* and *H. erectus* better established in the basin ecosystems than *H. habilis* and *H. rudolfensis*? What is the role of taphonomic factors in the preservation of some hominin species vs. others? Although questions of this nature have been explored elsewhere (Behrensmeyer, 1975, 1978, 1985; Bobe and Eck, 2001; Alemseged, 2003; Bobe and Behrensmeyer, 2004; Bobe and Leakey, 2009), a full analysis of hominin taphonomy in the context of the Omo-Turkana Basin remains a fertile topic for future research.

## Conclusions

The newly described *Paranthropus boisei* upper limb KNM-ER 47000 and the Ileret footprints attributed to *Homo erectus* from the Okote Member raise new questions about hominin diversity and adaptations at around 1.5 Ma. Here we show that the Okote hominins occurred in heterogeneous environments with extensive grasslands (including edaphic grasslands) and woodlands, and that these environments were highly dynamic, at least in part because of the effects of regional tectonics and volcanism. Assessment of paleosol stable isotopes and frequency of tephra deposition indicates that environmental variability was not limited to the Okote Member, but was a characteristic of the entire Omo-Turkana basin from at least 2 Ma to 1.4 Ma. Shortly after 2 Ma there is strong evidence of three or perhaps four hominin species in the Omo-Turkana Basin: *P. boisei*, *H. habilis*, *H. rudolfensis*, and *H. erectus* occur in the Upper Burgi and KBS members at East Turkana. Three of these species have also been documented from the Okote Member, but the LAD of *H. rudolfensis* in the KBS Member does not provide a high confidence level that this LAD corresponds to an extinction event, and the species may also have existed during the Okote Member times. We suggest that during the Okote Member times in particular, but more broadly in the time from 2 Ma to 1.4 Ma, environmental conditions in the Omo-Turkana Basin were highly variable both in time and space, and that this environmental variability would have facilitated a high diversity of mammalian taxa including hominins.

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## Figure captions

Figure 1. A: Map of the Omo-Turkana Basin including the lower Omo Valley of Ethiopia and the Lake Turkana Basin of Kenya. The Pliocene and Pleistocene Omo Group deposits include the Mursi, Usno, and Shungura formations in Ethiopia, and the Nachukui and Koobi Fora formations in Kenya. B: Satellite image (Google Earth) of the Ileret region in East Turkana showing the extent of paleontological collecting area 1A, the FwJj14E site, Il Eriet (seasonal river), the village of Ileret, and the location of the Turkana Basin Institute (TBI).

Figure 2. A: The Koobi Fora Formation in the context of the Omo Group deposits between 2.0 Ma and 1.2 Ma. This time interval includes the Upper Burgi, KBS, and Okote members of the Koobi Fora Formation, the Kalocho (upper), Kaitio, Natoo, and Nariokotome members of the Nachukui Formation, and members G (upper), H, J, K, and L of the Shungura Formation. The main dated tephras and their correlations within the Omo-Turkana Basin are highlighted. The ages of all tuffs are in Ma. The Geomagnetic Polarity Time Scale (GPTS) is shown next to the time axis. B: The Omo Group deposits were laid down by a major fluvio-lacustrine system relatively continuously from nearly 4.4 Ma to 1 Ma in the Omo-Turkana Basin. Major tephras provide a chronological framework and serve for correlations among different regions of the basin. The names of most members are indicated within the shaded rectangles; the names of key tephras are indicated to the right of the shaded rectangles, and the age of tephras in Ma are indicated to the left. The time span of major lacustrine intervals in the basin (from Feibel, 2011) is shown on the right of the figure.

Figure 3: Number of tephras in the Omo-Turkana Basin between 4.2 to 1.0 Ma. Data compiled and re-drawn from McDougall et al., 2012. Some of these tephras are airfall deposits from massive volcanic eruptions that likely produced major disruptions of regional ecosystems. One example of these thick volcanic deposits is the Chari Tuff, dating to 1.38 Ma and capping the Okote Member. Others tephras like the Okote Tuff Complex were fluvially deposited and reworked volcanic ashes that may have produce more localized and short-lived, but frequent, disruptions to the ecological systems of the Omo-Turkana Basin around 1.5 Ma.

Figure 4: Photo of the FwJj14E site in Area 1A with three tephras in an interval of less than 20,000 years. The *Paranthropus boisei* specimen KNM-ER 47000 and the series of hominin footprints derive from this part of the sequence measuring 8.5 m between the Lower Ileret Tuff and the Northern Ileret Tuff.

Figure 5: Paleosol stable carbon isotope values reflecting C<sub>3</sub> and C<sub>4</sub> vegetation in the Omo-Turkana Basin from 4.3 Ma to 1.0 Ma. These values derive from paleosols in the Omo Shungura Formation, the Nachukui Formation at West Turkana, and the Koobi Fora Formation at East Turkana. The vegetation categories of “Woodland”, “Wooded grassland”, and “Grassland” are derived from Cerling et al. 2011. The carbon isotope

values show that the basin underwent an important shift after 2 Ma, with values from the Omo becoming more similar to those elsewhere in the basin but the overall range of values in the basin becoming wider than they had been. Data from Quinn et al. 2007 and Levin et al. 2011.

Figure 6: The problem of first and last appearances in the fossil record. This figure illustrates the time range of a hypothetical species A (or taxon) from  $t_1$  to  $t_4$ . The terms First Appearance Datum (FAD =  $t_2$ ) and Last Appearance Datum (LAD =  $t_3$ ) refer to the earliest and the latest fossil records of the species, respectively. FADs almost always underestimate the true origin of a lineage. Likewise, LADs are almost always older than the true time of extinction of a lineage. “Nonfinds” are samples in which the species of interest was not found (fossil samples without species A in this figure). To place confidence intervals on FADs and LADs, we need to know the relative abundance of the species in the samples where it is found, and the abundance of the samples preceding and following the FAD and LAD. Thus, fossil “finds” can be as important as “nonfinds” in our understanding of the evolutionary history of a lineage

Figure 7: Frequency (modified NISP) of fossil mammal genera from the Okote Member in Area 1A at East Turkana. The three most abundant genera (*Kobus*, *Metridiochoerus*, and *Kolpochoerus*) had a  $C_4$  dominated diet, but  $C_3$  browsers like *Giraffa* and mixed feeders like *Hippopotamus* and *Tragelaphus* were also common. Specimens of aff. *Hippopotamus* are here included in *Hippopotamus*.

Figure 8: Time range of *Paranthropus* and *Homo* species in eastern Africa between 3 Ma and 1 Ma, with emphasis on the Omo-Turkana Basin. To the right of each time range bar there are selected hominin specimens with emphasis on those that constitute the first and last appearances of the species. For the 95% confidence intervals on species's FADs and LADs, see the Methods section. The green dashed box around 1.5 Ma corresponds to the time of the Okote Member.

Figure 9: Illustration of the four species of hominins that likely co-existed in the Omo-Turkana Basin after 2 Ma: *Paranthropus boisei* (KNM-ER 406), *Homo habilis* (KNM-ER 1813), *Homo rudolfensis* (KNM-ER 1470), and *Homo erectus* (KNM-ER 3733). Artwork by Vanessa Cannon.

Table 1

Table 1: Fossil mammal taxa and abundance (number of specimens) from the Okote Member of the Koobi Fora Formation

<b>Taxon</b>	<b>Number of specimens</b>
PRIMATES	
Hominini indet.	1
<i>Homo</i> indet.	1
<i>Homo erectus</i>	1
<i>Paranthropus boisei</i>	1
<i>Theropithecus oswaldi</i>	8
<i>Lophocebus</i> sp.	1
<i>Lophocebus</i> cf. <i>albigena</i>	1
CARNIVORA	
<i>Homotherium</i> sp.	1
<i>Panthera leo</i>	1
<i>Crocota</i> sp.	3
PERISSODACTYLA	
Equidae indet.	3
<i>Equus</i> sp.	3
<i>Hipparion</i> sp.	3
<i>Diceros</i> sp.	1
CERTARTIODACTYLA	
Bovidae indet.	20
<i>Tragelaphus</i> sp.	5
<i>Tragelaphus strepsiceros</i>	2
<i>Peloroavis oldowayensis</i>	5
<i>Peloroavis turkanensis</i>	2
<i>Aepyceros melampus</i>	4
Antilopini indet.	2
Reduncini indet.	18
<i>Kobus</i> sp.	10
<i>Kobus kob</i>	16
<i>Kobus sigmoidalis</i>	6
<i>Menelikia lyrocera</i>	1
Alcelaphini indet.	6
<i>Beatragus antiquus</i>	3
<i>Connochaetes gentryi</i>	1
<i>Damaliscus eppsi</i>	5
<i>Gazella</i> sp.	1
Giraffa indet.	4
<i>Giraffa jumae</i>	1
<i>Giraffa pygmaea</i>	1
<i>Sivatherium maurusium</i>	1
Hippopotamidae indet.	6
aff. <i>Hippopotamus aethiopicus</i>	5
<i>Hippopotamus gorgops</i>	1
Suidae indet.	2
<i>Kolpochoerus limnetes</i>	13
<i>Metridiochoerus compactus</i>	13
<i>Metridiochoerus andrewsi</i>	2
<i>Metridiochoerus hopwoodi</i>	1
PROBOSCIDEA	

Table 2

Table 2: Fossil hominin species across members of the Koobi Fora Formation at East Turkana, Kenya.<sup>a</sup>

Koobi Fora Formation						
	Upper Tulu Bor	Upper Burgi	KBS	Okote	Chari	Total
Hominini indet.	0	4	6	7	0	17
<i>Paranthropus boisei</i>	0	5	43	21	0	69
<i>Homo</i> indet.	1	26	29	11	0	67
<i>Homo habilis</i>	0	2	1	1	0	4
<i>Homo rudolfensis</i>	0	4	1	0	0	5
<i>Homo erectus</i>	0	4	9	11	0	24
Total hominins	1	45	89	51	0	186
Total larger mammals	132	1351	2089	978	8	4558
Abundance (%) of <i>Paranthropus</i>		0.37	2.06	2.15	0.00	1.51
Abundance (%) of <i>Homo habilis</i>		0.15	0.05	0.10	0.00	0.09
Abundance (%) of <i>Homo rudolfensis</i>		0.30	0.05	0.00	0.00	0.15
Abundance (%) of <i>Homo erectus</i>		0.30	0.43	1.12	0.00	0.53

<sup>a</sup>The table also provides the total number of larger mammals per member (excluding micromammals, i.e., Rodentia, Lagomorpha) as well as the relative abundance of hominin taxa as a percentage of the fauna.

Table 3

Table 3: Fossil hominin species across members of the Nachukui Formation at West Turkana, Kenya. <sup>a</sup>

Nachukui Formation								
	L. Lomekwi	U. Lomekwi	Lokalalei	Kalochoro	Kaitio	Natoo	Nariokotome	Total
Hominidae indet.	8	0	0	0	0	0	0	8
<i>Australopithecus</i> indet.	1	0	0	0	0	0	0	1
cf. <i>Kenyanthropus platyops</i>	29	0	0	0	0	0	0	29
<i>Kenyanthropus platyops</i>	2	0	0	0	0	0	0	2
<i>Paranthropus aethiopicus</i>	0	3	2	0	0	0	0	5
<i>Paranthropus boisei</i>	0	0	0	1	7	0	0	8
<i>Homo</i> indet.	0	0	0	1	0	0	0	1
<i>Homo erectus</i>	0	0	0	0	1	4	1	6
Total hominins	40	3	2	2	8	4	1	20
Total larger mammals	567	277	72	188	198	190	87	1012
Abundance (%) of <i>Paranthropus</i>		1.08	2.78	0.53	3.54	0.00	0.00	0.79
Abundance (%) of <i>Homo erectus</i>					0.51	2.11	1.15	0.59

<sup>a</sup>The table also provides the total number of larger mammals per member (excluding micromammals, i.e. Rodentia, Lagomorpha) as well as the relative abundance of hominin taxa as a percentage of the fauna.

Table 4

Shungura Formation

	B	C	D	E	F	G(L)	G(U)	H	J	K	L	Total
Hominidae sp.	13	25	13	10	28	37	0	1	0	0	0	114
<i>Australopithecus</i> indet.	8	9	0	0	0	0	0	0	0	0	0	9
<i>Paranthropus aethiopicus</i>	0	6	4	16	20	0	0	0	0	0	0	46
<i>Paranthropus boisei</i>	0	0	0	0	0	14	0	0	0	1	0	15
aff. <i>Homo</i> sp.	0	0	0	4	13	3	0	0	0	0	0	20
<i>Homo</i> indet.	0	0	0	0	0	1	0	0	0	0	1	2
<i>Homo</i> cf. <i>habilis</i>	0	0	0	0	0	7	0	1	0	0	0	8
<i>Homo habilis</i>	0	0	0	0	0	0	1	0	0	0	0	1
<i>Homo erectus</i>	0	0	0	0	0	0	0	0	0	1	0	1
Total hominids	21	40	17	30	61	62	1	2	0	2	1	216
Total larger mammals	2754	6406	1420	3660	6520	15250	1811	1130	352	671	750	37220
Abundance (%) of <i>Paranthropus</i>	0.09	0.28	0.44	0.31	0.09	0.00	0.00	0.00	0.00	0.15	0.00	0.16
Abundance (%) of <i>Homo habilis</i>							0.06	0.00	0.00	0.00	0.00	0.00
Abundance (%) of <i>Homo erectus</i>										0.15	0.00	0.003
Abundance (%) of <i>Homo</i> <sup>b</sup>				0.11	0.20	0.07	0.06	0.09	0.00	0.15	0.13	0.09

<sup>a</sup>The table also provides the total number of larger mammals per member (excluding micromammals, i.e., Rodentia, L

<sup>b</sup> aff. *Homo*, *Homo* indet. *H.* cf. *habilis*, *H. habilis*, *H. erectus*

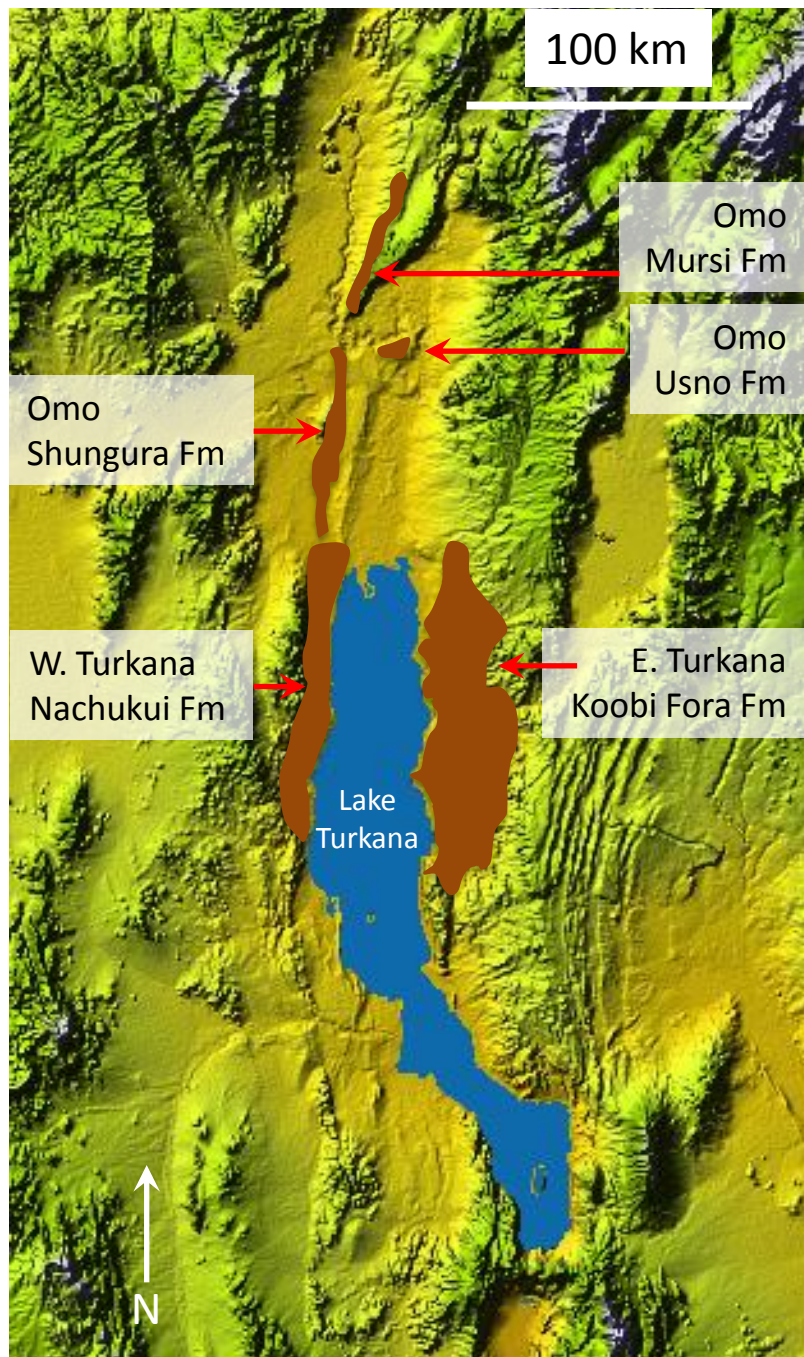
Table 5

	<i>P. aethiopicus</i>	<i>P. boisei</i>	<i>H. habilis</i>	<i>H. rudolfensis</i>	<i>H. erectus</i>
Regional FAD in Ma	2.7	2.3	1.9	2.03	1.9
Global FAD in Ma	2.7	2.3	1.9	2.4	1.9
Regional LAD in Ma	2.3	1.4	1.4	1.85	0.9
Global LAD in Ma	2.3	1.34	1.4	1.8	0.75
Species abundance (n)	51	92	5	5	31
Mammalian abundance (m)	18355	24018	8958	7119	9615
Relative abundance = n/m	0.0028	0.0038	0.0006	0.0007	0.0032
r1 = sample size first interval preceding FAD	446		15454	15454	15454
Pi = 1 – (1 – n/m)r	0.7109		0.9998	1.0000	1.0000
r2 = cummulative sample size adding second interval preceding FAD	3200				
Pi = 1 – (1 – n/m)r	0.9999				
r1 = sample size first interval following LAD		845	845	1839	
Pi = 1 – (1 – n/m)r		0.9610	0.3761	0.7253	
r2 = cummulative sample size adding second interval following LAD				2684	
Pi = 1 – (1 – n/m)r				0.8483	



# Figure 1

A.



B.

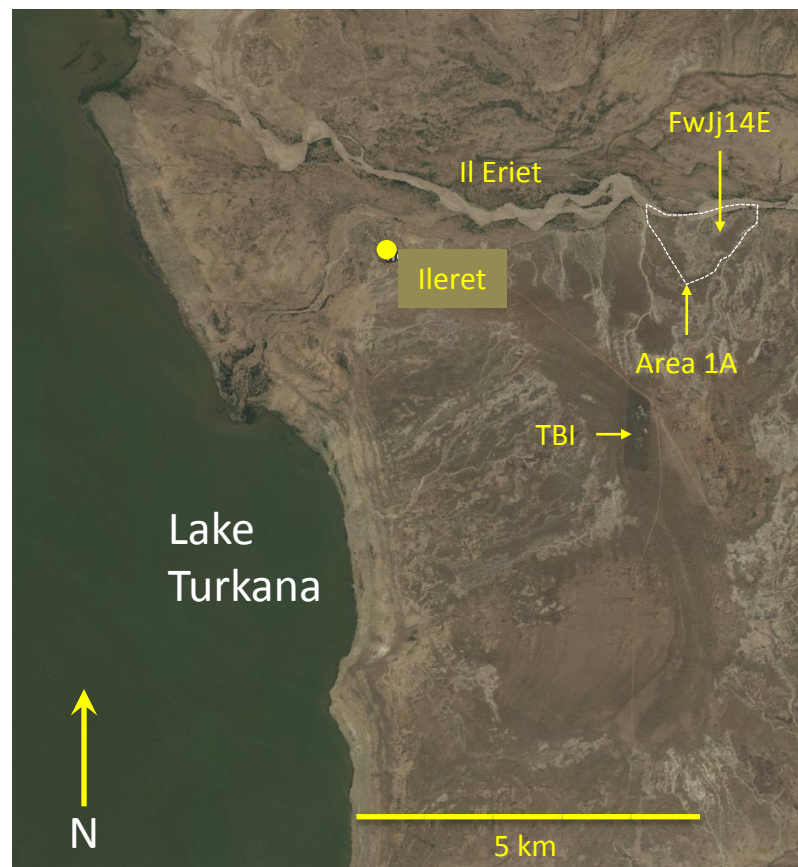


Figure 2A

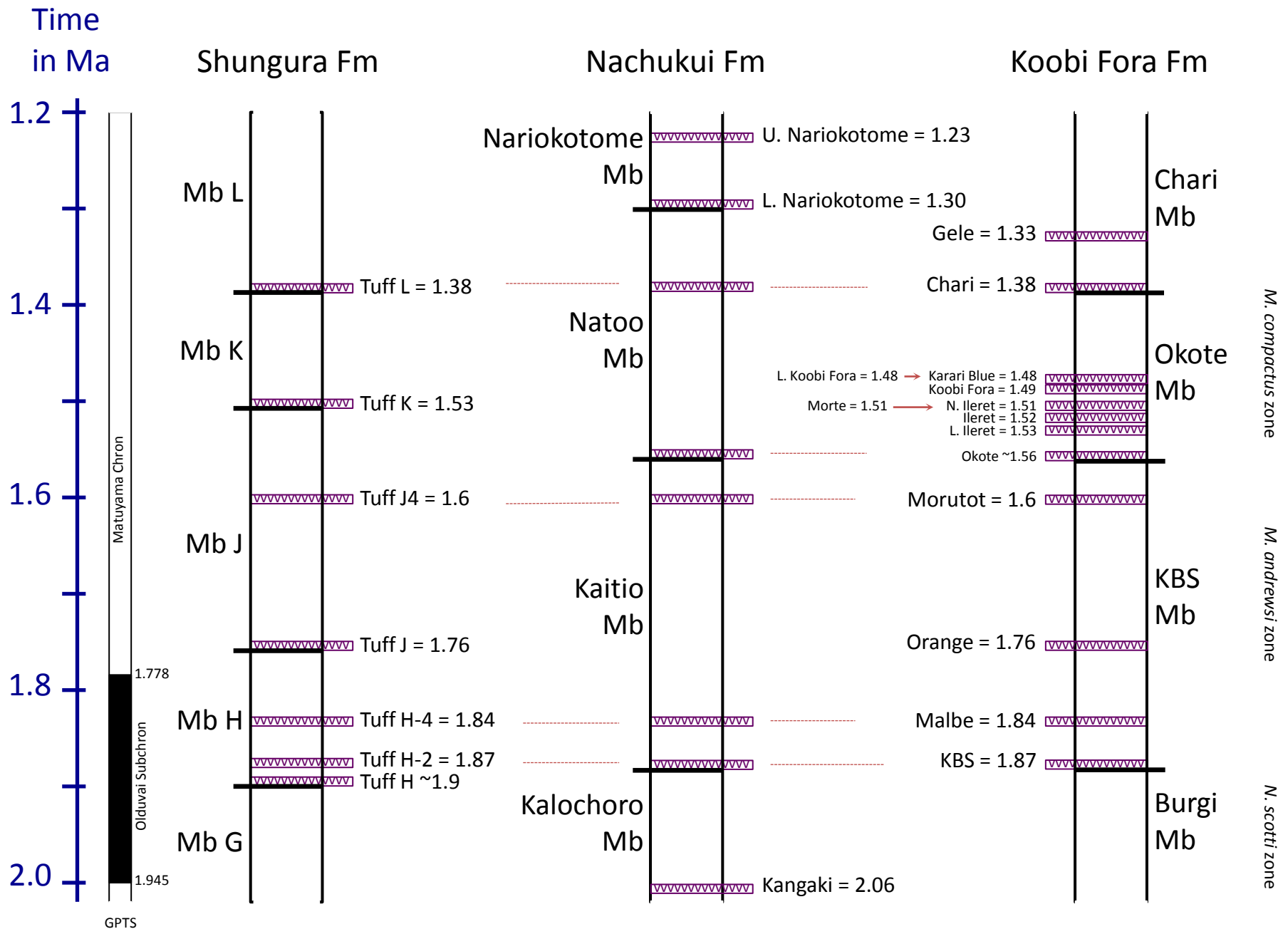


Figure 2B

Time in

Ma

0

1

2

3

4

5

Omo

West Turkana

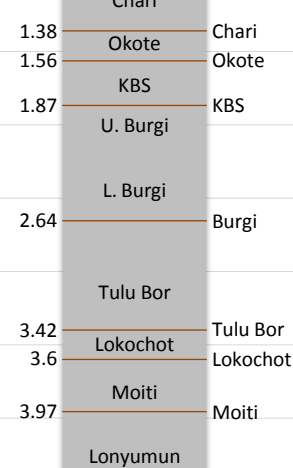
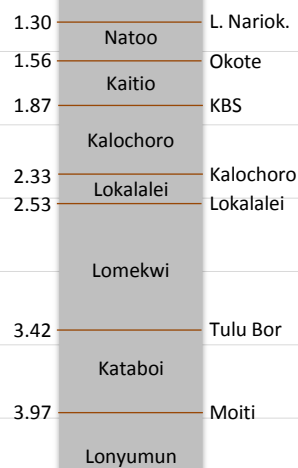
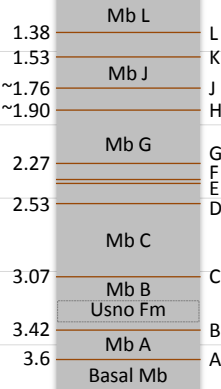
East Turkana

Major lakes

Shungura Fm

Nachukui Fm

Koobi Fora Fm



Lake Turkana

Lorenyang Lake

Lokochot Lake

Lonyumun Lake

Figure 3

# Number of tephras in the Omo-Turkana Basin between 4.2 Ma and 1.0 Ma

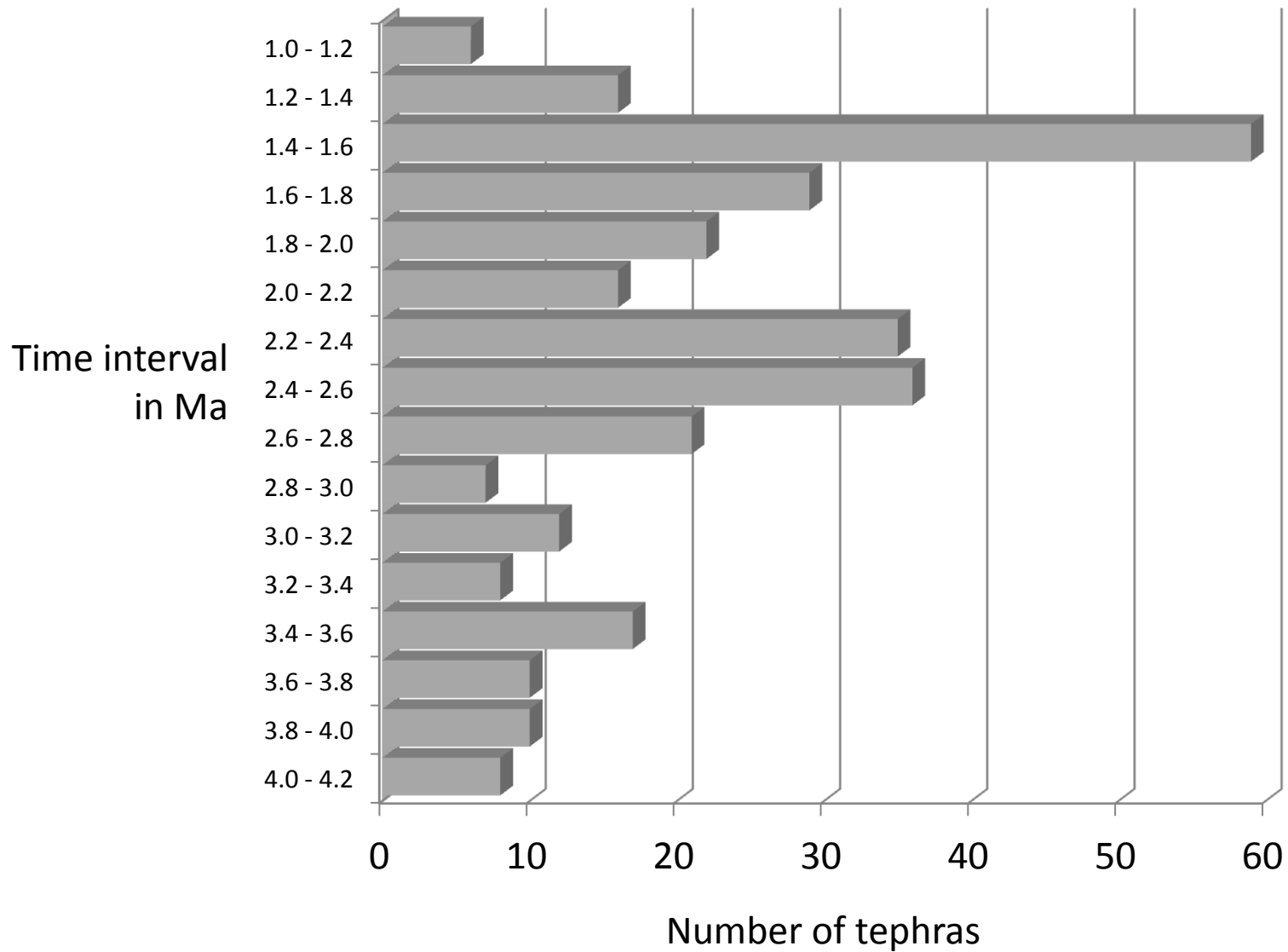




Figure 4



Northern Ileret Tuff 1.51-1.52 +/- 0.01 Ma

Ileret Tuff 1.52 +/- 0.01 Ma

← Hominin trackways

Hominin trackways

Lower Ileret Tuff 1.53 +/- 0.01 Ma

Figure 5

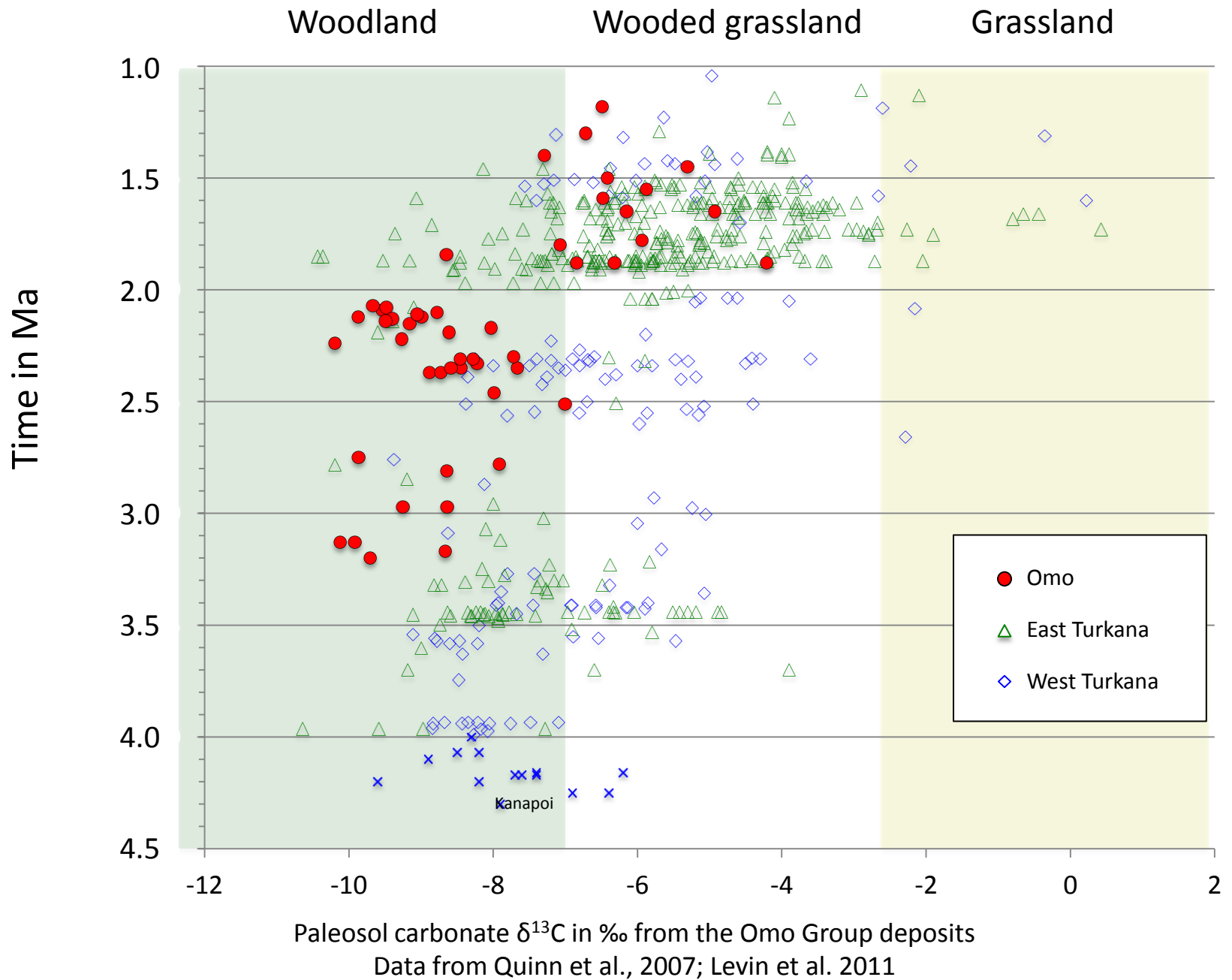


Figure 6

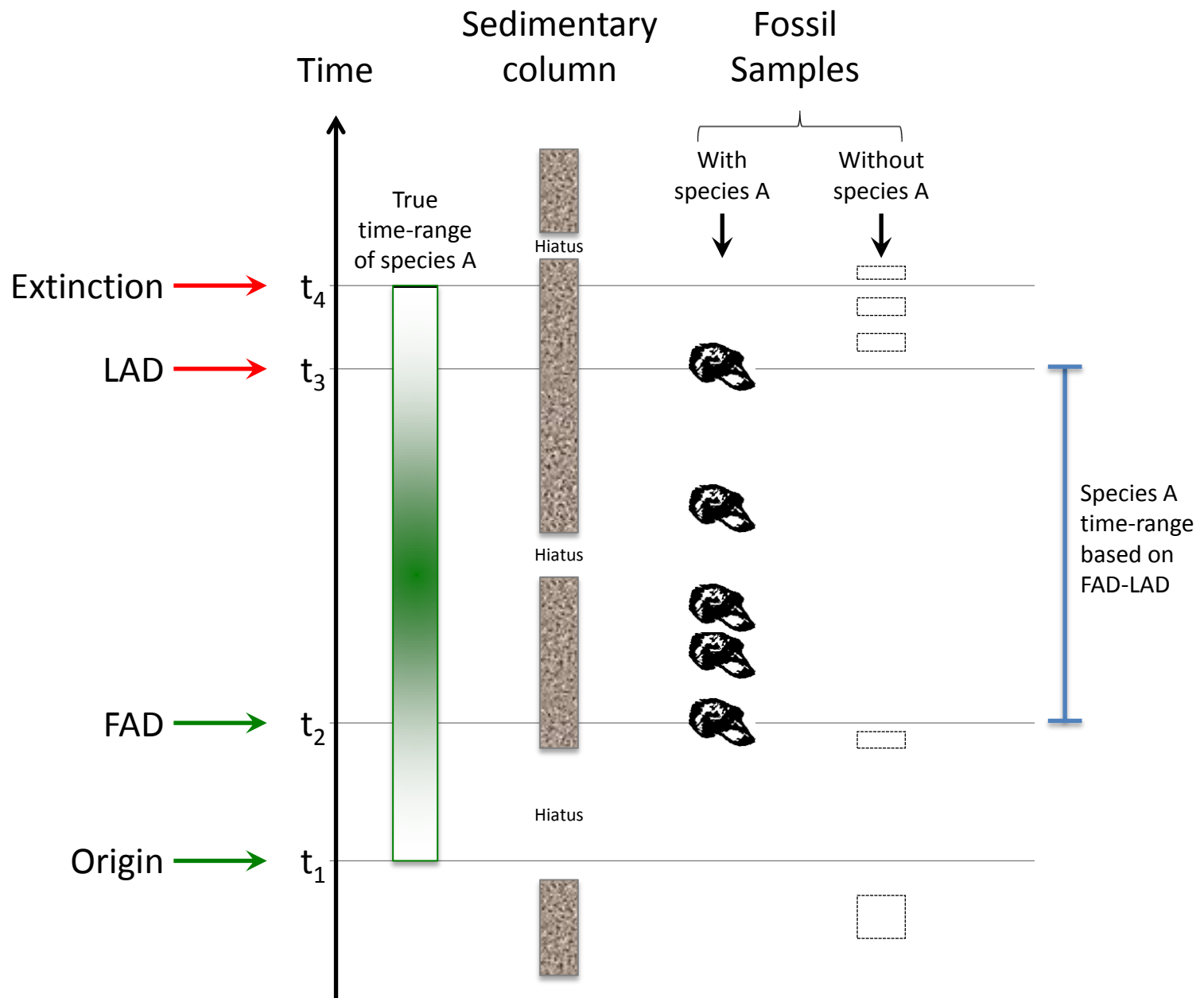


Figure 7



Genera of mammals from Okote Mb Area 1A

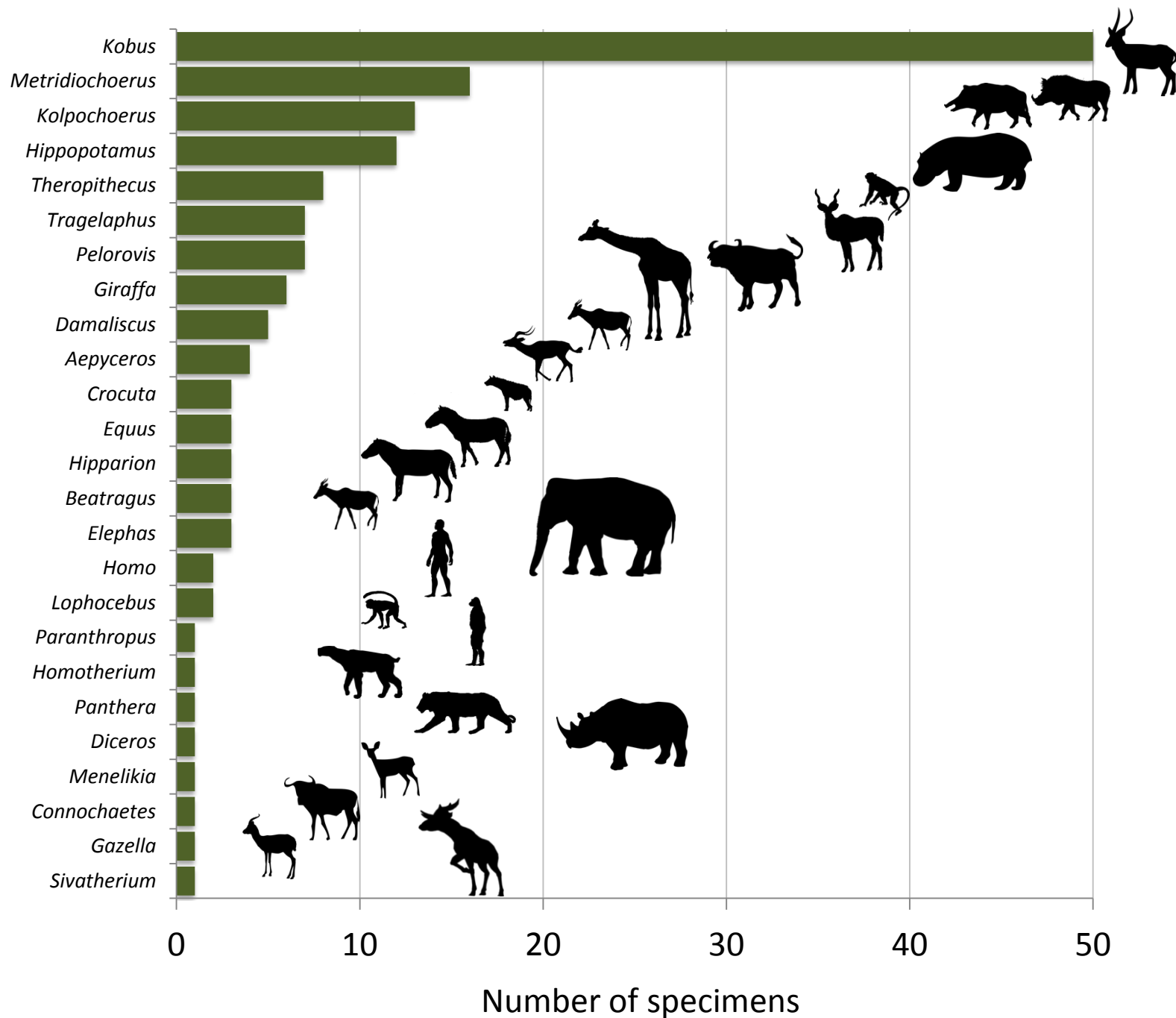




Figure 8

Time in Ma

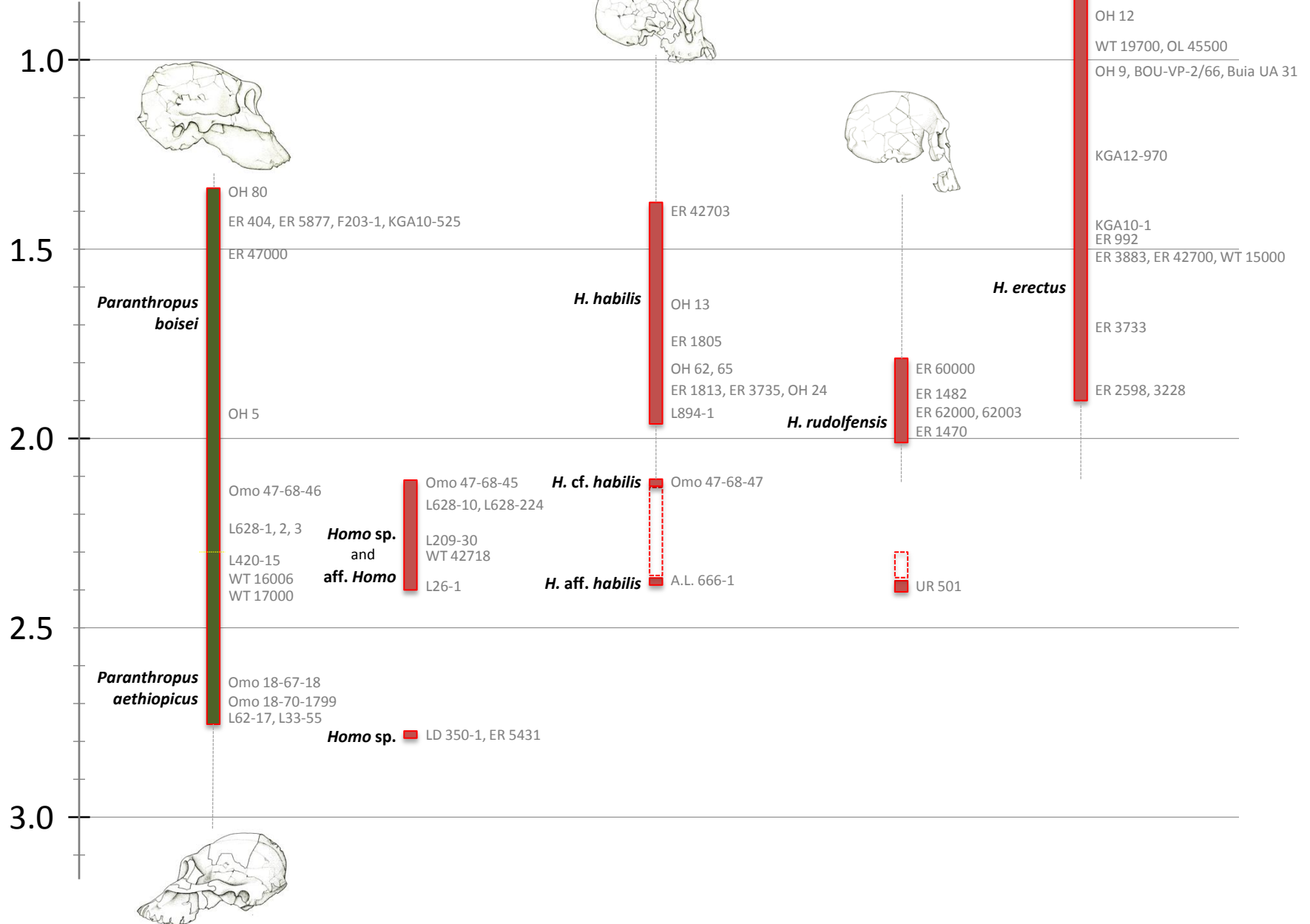
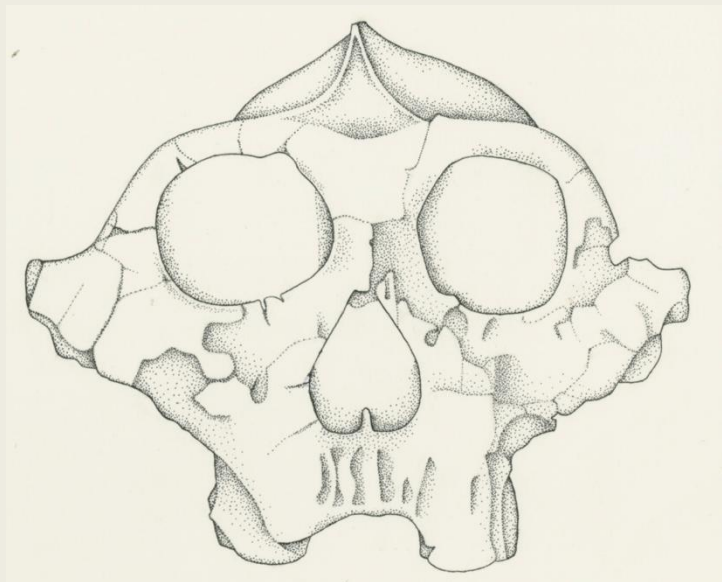
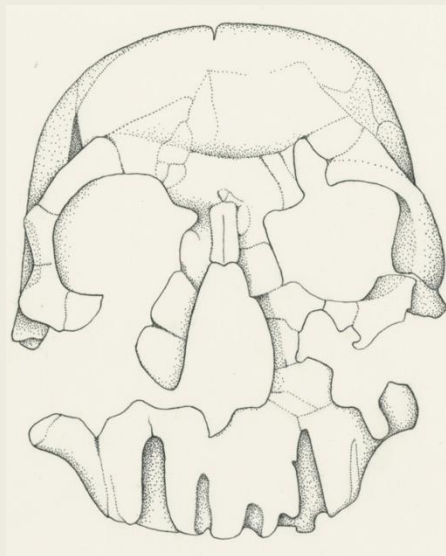


Figure 9

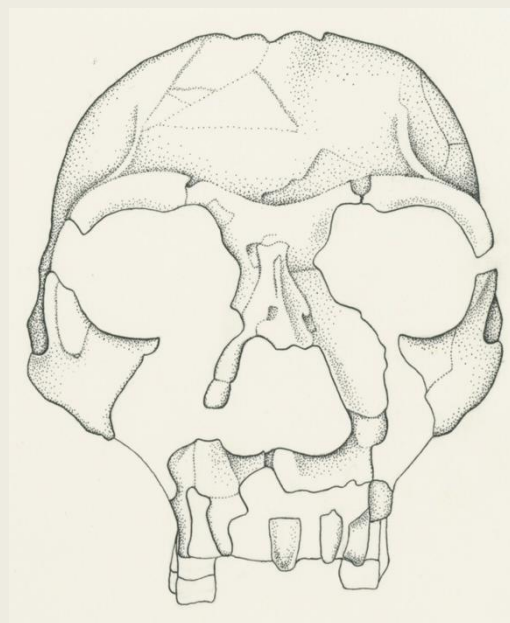
KNM-ER 406



KNM-ER 1470



KNM-ER 3733



KNM-ER 1813

