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Paleoecology of the Serengeti during the Oldowan-Acheulean transition at Olduvai Gorge, Tanzania : The mammal and fish evidence

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Abstract: Eight years of excavation work by the Olduvai Geochronology and Archaeology Project (OGAP) has produced abundant remains of a rich vertebrate fauna from several sites within and just below Middle Bed II, Olduvai Gorge, Tanzania. Study of these as well as the recently re-organized collections from Mary Leakey's 1972 HWK EE excavations here provides a synthetic view of the faunal community of Olduvai at 1.7-c.1.4 Ma. We expand the faunal list for this interval, including naming a new bovid species, clarify of the evolution of several mammalian lineages, and record new local first and last appearances. Compositions of the fish and large mammal assemblages support previous indications for the dominance of open and seasonal grassland habitats at the margins of paleo-Lake Olduvai. The mammals are mainly dominated by grazing bovids (alcelaphins) and equids, and the taphonomy of the fish assemblages supports reconstructions of fluctuating lake levels with mass die-offs in evaporating pools. No major turnover or paleoecological changes seem to be associated with the transition from Oldowan to Acheulean stone tool technologies within Middle Bed II.

Community profiles show that the Middle Bed II large mammal community is much more species-rich and includes a larger number of large-bodied species (> 100 kg) than its modern Serengeti analog. By comparison, extant Serengeti fits the profile of a 'downsized' community, similar to those that have been defaunated by human disturbance rather than by climate change alone. Despite these fundamental differences, trophic network analyses show that the Middle Bed II and extant Serengeti communities bear similar structural properties as concerns the distribution of feeding links among predator and prey species. The presence of a generalized hominin predator increases competition among carnivores and vulnerability among herbivores, but both the paleo- and extant webs include highly generalized predators that are highly resistant to the effects of herbivore extinctions. Both climatic and human-induced hypotheses for the loss of African Pleistocene large mammals require further testing.

Large Mammals and Fish from the Oldowan-Acheulean Transition at Olduvai Gorge, Tanzania, and the Paleoeecology of the Serengeti

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Abstract

Eight years of excavation work by the Olduvai Geochronology and Archaeology Project (OGAP) has produced abundant remains of a rich vertebrate fauna from several sites within and just below Middle Bed II, Olduvai Gorge, Tanzania. Study of these as well as the recently re-organized collections from Mary Leakey's 1972 HWK EE excavations here provides a synthetic view of the faunal community of Olduvai at 1.7-c.1.4 Ma. We expand the faunal list for this interval, including naming a new bovid species, clarify of the evolution of several mammalian lineages, and record new local first and last appearances. Compositions of the fish and large mammal assemblages support previous indications for the dominance of open and seasonal grassland habitats at the margins of paleo-Lake Olduvai. The mammals are mainly dominated by grazing bovids (alcelaphins) and equids, and the taphonomy of the fish assemblages supports reconstructions of fluctuating lake levels with mass die-offs in evaporating pools. No major turnover or paleoecological changes seem to be associated with the transition from Oldowan to Acheulean stone tool technologies within Middle Bed II.

Community profiles show that the Middle Bed II large mammal community is much more species-rich and includes a larger number of large-bodied species (> 100 kg) than its modern Serengeti analog. By comparison, extant Serengeti fits the profile of a 'downsized' community, similar to those that have been defaunated by human disturbance rather than by climate change alone. Despite these fundamental differences, trophic network analyses show that the Middle Bed II and extant Serengeti communities bear similar structural properties as concerns the distribution of feeding links among predator and prey species. The presence of a generalized hominin predator increases competition among carnivores and vulnerability among herbivores, but both the paleo- and extant webs include highly generalized predators that are highly resistant to the effects of herbivore extinctions. Both climatic and human-induced hypotheses for the loss of African Pleistocene large mammals require further testing.

Introduction

Fieldwork by the Olduvai Geochronology and Archaeology Project (OGAP) since 2008 has produced a large vertebrate fauna from Middle Bed II at Olduvai Gorge, Tanzania. The Olduvai fossil fauna, particularly the large mammals of Bed I, are well known from previous collections, mainly from excavations led by Hans Reck and then Louis and Mary Leakey (reviewed in Leakey, 1978).

The main fossiliferous beds at Olduvai are numbered from Bed I to IV (Fig. 1), from oldest to youngest, following the original stratigraphy developed by Hans Reck (e.g. in Leakey, 1951). Geological work over the last 100 years has clarified the chronostratigraphy at Olduvai. Bed I is the best constrained level, dated to 2.038-1.803 Ma (Deino, 2012), and is divided into Lower, Middle, and Upper units. Bed II is also divided into Lower, Middle, and Upper units (Leakey, 1971a), but dating is not as precise as for Bed I. The Bed II fauna has sometimes been treated as a single assemblage though the presence of at least several depositional hiatuses (unconformities) means that Bed II could span some 600,000 years (1.8-1.2 Ma, McHenry et al., 2016). Leakey (1971a) placed the boundary between Lower and Middle Bed II at the top of Tuff IIA, but Hay (1976b) later formally defined the Lemuta Member, of which Tuff IIA is just the middle of three 'tongues' of eolian tuffaceous sediment to the east. Following de la Torre et al. (this volume "New Excavations at the HWK EE" site; also Stanistreet et al, in prep, this volume "Stratigraphy of Middle Bed II") the disconformity at the bottom of the Lower Augitic Sandstone is now proposed as the boundary between Lower and Middle Bed II. Tuff IIC defines the boundary between Middle and Upper Bed II (Fig. 1). Tuff IIA, often found just below the Lower Augitic Sandstone, is dated to 1.71 Ma (Curtis and Hay, 1972). The Bird Print Tuff (BPT), found slightly above Tuff IIB, is correlated with a tuff dated to 1.664 Ma (Diez-Martín et al., 2015) (also McHenry and Deino, in prep, this volume "Tephrochnology of Middle Bed II"). Tuff IIC is not dated. Tuff IID is around 1.34 Ma in age (Domínguez-Rodrigo et al., 2013).

This article presents the large mammals and fish from new Bed II collections recovered by OGAP as well as the large collections from Mary Leakey's 1972 excavations of the HWK-EE site. The redefinition of the Lower-Middle Bed II boundary means a few specimens from lowermost Middle Bed II are now technically reassigned to the top of Lower Bed II. However, for convenience, we here continue to use the term 'Middle Bed II' to refer to the entire faunal assemblage between Tuffs IIA and IIC, compatible with previous studies. A small number of specimens from EF-HR and FLK West, which derive from Upper Bed II (above Tuff IIC), are also covered here.

It is common at Olduvai to find all four Beds exposed within close proximity at a single outcrop (Leakey, 1951). At site FLK, for example, Beds I-IV are all exposed within a section of about 60 m, and some sites have beds within even closer spacing. This naturally raises the concern that some of surface material collected at Olduvai, in particular many of the surface specimens collected by Reck and Louis Leakey, may be of uncertain stratigraphic origin. The new OGAP collections, along with those of Mary Leakey from HWK EE, provide an opportunity for the close examination of the large mammal community of Bed II using samples excavated *in situ* from well-controlled archeological contexts and within a newly developed geochronological scheme.

A central question within this time frame is whether the transition from Oldowan to Acheulean technology, and the accompanying emergence of *Homo erectus*, was driven by environmental changes. At Olduvai, these changes took place during Middle Bed II time, specifically before and after Tuff IIB (~ 1.66 Ma). The time interval documented by Middle Bed II covers the end of a 200,000 year-long phase of high moisture availability in eastern Africa, and a large reduction in the level of Lake Olduvai (Ashley, 2007; Barboni, 2014). Stable isotope data from both paleosols and fossil enamel of this age show increasing $d^{18}O$ values, documenting the appearance of drier conditions around this time (Cerling and Hay, 1986; Cerling et al., 1977)(also Uno et al, in prep, this volume).

Assemblages of similar age to the main Bed II fauna described here within eastern Africa are those from Interval 2-3 at Konso in Ethiopia (Suwa et al., 2003), Member J (1.76-1.53 Ma) of the Shungura Formation in the Lower Omo Valley, Ethiopia, and the upper part of the KBS Member (1.87-1.56 Ma) of the Koobi Fora Formation in East Turkana (dates from McDougall and Brown, 2006; McDougall et al., 2012).

We first describe the fauna and then reconstruct aspects of the paleoecology in Middle Bed II times. We assess and describe several community parameters including extinction patterns and analyze the Bed II large mammal community in comparison with the savanna fauna of the extant Serengeti including a trophic network analysis to describe the properties of the Olduvai Bed II large mammal food web, and the role that early hominins might have played in it.

Methods

All fossil specimens described here are housed at the Research Laboratory at Olduvai Gorge, Tanzania.

All anatomical and taxonomic identifications as well as metrics for teeth are given in Supplemental Table 1.

Only the most significant specimens are referred to here in the text.

OGAP specimens are numbered as follows: SITE TRENCH-LEVEL-SPECIMEN. For example, MNK T5-L10-2265 refers to site MNK, trench 5, level 10, specimen number 2265. Trenches are numbered consecutively across all sites, but each trench has its own level numbering system, and each level of each trench assigns a consecutive unique ID number (starting at 1) to each specimen. In the case of fossils from MNK Main and MNK Skull [named as such by Mary Leakey (1971)], an M and an S respectively follow the locality, before level and specimen number (e.g. MNK M-L6B-151 stands for locality MNK, Main site, archaeological unit L6B, specimen number 151). Accession codes (and specimen labels) at the main trenches at HWK EE and EF-HR do not include a trench number (e.g. HWK EE L2-395 refers to site HWK EE, main trench, level 2, specimen number 395). In this manuscript, we include an M for the main trenches at EF-HR and HWK EE, to avoid any confusion (e.g. HWK EE M-L2-395). Specimens collected by Mary Leakey's excavations at HWK EE are prefixed with HWK EE 1972, and then a specimen number. A few of Leakey's specimens from HWK EE were not originally given specimen numbers, and so they are here referred to by OGAP barcode consecutive numbers. Specimens housed at the Natural History Museum in London have the letter M prefixed with NHM (not to be confused with a 'main trench' designation).

Counts for relative abundance analyses of bovid tribes were taken on craniodental specimens only (isolated teeth, mandibles, maxillae) in order to minimize counting biases from differential preservation and identification of anatomical elements across taxa. Three comparisons of Bed I and II assemblages were made: 1, using dental specimens counts of Middle Bed II assemblages (IIA, IIB), and Upper Bed II from the OGAP & HWK EE 1972 specimens and of Bed I bovids from the literature (through the CODI database by Hlusko and Njau, olduvai-paleo.org, accessed August 2016); 2, number of individual specimen (NISP) counts for Beds I and II and from tables in Kappelman (1984); and 3, minimum number of individual (MNI) counts from Shipman and Harris (1988). The CODI, NISP, and MNI data are ultimately sourced mainly from Gentry & Gentry (1978a, c). Abundance data for large mammals for body size distribution and food web analyses were based on the same dental specimen counts and considered only mammals larger than 15 kg (herbivores) and 20 kg (carnivores). Taxa that were not definitely identified in the current collections, but were previously recorded from Middle Bed II (e.g. *Homo habilis*, *Diceros bicornis*) were given abundance counts of 1. Hippopotamids, being semiaquatic, are preferentially fossilized relative to other fully terrestrial large mammals, and although *H. gorgops* is well represented in Middle Bed II, its abundance was set to 1.

Adult body mass ranges for extant taxa were taken from the literature (e.g. Kingdon, 1997). Mass estimates for fossils were calculated using either metric (usually dental) regressions (Janis, 1990) and $\pm 50\%$ to create a minimum-maximum adult size range (e.g. fossil bovids in Bibi and Kiessling, 2015), or by

approximation to a similarly-sized extant relative (e.g. *Equus oldowayensis* and *E. grevyi*, *Giraffa jumae* and *G. camelopardalis*). For an approximation of young or neonate mass, we simply used 10% of the minimum adult body mass value (Supplementary File 2).

All alcelaphin upper and lower third molar lengths were analyzed in a combined cluster analysis to help assign specimens to size categories. This was performed in SAS JMP 11 using the Ward, and 'missing value imputation' options. The resulting classification was visually assessed with reference to the actual measurement data and to specimens of known taxonomic affinity (namely *Megalotragus isaaci* and the small alcelaphin species). Results are given in the 'Alcelaphini indet. (teeth)' section. For the body size and community abundance analyses, we divided all Alcelaphini teeth in the OGAP collection (n=268) according to the ratios found by the third molar classification analysis (48 for *M. isaaci*, 180 among two *Parmularius* spp. and *Damaliscus niro*, and 40 for the small alcelaphin).

For trophic network (food web) analyses, predator species were assigned a preferred prey body size range based on analogy with their nearest living relative, including assumptions about possibilities for group hunting (which allows for larger prey capture). The Bed II hominin (*H. habilis* in lower Middle Bed II, possibly *H. erectus* in upper Middle Bed II, in addition to *A. boisei*) was modeled as a single taxon with the properties of a generalist predator with a wide range of prey (e.g. Ungar et al., 2006). We did not differentiate between different modes of predation (e.g. hunting, scavenging, kleptoparasitism). Species data for Serengeti was taken from a recent census by the Tanzania Wildlife Research Institute (TAWIRI, 2010).

Trophic links between predator and prey species were assigned based on body size preferences (e.g. Nenzén et al., 2014), including allowing predators to prey upon neonates of large species when they fit into their preferred body-size ranges. We assume that prey availability is an additional determinant of the strength of interactions and we used prey abundance to weight trophic links. Abundance was calculated using the number of dental specimens for fossil data (as above) and from census data for Serengeti.

We calculated the following 10 food web metrics using the bipartite R package (Dormann et al., 2008; R_Core_Team, 2014):

- *Connectance*: the number of realized links / number of potential links in the food web.
- *Links per species*: mean number of links per species.
- *linkage density*: (vulnerability + generality) / 2 (see below)
- *Degree distribution*: distribution of links per species. We distinguish out-degree (predators) and in-degree distributions (prey).
- *Nestedness*: From 0 (high nestedness) to 100 (chaos) (Rodríguez-Gironés and Santamaría, 2006).

- *Weighted nestedness*: like nestedness but takes into account the strength of the interactions. From 1 (high nestedness) to 0 (chaos) (Galeano et al., 2009).
- *Generality*: Weighted mean effective number of prey species per predator.
- *Vulnerability*: Weighted mean effective number of predators per prey species (apparent competition) (Bersier et al., 2002; Tylianakis et al., 2007).
- *Niche overlap*: Horn's (1966) index.
- *Predator-prey ratio*: number of predators / number of prey species.

In order to explore the role of early *Homo* sp. in its food web, we calculated the structure of the Olduvai Bed II food web (as per above) removing one carnivore species at a time. We used the results as a null model against which to compare the effect that *Homo* had on the structure of the food web. We also ran three simulations removing herbivore species one at a time in order to examine the robustness of each web to extinction. This was done based on prey abundances (rare species disappearing first), based on vulnerability (prey with more predators disappearing first), and randomly. We used the R package bipartite (Dormann et al., 2008) to calculate the number of secondary extinctions that occurred when species were removed from the food web (function 'secondary extinction') and to calculate the area below the secondary extinction curve ('robustness').

Systematic paleontology of the large mammals

All specimen numbers, anatomical and taxonomic determinations, as well as dental metrics, are given in Supplemental Table 1. Only the most significant specimens are referred to here in the text.

ARTIODACTYLA Owen, 1841

Bovidae Gray, 1821

Bovini Gray, 1821

Pelorovis Reck, 1925

Pelorovis oldowayensis Reck, 1928

Description – A few teeth of Bovini, mostly isolated upper molars. *Pelorovis oldowayensis* has larger teeth than fossil and extant *Syncerus* (Gentry and Gentry, 1978a fig. 8), with the exception of *S. antiquus*, which is not known from Olduvai. The OGAP bovin teeth are on average larger than those of extant *S. caffer*, and

within the range of *Pelorovis* (upper molars consistently longer than 30mm). The best specimen is HWK EE T27-L31-28, a right maxillary fragment with M2-3 (Fig 2A). It is estimated to have had an M1-3 length of about 100 mm, which is within the range of previously reported remains of *P. oldowayensis* from Olduvai Bed II (Gentry, 1967 fig. 9; Gentry and Gentry, 1978a fig. 8).

Discussion – Both *Syncerus acoelotus* and *Pelorovis oldowayensis* have been previously recorded from Middle Bed II (Gentry and Gentry, 1978b), but the former is much less common, and appears not to be represented in the new OGAP collections.

Tragelaphini Blyth, 1863

A few specimens representing the greater kudu and possibly an eland. Gentry & Gentry (1978a) mention a distal tibia of a bushbuck-sized tragelaphin from SHK (Middle Bed II). There is no evidence for a small tragelaphin in the current collections.

Tragelaphus de Blainville, 1816

Tragelaphus strepsiceros (Pallas, 1766)

Description – Tragelaphin dental specimens referred to *T. strepsiceros* on the basis of their size, which is large and within the range of the extant species. HWK EE 1972-3916 is a right maxillary fragment with M2-3 (Fig. 2C). Two lower p4s (MNK M-L1-179, MNK T5-L10-44) have a fused metaconid-paraconid (closed lingual wall). Specimen HWK EE 1972-3916 (M2 and M3 length c 22 mm each) falls among smaller individuals of extant *T. strepsiceros*. In contrast, five lower premolar specimens from MNK (measuring ~18-21 mm in length) are at the larger end of extant *T. strepsiceros*, or the smaller end of extant *T. oryx*.

Discussion – Fossil greater kudu specimens are already well known from Olduvai. Gentry & Gentry (1978b) follow Leakey (1967) in recognizing two subspecies: *T. s. maryanus*, present in Bed I-early Middle Bed II, and *T. s. grandis*, from Middle Bed II to Bed IV. The latter was diagnosed as having slightly larger size than extant individuals.

cf. *Tragelaphus (Taurotragus)* (Wagner, 1855)

Description – MNK T5-L10-2124 (Fig. 2B) is the distal half of a left upper M3 that is very large, but too high-crowned, straight-walled (not bulbous), and with an outer surface too smooth to belong to a giraffid. It lacks the hypsodonty, rounded cusps, basal pillars, projecting ribs, and convoluted enamel ridges of Bovini. Mesodonty, pointed lingual cusps, projecting styles, and simple enamel cavities match tragelaphin morphology. Preserved tooth width is 24 mm, and length when complete is estimated to have been about 35-40 mm (20 mm is preserved). This would put this specimen within the range of a large extant individual of *T. oryx*.

Discussion – Eland are tragelaphins distinguished by their large size and tightly spiraled horns. Previously placed in the genus *Taurotragus*, molecular phylogenetic work has shown that the two extant species belong within the *Tragelaphus* clade, but *Taurotragus* may be retained as a subgenus. Ecologically, eland differ from other tragelaphins in venturing into open grassland habitats. Especially during the wet season, they may frequently be found alongside grazers such as wildebeest and zebra, though their diets remain centered around browse and herbs (Cerling et al., 2003; Kingdon, 1982). Enamel $\delta^{13}\text{C}$ from MNK T5-L10-2124 was measured at -2.8‰ which indicates a diet dominated by C₄ (grass) biomass (Uno et al. this volume). Such a high intake of grass contrasts with the measured diets of extant tragelaphins, but is not uncommon in the Pliocene and Pleistocene (Bibi et al., 2013; Cerling et al., 2015).

Early Pleistocene eland fossils are rare. Previously, the oldest record from Olduvai was a single surface find from Upper Bed II (NHM M 29415, partial right horn core from BK, Gentry and Gentry, 1978a). The molar fragment described here, found in situ at MNK, suggests the occurrence of *T. (Taurotragus)* in Middle Bed II times.

Alcelaphini Rochebrune, 1883

Alcelaphins constitute the most abundant bovid tribe at Olduvai, and Middle Bed II is no exception. Horn core and dental remains indicate the presence of at least six species, which is impressive considering that no more than three occur sympatrically in Africa today. Most notable are the presence of a very small species only slightly larger than a Thomson's gazelle and a massive species larger than a wildebeest (*Megalotragus isaaci*).

Parmularius Hopwood, 1934

Parmularius angusticornis (Schwarz, 1937)

Description – The most abundant alcelaphin species in Middle Bed II, represented by numerous horn cores and partial crania (Fig. 3A-B). Long horns with wide bases, arising with low (20°) divergence basally in anterior view, then diverging more strongly (40°) slightly above the base. In side view relatively straight but with clear undulation, then with posterior recurving of the tips. No torsion. Base with no compression or weak mediolateral compression, with posteromedial basal swelling present. Base lowest posterolaterally, highest medially; medial surface less convex than lateral surface, some flattening of posterolateral surface. Weak transverse ridges present midway and distally. Long and wide postcornual groove. Braincase with strong temporal musculature forming a depression on dorsal parietals and a raised area at the midline, which is not a true parietal boss, as in *Damaliscus*, but a raised surface defined by the surrounding temporal musculature. Strong median nuchal crest present. Occipital in posterior view has a rounded triangular outline. Wide mastoids. Frontoparietal suture anteriorly indented. Basioccipital with long and thick ridges connecting posterior and anterior tuberosities, these having a thin ventral edge and becoming slightly weaker midway. Anterior tuberosities about as wide as posterior tuberosities, giving the basioccipital a fairly parallel-sided outline.

Discussion – *Parmularius angusticornis* is descended from the Bed I *P. altidens*, differing from it mainly in larger size and in the longer and more massive horn cores (Gentry and Gentry, 1978b). This is the most common bovid species in Middle Bed II, at least among the identifiable cranial remains, and was a medium-large alcelaphin, about the size of the extant hartebeest.

Parmularius maasaicus sp. nov.

Synonymy — *Parmularius* aff. *rugosus* Gentry & Gentry 1978 (Pl. 32, 2-3)

Etymology – Named in honor of the Maasai people who live in the Olduvai Gorge area.

Age and stratigraphy – Known only from Olduvai Gorge. The holotype comes from site HWK EE between Tuffs IIA and IIB. Other specimens come mainly from Middle Bed II, with possible occurrences from Bed I and Lower Bed II (see below).

Holotype — HWK EE 1972-2181, frontlet with both horn cores, recovered in 1972 by Mary Leakey (Fig. 4A)

Referred specimens — HWK EE 1972-2061, frontlet with both horn cores (Fig. 4B). HWK EE 1972-285, right frontlet with complete horn core. HWK EE 1972-954, right horn core (possible female). HWK EE M-L4-7, right frontlet with horn core. HWK EE M-L4-382, frontlet with both horn cores.

Other specimens mentioned by Gentry & Gentry (1978a: 393) but not seen by us are: from Middle Bed II: SHK II 1952-no number, basal right horn core; HWK East II 1962.068/6649, immature frontlet with both horn cores (pl. 32 fig. 2). From Lower Bed II: HWK 1960.58, left horn core (pl. 32 fig. 3); HWK 067/5523, right horn core; HWK (1960?).054, distal right horn core. From Bed I: NHM M 14516 (1931), left horn core with frontal; NHM M 29421 (1932?), left horn core. Tentatively referred is FLK (surface) 1955 P.P.F.4., a left horn core (Gentry and Gentry, 1978b: 393; Leakey, 1967:65, pl.88).

Species diagnosis — A medium-sized alcelaphin. Horns intermediate in length. Arising close together, behind the orbits, with bases inclined to the same plane as the anterior frontal. In anterior view they are lyrate, diverging posterolaterally above the base, then recurving to point upwards at the tips. In lateral view they are sigmoidal, weakly curving posteriorly at the base, then recurving to point upwards at the tips. Posteromedial swelling at the base, with a discrete posteromedial tuberosity, variably present. Basal horn core with flattened posterior surface. Resulting basal cross-section is not symmetric, with the anteroposteriorly widest portion located slightly laterally. Torsion present, though very weak, and heteronymous (not more than ~45° along the entire horn core). Transverse ridges present, broad and best developed on the lateral surface from the midsection up. Pedicels are tall, located far above the level of the orbits, but not as high nor united as in *Alcelaphus*.

Differs from *P. rugosus* in the much stronger lateral curvature at the base, and the stronger sigmoidal curvature overall, in the presence of posteromedial (rather than posterolateral) basal swelling, posterior flattening, and possibly in the anteroposterior compression. The horn cores also seem larger than those of the type specimen and the right horn core figured by Gentry & Gentry (1978a pl. 26 fig 3), which appear to be

quite slender. This slenderness is unlikely to be a result of sexual differences as it would exceed the dimorphism observed in alcelaphins today (which is weak relative to other bovid tribes). Additionally, there is no stratigraphic overlap with *P. rugosus*, which is known only from Beds III and IV.

Heteronymous torsion is a similarity to *Beatragus* spp., including fossil species such as *B. antiquus*. The new species differs from these in the much taller pedicels and the greater closeness, anteroposterior compression, and posterior flattening of the horn cores, and their resulting asymmetric cross-section, and in the lack of the straight distal ends typical of *Beatragus* species such as *B. antiquus* and *B. hunteri*.

The basal lateral divergence and upwards recurvature along with the shape of the cross-section and tall pedicels are reminiscent of horn shape in living hartebeest (*Alcelaphus buselaphus*), especially subspecies *A. b. cokei* or *A. b. tora*. The new species clearly differs from hartebeest in smaller size, shorter and less complex horn curvature, weaker divergence, and the far less raised pedicels, which in the hartebeest are very tall and united. Additionally, in hartebeest the horns recurve strongly anteriorly at their midsections, while in *P. maasaicus* they remain directed posterolaterally. The fossil species has weak, but noticeable, heteronymous torsion, while in hartebeest it is homonymous.

Description — The main features of all specimens may be deduced from the diagnosis. Metrics are given in Table 2. Most characteristic is the shape of the horn cores. Viewed from anterior, these are basically lyrate, diverging at an angle of around 100° at the base, followed by recurvature in the midsections such that the distal horn core tip is pointing posterodorsally. Viewed from the side, it can be seen that the horn cores have a well-developed posterior curvature at their bases, followed by a strong recurvature in the midsections, and dorsal recurvature towards the distal ends. Torsion is weak, but consistently present, and heteronymous. The swelling at the postero-medial corner of the basal horn core can be quite variable, and this can be seen in anterior or posterior views; it is poorly developed in the holotype (Fig. 4A) but well developed in HWK EE-1972-2061 (Fig. 4B). HWK EE 1972-954 is a slender right horn core with a small base and only a weak posteromedial swelling. However, it is of similar total curved length (170 mm) and exhibits well-developed basal curvature, indicating this was probably an adult, and not a juvenile. In all extant alcelaphin species females bear horns, though these are typically more slender (but commonly of the same length) than those of males, and we believe HWK EE 1972-954 could represent an adult female horn core. Gentry & Gentry (1978a: pl.32 fig. 2) illustrated an immature specimen (HWK East 1962.068/6649) which, in contrast to HWK EE 1972-954, shows a lack of development of the basal curvature and swelling.

Discussion — Gentry and Gentry (1978a) proposed that *P. aff. rugosus* in Beds I and II could be an ancestral form of the *P. rugosus* of Beds III and IV. However, the morphological differences between the two species are quite stark, with *P. rugosus* being more slender, with less complex curvature. A lineage relationship remains possible, but would require the loss of the horn shape complexity in *P. maasaicus* over time.

An alternate (perhaps not exclusive) scenario could place *P. maasaicus* on the ancestry to the extant hartebeest. An increase in size, raising of the pedicels, and increasing complexity of the horn core curvature producing a redirection of the horn core midsection anteriorly are conceivable. In fact, *P. maasaicus* may make a better candidate for the ancestry of *Alcelaphus* than *Numidocapra* (= *Rabaticeras*) *arambourgi*, which was previously proposed as an ancestor (Gentry and Gentry, 1978b; Vrba, 1997) (but see Gentry, 2010). Similarities in general shape of the horns in these two species suggest a similar fighting style. Horn bases in line with the facial plane permit head pushing, raised pedicels increase reach, enlarged horn bases add clout, and a lyrate midsection permits grappling. The less complex shape of the horns in *P. maasaicus* may indicate a less complex fighting (grappling) repertoire than seen in hartebeest.

Damaliscus Sclater & Thomas, 1894

Damaliscus niro (Hopwood, 1936)

Description — Two horn cores. MNK M-L6B-149, a complete right horn core (Fig. 3D), is larger in basal dimensions (72.4 x 51.8 mm) than any other Olduvai specimen recorded by Gentry & Gentry (1978b), but otherwise is a morphological match with the *D. niro* holotype (M14561 in the NHM). The horn core is long with gradual posterior curvature, strong mediolateral compression, flattening of both medial and lateral surfaces, rounded anterior and posterior surfaces, no keels, no torsion, widest part of the cross-section located far anteriorly, with prominent and widely spaced transverse ridges, and low pedicels (for an alcelaphin). The horn arises close to the midline and above the orbit. Distally, the horn core becomes more compressed and the posterior edge sharper. A weak postcornual groove is present.

HWK EE T29-L51-274 is a right frontlet with horn core with basal dimensions (45.1 x 33.4 mm) about the size of *D. pygargus*. The horn core arises upright, with weak posterior curvature, incipient heteronymous torsion, mediolateral compression, weak posteromedial swelling, weak flattening of the lateral surface, narrow but deep longitudinal grooves on the posterior surface, no transverse ridges, hollowed pedicels, and tall pedicels anteriorly. It is too curved to belong to *P. angusticornis* (even considering possible female morphology), and far less compressed and smaller than *D. agelaius*. It is a better match for some of

the specimens distinguished by Gentry & Gentry (1978b) as *D. niro* 'Type B', but is smaller in basal dimensions.

Discussion — *Damaliscus niro* was first described from Olduvai, and has since been widely recorded from Pleistocene sites in eastern and southern Africa. Gentry & Gentry (1978b) described a variety of horn core shapes and sizes attributed to this species. The two horn cores assigned here, possibly the largest and smallest specimens assigned to *D. niro* from Olduvai, exemplify this range of variation. Gentry & Gentry wondered if 'Type B' *D. niro* could represent female individuals but, considering the current specimens, this may require levels of sexual dimorphism beyond the limits observed among living alcelaphins (in which sexual dimorphism is quite low). The assignment of the HWK EE specimen to *D. niro* may later be revised.

Megalotragus van Hoepen, 1932

Megalotragus isaaci Harris, 1991

Description – A number of horn cores and teeth are assigned to this species. These include MNK M-L6B-151, a right horn core; MNK M-L6B-152, left frontlet with complete horn core (almost certainly the same individual as #151 – Fig. 3C); FLK T69-L26-231, right and left frontlet with complete horn cores (in matrix); and MNK T5-L10-1733, left mandible with p3-m3. Horn cores are long, strongly divergent (~100° in anterior view), weakly curving posterolaterally at their base, then gradually recurving anteromedially towards the tips. Basal cross-section is rounded with weak anteroposterior compression variably present. Distinct (though weak) homonymous torsion present, completing about 45° from base to tip. Transverse ridges absent. Mid-frontal suture well-fused and barely discernible. Teeth are immediately distinguished by their large size (m3 lengths mainly 38-42 mm, which is larger than extant *Connochaetes*, Fig. 5), and simple occlusal morphology (Faith et al., 2011; Gentry and Gentry, 1978b). The single complete mandible confirms the loss of the second premolar in this species.

The large basal size, great length, and weak curvature of these horns, and the large size of the teeth, are a match for *Megalotragus*, specifically to larger specimens assigned to *M. isaaci* from deposits of ~2.3-1 Ma in age, such as the Upper Burgi to Okote Members of the Koobi Fora Formation (Harris, 1991) or Shungura Members G-L (Gentry, 1985).

Discussion – *Megalotragus kattwinkeli* was named on material collected by Reck's expeditions at Olduvai in 1911-1913. That type material, thought lost in World War II, has been rediscovered and is today housed in Munich (Gentry et al., 1995). Its stratigraphic provenience is uncertain, but Dietrich (1933: 301) lists this species (= '*Rhynotragus semiticus*') as occurring in Bed IV. Author FB's examination of the Munich type series reveals that the abundant cranial and postcranial remains of this species appear mainly to have come from excavations (i.e. *in situ*), mostly from within close proximity (elements with different site numbers were found to conjoin), and with similar preservation. All bones and teeth have a reddish-brown color (and some retain a brick-red matrix), which is indicative of Beds III and IV (IdIT and MP, pers obs). The type series dental remains are not very large. Nine lower third molar lengths range 30-36 mm, which falls within the range of *C. taurinus* (Faith et al., 2011 fig. 5). Dental rows of *Megalotragus kattwinkeli* are in fact similar in size to those of *Rusingoryx atopocranion*, which by all accounts appears to be referable to *Megalotragus* (Harris, 1991; O'Brien et al., 2016; Vrba, 1997). O'Brien et al. (2016) discuss further cranial differences among *Megalotragus* species. It is more convenient to maintain a species level distinction between *M. isaaci* and *M. kattwinkeli*, recognizing they are almost certainly chronospecies on the same lineage, rather than treat them all as a single polymorphic species.

On that basis, *Megalotragus isaaci* comprises the early and large *Megalotragus* best known from the Koobi Fora Formation. At Olduvai it is known from Bed II, from specimens referred here and those described as *M. kattwinkeli* by Gentry and Gentry (1978b). The youngest known record of *M. isaaci* may come from the Daka Member of the Bouri Formation in the Middle Awash, Ethiopia (1 Ma, Gilbert, 2008b), comprising cranial and dental remains of appropriate size.

Connochaetes Lichtenstein, 1814

Connochaetes cf. *C. gentryi* Harris, 1991

Description – A single specimen, HWK EE M-L0-635, a horn core midsection, is large, and bears a rounded cross-section and moderately strong curvature similar to horn midsections in *Connochaetes* species, particularly the more weakly curved horns of early Pleistocene species such as *C. gentryi* or *C. africanus*. This is a surface find, and therefore of uncertain provenience.

Discussion – Gentry and Gentry (1978a) recognized the presence of three species of *Connochaetes* in Lower to Middle Bed II: *C. africanus*, and a single lineage represented by *C. gentryi* and *C. taurinus*. The evidence

for *C. taurinus* from Middle Bed II is a single partial horn core (MNK 2716) which Gentry and Gentry (1978a) only tentatively referred to this species. A horn core from HWK EE II 2315 (original not seen by us, but a replica in NHM) was first assigned to *C. gentryi* by Gentry and Gentry but later to *C. africanus* by Gentry (2010). The holotype cranium (and only other known specimen) of *C. africanus* comes from an unknown level in Bed II, and is in our opinion only arguably different from *C. gentryi* (Bibi et al. in press). The identity and status of *Connochaetes* in Bed II is far from clear. Wildebeest appear to have been far less abundant in the early Pleistocene community than they are in the Serengeti today.

Alcelaphini 'small sp.'

Synonymy – Alcelaphini sp. 4 (Gentry and Gentry, 1978a) in part (at least some of the dental specimens)

Description — Known only from dentitions (Fig. 2F, L–N). Best specimens are EF-HR M-L2-302, right mandible with dp3 alveolus and dp4-m2; HWK EE 1972-4302, left mandible with p3-m1; HWK EE M-L10-575, left mandible with m1 and m3, and p3-4 and m2 alveoli; HWK EE T27-L32-608, right maxilla with P4-M3 (Fig. 2F). HWK EE 1972-1156, left mandible with m1-3 (Fig. 2M); MNK SKULL-L10-5, left maxilla with M1-2.

This is a small alcelaphin, with teeth slightly smaller than those of extant *Damaliscus pygargus* or the late Pleistocene *D. hypsodon* (Faith et al., 2012). Lower molar row length is around 45 mm, giving an estimated body mass of around 30-55 kg (Janis, 1990), or about the size of extant springbok (*Antidorcas marsupialis*). Mandibles show a greatly reduced premolar row, with p2 absent and p3 greatly shortened. The metaconid and paraconid of p4 are unfused in HWK EE 1972-4302.

Discussion – A small alcelaphin of this size was previously reported from Bed I and Lower and Middle Bed II ('Alcelaphini sp. 4' in Gentry and Gentry, 1978a). Gentry & Gentry state that mandibles mainly from Bed I retain a small p2, which may be a difference from the currently referred specimens, or represent an earlier form of the species. Gentry (1985:169) described an older small alcelaphin from the Shungura Formation Members D-G (~2.5-2.0 Ma), which is of similar size but already lacked lower second premolars. Lack of metaconid-paraconid fusion on p4 is similar to the state reported for other Olduvai specimens and a difference from the small Shungura alcelaphin.

The small Olduvai alcelaphin is also close in size to the much younger *D. hypsodon* (Faith et al., 2012). Lack of paraconid-metaconid fusion in p4, and loss of second premolars are also similarities. Hypsodonty was measured on an unworn upper third molar, an unnumbered specimen from the HWK EE Leakey collections (OGAP barcode 60648, AP x T x Ht = 16.4 x 11.4 x 34.8 mm). This is quite hypsodont, but still less than in *D. hypsodon*, in which upper M3 height can be 2.5 or more times the length, and over 4.5 times the width (Faith et al., 2012 and data from T. Faith pers. comm.).

Alcelaphini indet. (teeth)

Isolated alcelaphin teeth were sorted into three gross size categories, representing *Megalotragus isaaci* on the large end (Fig. 2G), the small alcelaphin species on the small end (Fig. 2F, L–N), and an intermediate category (here Alcelaphini indet.) that potentially includes species such *Parmularius angusticornis*, *P. maasaicus*, *Damaliscus niro*, and possibly *Connochaetes* (Fig. 2 J-K, see Methods).

Lower and upper third molars were tabulated to provide some sense of the relative abundance of these categories. Out of 40 measurable lower m3 specimens (isolated or from more complete specimens), nine (22.5%) are attributable to *Megalotragus* on account of very large size (m3 lengths 39–49 mm) and six (15%) belong to the small alcelaphin (m3 lengths 18–22 mm). The remaining 25 (62.5%) specimens are intermediate in size (m3 lengths 25–35 mm). Out of 32 upper third molar specimens, five (16%) are attributable to *Megalotragus* (lengths ~29–31 mm), four (13%) to the small alcelaphin (~15–20 mm), and the remaining 24 (75%) to the intermediate size category (~22–27 mm). Tooth size (and, by proxy, body size) ranges are displayed graphically in Fig. 5.

Upper and lower third molar counts are compatible. *Megalotragus* represents some 15–25% of alcelaphin remains, the small alcelaphin around 10–15%, and the intermediate species the remaining 60–75%. In the extant Serengeti fauna, the intermediate size category covers the entire size range from hartebeest (*Alcelaphus buselaphus*) to wildebeest (*Connochaetes taurinus*).

Antilopini Gray, 1821

Two or three species minimum, the most abundant being *Antidorcas recki*. Others are '*Gazella*' *praethomsoni* and a larger indeterminate species known only from teeth. The latter is not certainly antilopin and could be impala, which is very rare at Olduvai.

Antidorcas Sundevall, 1847

Antidorcas recki (Schwarz, 1932)

Description – Five horn cores (all from HWK EE) are assigned to this species (Fig. 3G-H). Horn cores show mediolateral compression, are rotated to the midfrontal plane (but not as much as in *G. praethomsonii*), arise upright above the orbits, are weakly curved at the base and then strongly bent backwards just above, ending with straight distal portions. Transverse ridges are present and closely spaced. Pedicels are tall and hollowed internally by frontal sinuses. Dorsal surface of the frontal is strongly curved, postcornual fossa shallow. Weak homonymous torsion, if present. In these features, in addition to their medium-small size, these horn cores are a match for *Antidorcas recki*.

Numerous dental specimens of antilopin morphology are within the size range of previously described Olduvai *A. recki* (Gentry and Gentry, 1978a). Mandibles retain p2 (or its alveolus) and this tooth is not greatly reduced, matching *A. recki* and in contrast to *A. marsupialis*, in which p2 is typically absent.

Discussion – While springbok is today known only from southern Africa, *A. recki* was a common occurrence across much of sub-Saharan Africa. Originally described from Olduvai from specimens collected by the Reck expeditions, *A. recki* has since been found in South Africa, the Turkana Basin, and even Chad (reviewed in Gentry, 2010). It is known from abundant material, including remains of a herd from Middle/Upper Bed II (site SHK, Gentry, 1966).

Gazella de Blainville, 1816

Gazella sp. 'aff. *rufifrons*' *sensu* Gentry, 2010

Description – Several cranial and horn core specimens belong to a gazelle, the best among these being HWK EE T28-L40-96, HWK EE 1972-2396 (Fig. 3F), and HWK EE 1972-1211. Horn cores are mediolaterally compressed, with the lateral surface noticeably flatter than the medial surface, bear deep longitudinal grooving, and no transverse ridges. They are quite upright in lateral view, with only weak posterior curvature basally that becomes straighter distally with a hint of anterior recurvature at the tips. The basal cross-section long axis is rotated at almost 45° to the midfrontal plane. Pedicels are short, and frontal sinuses are absent.

Frontal dorsal surfaces are depressed, sutures are complex, and the midfrontal suture forms a raised ridge. Postcornual fossa is a vertical oval, large, and moderately deep.

HWK EE 1972-2396 was described as *Gazella* sp. by Gentry & Gentry (1978b), later referred to *Gazella* aff. *rufifrons* by Gentry (2010). This differs from a second Olduvai gazelle referred to *Gazella* 'sp. 3' by Gentry (2010) (= Antilopini sp. 1 in Gentry and Gentry, 1978b), which is similar but has more upright horn bases, with less flattening of the lateral wall, and heteronymous torsion (lyration) in longer specimens. *Gazella* aff. *rufifrons* horns are also very similar to those of larger individuals of *G. praethomsoni*, and to those of extant *Eudorcas thomsoni*, but less mediolaterally compressed.

Discussion – Gentry (2010) grouped together gazelle specimens from Olduvai, Peninj, Elandsfontein, Turkana, and Melka Kunture under the name *Gazella* aff. *rufifrons* and we maintain his designation here. This species, *G. praethomsoni*, and Gentry's '*Gazella* sp. 3' must have been a closely related group of species, from which the extant *E. thomsoni* and *E. rufifrons* are likely to have arisen.

Antilopini sp. indet. 'large'

Description – About five teeth appear to represent a large antilopin. The most complete specimen is HWK EE M-LCHA-537, which comprises right upper P2-M3 slightly smaller than extant *Nanger granti* (P2-4 length is 25.2 mm, M1-3 is 44.8 mm). Large antilopin teeth (particularly upper molars) may be difficult to distinguish from those of impala, and these specimens are also close to the size of *Aepyceros melampus*. The lower teeth assigned here are more certainly antilopin (e.g. HWK EE 1972-4173, a left lower m3) on account of the very weak lingual stylids and weak ribs resulting in a very flattened lingual surface, and simple slit-like central cavities.

Discussion – Absence of large antilopins in the Pliocene means isolated impala teeth can often be distinguished quite easily, but the situation becomes more complicated in the Pleistocene when the presence of large antilopins (e.g. Grant's gazelle size) becomes a possibility. Remains of impala are very rare at Olduvai, in contrast to their abundance at sites in Turkana and the Afar. Gentry and Gentry (1978a) documented a few specimens of *Aepyceros melampus* from Lower Bed I (THC), possibly the upper part of Middle Bed II (SHK), and Upper Bed II (BK), and so presumably impala were also present at sites like

HWK EE though we have found no conclusive evidence of them. Evidence for larger gazelles such as *N. granti*, in the early Pleistocene record has also been very spotty (Gentry, 2010).

This larger antilopin separate nicely from *Antidorcas recki* on the dietary spectrum as well, with the springbok grazing (in contrast to living springbok) and the larger species browsing and mixed-feeding (Uno et al, this volume).

Bovidae incertae sedis

?Antilopini gen. et sp. indet.

Description – HWK EE M-L1-1860 (Fig. 3E) is a left horn core that would be on the large side for an antilopin (DAP x DT: 42.4 x 30.2 mm, total length ~300 mm). It is strongly mediolaterally compressed, with the basal long axis weakly rotated to the midfrontal plane, with gradual posterior curvature that straightens out distally then weakly recurves anteriorly at the tips, inclined to the braincase at about 60°, and weak (~45°) heteronymous torsion resulting in a lyrate shape. Keels absent, transverse ridges very prominent and closely spaced (about 1 cm apart) along the entire anterior surface. No flattening of lateral or medial surfaces. Frontal sinuses expanded but ending in the anterior pedicel, frontals thin at the midfrontal suture (~12 mm maximum thickness), and pedicels short. Frontal between horn cores not raised, nor is the dorsal frontal area depressed (which suggests that the midfrontal suture was not raised either). Fronto-parietal suture complex.

Main comparisons are with *Aepyceros*, and among Antilopini with *Litocranius*, the Olduvai *Gazella* aff. *rufifrons* (above), *Antidorcas recki*, and *Nanger granti*, and among Alcelaphini with some specimens of *Damaliscus niro*, and Olduvai horns assigned to 'Alcelaphini sp. 4' by Gentry & Gentry (1978b).

HWK EE M-L1-1860 differs from horns of *Aepyceros* spp. in the strong mediolateral compression (and resulting oval, rather than more circular, basal cross-section), the far less-developed lyration, the lack of a posterolateral keel, the close spacing of the transverse ridges, and the lack of a fully hollowed pedicel.

The specimen bears some similarity to the overall course of horns of the gerenuk (*Litocranius walleri*, for which no fossil record is known) but differs in the expansion of the frontal sinuses (not expanded in gerenuk, Farke, 2010), in the greater mediolateral compression, the prominent transverse ridges (absent on the horn core in gerenuk), and lack of deep longitudinal grooving. It is far larger than *Eudorcas thomsoni* and *Gazella* aff. *rufifrons* described above, and differs further in the expanded frontal sinuses, presence of transverse ridges, lack of flattening of the lateral horn core surface, and lack of strong longitudinal grooving

along the horn core. It differs from *Antidorcas recki* in larger size and longer horns that are more compressed, that lack a strong backward bend, spiral in the opposite direction, with better developed and more closely spaced transverse ridges, and less expanded frontal sinuses. HWK EE L1-1860 differs from horns cores of extant *Nanger granti*, which are larger, with torsion that when present is homonymous, lacking transverse ridges, lacking anterior recurvature at the distal horn core (only the horn sheath), and with unexpanded frontal sinuses (Farke, 2010).

HWK EE M-L1-1860 is somewhat similar to horn cores from site BK that Gentry & Gentry (1978b: 396) doubtfully referred to as *Damaliscus niro* under the designation 'Type A' ('Gazellae indet.' in part, Leakey, 1967: 65, pl. 86), or *D. cf. niro* from Turkana (Harris, 1991). Compared to the type material of *D. niro* (which is mostly younger), these horns are smaller, shorter, with slightly less mediolateral compression on average, anterior recurvature of the distal tips, and more closely spaced transverse ridges. HWK EE L1-1860 superficially fits these features, and is of about the same length, but differs from Type A (and any *D. niro* for that matter) in being smaller, lacking any flattening of the lateral or medial surfaces, lacking the more sudden backward bend about halfway up the horn core, with better developed heteronymous torsion, and less prominent transverse ridges that are much more closely spaced. Perhaps the most telling difference from all alcelaphins is the limited sinus expansion and lack of pedicel hollowing in HWK EE M-L1-1860 (expanded frontal sinuses are usually also associated with greatly thickened frontals and tall pedicels, absent in this specimen). Gentry and Gentry (1978b) mention that *D. niro* has less developed sinuses than in living *Damaliscus*, but these still extend 'beyond the pedicel top', which is not even remotely approached here.

HWK EE M-L1-1860 resembles horn cores from Bed I tentatively attributed to the Olduvai small alcelaphin (Gentry and Gentry, 1978a) in the posterior curvature and possibly the obliqueness of the inclination and the torsion (if this were confirmed to be heteronymous in the previously described FLKN I specimens). HWK EE M-L1-1860 differs from these in being larger, bearing transverse ridges, a stronger backwards curvature, and in lacking the alcelaphin condition of a fully hollowed pedicel. While this specimen does not appear to match any known antilopin, it seems to be an even poorer match with alcelaphins.

Discussion – This horn core of uncertain taxonomic identity represents a medium-sized antelope with heteronymous torsion and slightly expanded frontal sinuses. The mediolateral compression, limited frontal sinus expansion, and the closely spaced transverse ridges may be more like an antilopin than an alcelaphin. It

is interesting that this horn core does not seem to match any previously described bovid from Olduvai Gorge, despite over 100 years of discovery there.

Reduncini Lydekker & Blaine, 1914

Kobus A. Smith, 1840

Kobus ellipsiprymnus Arambourg, 1941 / *sigmoidalis* (Ogilby, 1833)

Description – HWK EE 1972-4356 is a basal fragment of a left horn core that may be reduncin. It is large with only slight mediolateral compression (49.3 x ~45e mm), with transverse ridges that dip medially, a hint of heteronymous torsion, a flattened lateral surface, indications of a posterolateral keel, and no sign of sinuses at the base. These features are suggestive of the *K. sigmoidalis-ellipsiprymnus* (waterbuck) lineage. However, the surface texture, though greatly eroded, does not seem rugose enough for Reduncini, and the basal horn core seems far too developed vertically and the lamination too strong for waterbuck.

Large reduncin molars may be difficult to distinguish from those of hippotragins as both have basal pillars, and lowers with goat folds. Reduncin molars normally have better developed ribs and more pinched labial/lingual cusps on lowers/uppers, but morphology varies with wear. Size is often an indicator, but teeth of *Kobus sigmoidalis* can overlap smaller *Hippotragus* individuals. Several molars are here assigned to a reduncin that, on the basis of large size, could only be the *K. sigmoidalis-ellipsiprymnus* lineage. The size of these specimens is in the intermediate to larger range of extant waterbuck (Figs. 2I, 5).

FCE T30-L60-535 is a fragment of a lower molar that seems slightly smaller than the remaining teeth assigned here, and may represent a second, smaller reduncin, such as *Kobus kob* or a *Redunca*.

Discussion – Reduncins from Olduvai have previously mainly been reported from Bed I, and especially Middle Bed I (see below). Their rarity at Olduvai suggests a significant lack of wetland vegetation. The *K. sigmoidalis-ellipsiprymnus* lineage is the main large reduncin of the eastern African Pleistocene, and can be quite common at sites in the Turkana Basin or Afar. They are extremely rare in Middle Bed II, with only a handful of specimens, including HWK EE 1972-1123, the single tooth previously attributed to *K. sigmoidalis* by Gentry & Gentry (1978a). These authors also assigned a few Middle Bed II specimens to *Kobus kob*, including a female skull with partial skeleton from site MNK. Kob are not known from the Serengeti region today, but Kingdon (1982) records them as formerly present on the east side of Lake Victoria.

Hippotragini Retzius & Loven, 1845

Hippotragus gigas Leakey, 1965

Description – A handful of dental specimens are attributable to *Hippotragus gigas* (giant sable), the only large hippotragin known from the early Pleistocene. Molars are characterized by large size, rounded cusps, tall and large basal pillars, rounded ribs, and large goat folds on lower molars. Lower third molar distal lobe lingual wall is located lingually and in line with remainder of the tooth. Size is comparable with or even slightly larger than the largest individuals of extant *H. equinus* (Fig. 5). Best specimen is FLKW T69-L22-596 (Fig. 2H), a partial mandible with m1-3 (length m1-3: 83.5 mm), size of which is slightly outside the range of waterbuck and within the range of both *H. gigas* and *H. equinus* (Gentry and Gentry, 1978a figs. 12 & 17).

Discussion— It is difficult to distinguish isolated molars of Hippotragini from those of large Reduncini (i.e. *Kobus*), especially lowers, and both taxa are uncommon at Olduvai. Molar rows of *H. gigas* are larger than those of both Bed I *K. sigmoidalis* and extant *K. ellipsiprymnus* (Fig. 5). There is also the possibility of confusion of isolated molars of *H. gigas* with those of the bovin *Syncerus acoelotus*, which is present in Middle Bed II (Gentry and Gentry, 1978a), especially as these overlap in size. Lower molars in *Hippotragus* can easily be distinguished by large goat folds, and both uppers and lower molars by weaker ribs. No teeth in the current assemblage are assigned to *Syncerus*.

Though its horn bases may have been larger, *H. gigas* was not much larger in molar (and, by extension, body) size than extant roan, and probably had males also in the 200-300 kg range. *Hippotragus gigas* differs from the roan and sable in only very few features, but a more reduced premolar row than in either extant species (Gentry and Gentry, 1978a: fig. 17) is a derived trait that suggests it may not have been ancestral to either.

Caprini Gray, 1821

Caprini sp. indet.

Description – HWK EE M-L0-172 is a left lower p4 that is very hypsodont, very long and narrow, with a greatly elongated metaconid and totally closed lingual wall. It retains thin traces of cementum. Its

morphology is characteristic of Caprini (including 'Ovibovini') and it is about the size of the takin, *Budorcas taxicolor*.

Discussion – With the exception of the Ethiopian walia (*Capra walie*), caprins are entirely absent today from sub-Saharan Africa. The fossil record, however, establishes their presence through much of the Pliocene and Plesitocene, until quite late in South Africa (Brink, 1999). Even as fossils, however, they are extremely rare in the eastern African record (less so in South Africa). Gentry & Gentry (1978a) and Leakey (1967) had previously referred a horn core and some metapodials from Bed I to Caprini (= 'Caprinae'). A horn core from Bed I (Gentry and Gentry, 1978a: pl. 41) resembles those of *Budorcas*, in particular the fossil *B. churcheri* from Hadar (Gentry, 1996). HWK EE M-L0-172 provides evidence for the presence of a large caprin (possibly the same species) in Middle Bed II. Unfortunately this was a surface find, and its preservation differs slightly from specimens found *in situ* at HWK EE. Bed III is also widely exposed and steeply inclined above the HWK EE site level.

Giraffidae Gray, 1821

A small number of specimens confirm the presence of at least two giraffid species in Middle Bed II.

Sivatherium Cautley & Falconer, 1835

Sivatherium maurusium Pomel, 1893

Description – Referred dental specimens include HWK EE 1972-377 and HWK EE 1972-634 (Fig. 6B), both right mandibles preserving p2-m3. These are massive giraffid teeth that are within the metric ranges of *Sivatherium maurusium* (Singer and Bone, 1960). FCW M-L14-147 is an upper M3 that is at the smaller end of the *Sivatherium* range. These teeth are larger and more hypsodont than those of *Giraffa*. Three lower third molars in early wear allow rough assessments of hypsodonty in this species (m3 height / width) as between ~1.5 and 1.8. The same index in extant *Giraffa* and *Okapia* is around 1.2 (Janis, 1988).

Discussion – Two African *Sivatherium* species are known, *S. hendeyi* and *S. maurusium*. Both have similar dental size and morphology, *S. hendeyi* differing mainly in its shorter posterior ossicones and longer metacarpals (Harris, 1976b), and being an earlier (late Miocene, early Pliocene) species. Later Pliocene and

Pleistocene material is assigned to a single species, *S. maurusium*, which at many sites, including Olduvai, had become a grazer (van der Merwe, 2013).

Giraffa Brisson, 1762

Giraffa cf. *stillei* (Dietrich 1942)

Description – HWK EE M-L4-339, a right upper P3 or P4 (AP x T: 19.7 x 24.3), falls at the smaller end of the size range of *G. camelopardalis* (Singer and Bone, 1960), with a low crown matches *Giraffa* rather than *Sivatherium*. HWK EE M-L4-339 bears a posterolateral spur extending from the posterior protocone into the fossette, a character Harris (1976a) noted in *Giraffa* (but not in *Okapia*).

This specimen is smaller than *G. jumae*, which is the size of large individuals of extant *G. camelopardalis*. HWK EE M-L4-339 is smaller than specimens of *G. stillei* (= '*G. gracilis*') from East Turkana, but similar in size to the syntype of *G. gracilis* from the Shungura ('OMO 1947' in Harris, 1976a). At 19.7 mm in length, HWK EE M-L4-339 is probably too large for *Giraffa pygmaeus*, which is even smaller than *G. stillei* but for which no upper premolar measurements are available in the original description (Harris, 1976a). Seeing as P3 and P4 are about two-thirds the length of M2 or M3 in *G. camelopardalis* (Singer and Bone, 1960 table 7), the upper premolars in *G. pygmaeus* are estimated to be about 14-16 mm. Among the different fossil *Giraffa* species, size suggests a best match with *G. stillei*.

EF-HR T2-L2-1410 is a lower p2 (AP x T: 17.7 x 12.1 mm) that falls comfortably within the size range of both extant *G. camelopardalis* and two specimens referred by Harris (1976a) to *G. jumae* (one from East Turkana, one from Rawe). It also matches the size of p2s of *G. stillei* from Laetoli (Harris, 1976a tables VIII and X) but is larger than Upper Laetolil specimens referred by Robinson (2011) to *G. stillei*, but similar to specimens he referred to *Giraffa* aff. *jumae*. Size overlap among multiple fossil species precludes any confident assignment for this specimen.

Discussion – *Giraffa stillei* (originally '*Okapia stillei*' Dietrich 1942:113) was established for a small giraffid from much older material from Laetoli. It has since been described from Olduvai and from the Shungura and Koobi Fora Formations, among other sites, and is the senior synonym of *G. gracilis* (Harris et al., 2010). All three known African fossil species of *Giraffa* — *G. jumae*, *G. stillei* (= *G. gracilis*), and *G. pygmaeus* — have previously been recorded from Olduvai Beds I and II (Harris et al., 2010; Harris, 1976a), including a well-preserved cranium of *G. jumae* from site EF-HR (Leakey, 1970). These three species differ from each

other (and from extant *G. camelopardalis*) in average size but the assignment of isolated dental material is problematic as there is large overlap.

Hippopotamidae Gray, 1821

Hippopotamus Linnaeus, 1758

Hippopotamus gorgops Dietrich 1926

Description – Numerous teeth (Fig. 6D) and postcranial elements. There is also a partial skeleton from FLKW T69 that is still being excavated and prepared. *Hippopotamus gorgops* is distinguished from extant *H. amphibius* by larger size in addition to cranial differences such as more elevated orbits and sagittal crest as well as higher-crowned teeth (Weston and Boisserie, 2010). Teeth are here referred to *H. gorgops* on account of their large size. Specimen HWK EE M-L10-1522 is a right lower m2 that is very large, even larger than the lower m3 MNK T5-L10-1511, which is highly unexpected within a monospecific assemblage of *Hippopotamus*, even accounting for different wear stages. This could indicate the presence of a separate species (even larger than *H. gorgops*), or else it represents a degree of intraspecific variation that is unparalleled in the extant hippopotamus.

Discussion – *Hippopotamus gorgops* was first described on a cranium from Olduvai (Dietrich, 1926, 1928) where it is known from Beds I-IV. A second, small hippo species has been reported from Bed II (Coryndon, 1970; Weston and Boisserie, 2010), but no remains of it have come to light in the new OGAP collections.

Suidae Gray, 1821

The new collection preserves specimens that belong to the suid genera *Kolpochoerus* and *Metridiochoerus*. As in the Konso Formation at ca. 1.6 Ma (Suwa et al., 2014), *Kolpochoerus* is the most abundant and is represented by the two lineages that predominate in the Pleistocene African fossil record: *K. majus* and *K. limnetes* (and its more derived descendant usually named *K. olduvaiensis*, but here named *K. paiceae*, see discussion below). Both *K. limnetes* and *K. paiceae* are identified in the new Middle Bed II assemblage, giving a better understanding of the morphological and temporal transition between those two chronospecies. *Metridiochoerus* is represented by fewer remains and these are more difficult to identify to specific rank with confidence. The most diagnostic specimens are here assigned to the large sized species *M. compactus*. Stable carbon isotopes from various African sites indicate that all those species present at

Olduvai feed predominantly on C₄ plants, likely grasses (Harris and Cerling, 2002; Souron, in press)(Uno et al., this volume). It is still unclear how these various large-sized suids were dividing resources on the landscape but stable oxygen isotopes seem to indicate that *Kolpochoerus* spp. were more water-dependent than *Metridiochoerus* (Harris and Cerling, 2002).

Kolpochoerus limnetes (Hopwood, 1926)

Description – Two specimens are confidently assigned to *K. limnetes*. HWKEE 1972-4186 (Fig. 6J) is a complete right lower m3 that bears four pairs of main pillars and no terminal pillar (complexity score of 4 according to Souron, 2012) and measures 50.6 mm in mesiodistal length (Fig. 6). HWKEE 1972-4326 is a complete right upper M3 that measures 47.8 mm in length. Both specimens are relatively short and low crowned (around 20 mm unworn height), with a weakly sloping cervix in the distal part of the crown.

Discussion – We use the species name *K. limnetes* in contrast to recent publications that prefer the name *K. heseloni* (e.g. Bishop, 2010). The holotype of *Sus limnetes* Hopwood, 1926 is a right upper M3 (NHM M 12614) that comes from the Kaiso Formation, Uganda. In contrast to Pickford (1994) who stated it belonged to *Nyanzachoerus*, *S. limnetes* is indistinguishable from the classic *Kolpochoerus* documented in numerous sites across eastern Africa between 2.9 Ma and ca. 1.6 Ma. Cooke (1997) also concluded that the morphology and morphometrics of the *S. limnetes* holotype specimen were perfectly aligned with other eastern African *Kolpochoerus*, but he chose to use the specific name *K. heseloni* (Leakey, 1943), as he had some doubts regarding the stratigraphic provenience of this specimen based on preservation features noted by Pickford (1994). We do not consider this a sufficient reason to invalidate a species name, and we therefore retain use of the name *K. limnetes*.

Based on their morphology and metrics, the two aforementioned specimens belong to a late stage of *K. limnetes*, similar to what is observed in Member H and the lower part of Member J of the Shungura Formation, Ethiopia (Sahnouni and Van der Made, 2009; Souron, 2012). The third molars of this late stage are plesiomorphic compared to those of the younger *K. paiceae* as they are composed of fewer main cusps (lower complexity score according to Souron, 2012) and their crowns are lower. Both specimens come from site HWKEE, from between Tuffs IIA and IIB.

Kolpochoerus paiceae (Broom, 1931)

Description – Three specimens are assigned with certainty to *K. paiceae*. FCW M-L10-194 (Fig. 6I) and FCW M-L8-656 are both complete unworn left lower third molars (complexity scores of 5 and 4.25 respectively, Souron, 2012), and FCE T30-L62-130 is a complete right upper M3. These teeth are differentiated from those of *K. limnetes* by slightly longer crowns (respectively 59.6 mm, 52.1 mm, and 53.7 mm) that are higher crowned (ca. 30 mm unworn height).

Discussion – Leakey (1942) diagnosed *K. olduvaiensis* (then classified in the genus *Mesochoerus*) by its lower third molars with a higher number of lateral pillars (five pairs instead of four in more primitive *K. limnetes*). In lower third molars of *Kolpochoerus*, the number of pairs of lateral pillars is strongly correlated with crown mesio-distal length (Souron, 2012). The name *K. olduvaiensis* has thereafter been widely used for east African specimens with third molars more elongated than those of *K. limnetes* (e.g. Bishop, 2010; Gilbert, 2008a; Suwa et al., 2014). However, it subsequently became clear that specimens from Beds III and IV at Olduvai Gorge that were assigned to *K. olduvaiensis* were extremely similar in terms of metrics and morphology to South African specimens assigned to *K. paiceae* (Braun et al., 2013, and AS in prep.). This observation extends to the current specimens from Middle Bed II.

Kolpochoerus paiceae was previously considered to be endemic to southern Africa but it seems more likely that some of the specimens from eastern Africa, including the current sample from Olduvai, represent *K. paiceae*. The morphological diagnosis and the biogeographic and chronological ranges of the whole complex comprising *K. limnetes*, *K. "olduvaiensis"*, and *K. paiceae* are currently being revised (AS, unpublished data) and reveal a wide-ranging *K. paiceae* spanning southern Africa, part of eastern Africa, and even possibly the Levant; morphological diversity among eastern African sites is notable, with specimens from the Turkana and Afar basins displaying longer third molars.

The transition between the late stage of *K. limnetes* and early *K. paiceae* in eastern Africa is best documented in the Konso Formation and takes place between 1.75 Ma and 1.45 Ma. Suwa et al. (2014) used the name *K. limnetes/olduvaiensis* for this transitional sample. OGAP specimens assigned to *K. paiceae* come from sites FCW and FCE, located between tuffs IIB and IIC, and are younger than those assigned to *K. limnetes*. Two specimens tentatively assigned to *K. cf. limnetes* come from sites FCE and FCW. If confirmed by further studies, these could indicate the coexistence of the ancestral *K. limnetes* and its descendant *K. paiceae* in Middle Bed II. These fossils promise a better understanding of the transition between late stage *K.*

limnetes and early *K. paiceae* in eastern Africa, in complement to the large samples from the Konso Formation.

Kolpochoerus majus (Hopwood, 1934)

Description – Four specimens are assigned to *K. majus*. HWKEE 1972-4349 is a complete left upper M3. FCE T67-L12-23 is a complete right upper M1. HWKEE M-L10-69 is a near complete right lower ml. FCW T62-L54-54 is a right mandibular ramus fragment with complete p3 to m1. All these specimens display molar morphology typical of *K. majus*, with mesiodistally compressed main pillars, and (where observable) simple, rounded wear patterns lacking clear enamel infoldings (Gilbert, 2008a; Souron et al., 2015).

Discussion – *Kolpochoerus majus* is a long-lived species that likely originated from the early Pleistocene *K. phillipi* (Souron et al., 2015; Suwa et al., 2014) and became extinct close to the end of the Pleistocene (Souron, 2012 and references therein). The samples from the Konso Formation were originally attributed to *K. majus* (Suwa et al., 2003) and then to *K. cf. majus* (Suwa et al., 2014), to reflect the uncertainty of their taxonomic status. Indeed, based on cranio-mandibular remains, the Konso specimens appear intermediate between the earlier *K. phillipi* and the younger definite *K. majus* from sites younger than 1 Ma (Gilbert, 2008a; Souron, 2012; Suwa et al., 2014). The OGAP specimens, being restricted to teeth, are here assigned to *K. majus* for the sake of simplicity. The OGAP specimens are too few and too fragmentary to give further information on the evolution of this species, which is in all cases a poor biostratigraphic indicator. As mentioned above for the *K. limnetes* / *K. paiceae* lineage, further collections from Middle Bed II could better clarify the transition from *K. phillipi* to typical post-1 Ma *K. majus* in eastern Africa.

Metridiochoerus compactus (Van Hoepen, 1932)

Description – Three specimens are assigned to *M. compactus* (although completely ruling out a very late stage of *M. andrewsi* is difficult, see discussion below). FCW T65-L79-2 is a nearly complete left lower m3. Dimensions and morphology are a match with *M. compactus*. HWKEE 1972-2065 is a complete right upper M3 partly enclosed in maxillary bone. MNK T5-L10-3028 is a right fragmentary mandibular ramus with p4 to m2 and erupting m3. The molars display an H-shaped wear pattern typical of *Metridiochoerus*, with straight lateral edges of the main cusps. The third molars are very much elongated and high crowned. The

dimensions and morphology of these specimens align them with the latest stage of *M. andrewsi* or its more derived descendant *M. compactus*. They are a good fit with *M. compactus* from the Konso Formation dated to between ca. 1.6 Ma and ca. 1.3 Ma (Suwa et al., 2014).

Discussion – There is the possibility of confusion between *M. compactus* and *M. hopwoodi* in younger deposits (Bed III and IV at Olduvai Gorge) as *M. hopwoodi* third molars become higher and longer, approaching the size of *M. compactus*. However, that is likely not the case in Bed II as both species are well discriminated metrically in the pene-contemporaneous or slightly younger levels of the Konso Formation (Suwa et al., 2014).

Metridiochoerus compactus is presumed to be a descendant of *M. andrewsi*, although the transition is poorly known. White (1995) places the temporal limit between *M. andrewsi* and *M. compactus* at around 1.6 Ma, with the possibility of overlap between the two species. The latest *M. andrewsi* and earliest *M. compactus* overlap slightly in terms of third molar dimensions and morphology (Cooke, 2007), and are mostly distinguished by the more derived canine morphology (and associated craniomandibular features) displayed by *M. compactus* (Harris and White, 1979). The new OGAP specimens here assigned to *M. compactus* could therefore be temporally close to the transition between *M. andrewsi* and *M. compactus*.

Some specimens assigned to *Metridiochoerus* sp. are not diagnostic enough to be identified to species. It is possible that other *Metridiochoerus* species (and especially the large-sized *M. hopwoodi*) are represented by some of these specimens. Both *M. hopwoodi* and *M. modestus* were reported from most levels at Olduvai Gorge (Bishop, 2010; Harris and White, 1979; Leakey, 1942, 1958). An edentulous mandibular symphysis, HWKEE M-L4-1090, could represent a species of *Metridiochoerus* other than *M. compactus* or even possibly an early *Phacochoerus* (which is itself a descendant of *Metridiochoerus*).

Primates Linnaeus, 1758

Cercopithecidae Gray, 1821

Papionini Burnett, 1828

Theropithecus oswaldi (Andrews, 1916)

Description – A few dental specimens including FCE T30-L64-16, a left maxillary fragment with M1-2 (Fig. 6N), and HWK EE 1972-4403, a left mandible fragment with m3 (Fig. 6O). These are papionin teeth of large size, with high crowns and columnar cusps indicative of *Theropithecus*. Size is larger than *T. brumpti* and

matches *T. oswaldi* from Koobi Fora (Jablonski and Leakey, 2008). The broken molar fragment HWK EE 1972 (barcode 61417) appears smaller, and is not certainly *Theropithecus* rather than *Papio*. Several postcranial remains are tentatively referred to *T. oswaldi* including FCE T67-L12-223, a proximal left humerus that is much larger than those of extant *Papio* and is comparable to a *T. oswaldi* humerus from Koobi Fora (Jablonski and Leakey, 2008).

Discussion – *Theropithecus oswaldi* was a medium-large sized terrestrial species common at Pleistocene sites across much of Africa until its last record at about 250 ka (Jablonski and Frost, 2010).

cf. Hominidae Gray, 1825

cf. Hominini Gray, 1825

Description – HWK EE M-L1-2792 is an upper premolar root fragment that may be hominin. EF-HR T2-L2-573 is an upper molar fragment that might be from a hominin or a large monkey.

Discussion – Olduvai is famous for its hominin fossils, and finds from Middle Bed II include the *Homo habilis* partial skull OH 13 from the MNK Skull site (Leakey et al., 1964). The contemporaneous presence of *Homo erectus* in Middle Bed II is not certain, but has been assumed on the basis of Acheulean stone tool technology, and by some indeterminate cranial fragments from SHK (Domínguez-Rodrigo et al., 2012). Presumably *Australopithecus boisei* was there too, as evidenced by remains from Bed I (Leakey, 1959) and Upper Bed II (Domínguez-Rodrigo et al., 2013). And yet hominins are among the rarest large mammals in the community. While abundant stone tools demonstrate without a doubt that hominins were active at Olduvai lake margin sites, the paucity of their skeletal remains suggests that they never reached high densities at these depositional sites, comparable, say, with the low fossil abundance of large felids. If hominins reached high densities, they may have preferentially kept to (and died in) non-depositional habitats, only rarely becoming preserved in these lake margin settings. Perhaps early *Homo* spp. favored wooded or mesic habitats, venturing into the open lake margins mainly for the acquisition of carcass foods or water.

PERISSODACTYLA Owen, 1848

Rhinocerotidae Owen, 1838

Ceratotherium Gray, 1868

Ceratotherium simum (Burchell, 1817) or *C. germanoaffricanum* Hilzheimer, 1925

Description – A few dental specimens are attributable to *Ceratotherium* (Fig. 6E-F). They are of similar size to teeth of *Diceros* but distinguished by taller crowns with much straighter labial walls on uppers and lingual walls on lowers, better-developed enamel bands and lophs, flatter wear surfaces, upper with a more curved protoloph, narrower and more oblique metaloph, and medifossette closed at an early wear stage (Geraads, 2010; Hernesniemi et al., 2011).

The Middle Bed II upper cheek teeth have strong protocone folds, suggestive of *C. germanoaffricanum*, but differences with extant *C. simum* are clearest on M3 according to Hernesniemi et al. (2011), but we do not have a good example of this tooth. Anterolabial corners are damaged in both upper teeth, but judging from the preserved anterolabial surface in HWK EE 1972-4172 (Fig. 6E), the parastylid groove may not have been so pronounced, unlike the state in *C. simum* (Hernesniemi et al., 2011). However, the protolophs curve quite smoothly towards the distal end, which is more like *C. simum*, and not just at the mesial end as in *C. germanoaffricanum*. Accepting that they are two separate species, the weight of the available evidence suggests the Olduvai Bed II rhino is more like *C. simum* than *C. germanoaffricanum*.

Discussion – *Ceratotherium 'germano-affricanus'* was named by Hilzheimer (1925) on a skull from Olduvai, but has mostly been treated as synonymous with *C. simum* (see Geraads, 2010). It is safe to say that a large grazing rhinoceros similar, if not identical, to the living white rhino was present in Middle Bed II at Olduvai.

?*Diceros* Gray, 1821

?*Diceros bicornis* (Linnaeus, 1758)

Description and Discussion – FCE T30-L60-217 is the lingual portion of an upper molar that is unfortunately in late wear and not diagnostic. Its stable carbon isotope values indicate that it belonged to an obligate browser (Uno et al. this volume). Black rhinoceros, *Diceros bicornis*, has previously been documented from Lower, Middle, and Upper Bed II (Geraads, 2010; Leakey, 1971a). It is possible, even likely, that this tooth represents this species, rather than the more abundant *Ceratotherium*.

Equidae Gray, 1821

Two species are present, one large and one small (a common pattern in many African fossil faunas). The larger of these, *Equus oldowayensis*, is the most abundant identified mammal species in Bed II. Churcher (Churcher, 1982) described the oldest African ass (*E. africanus* / *E. asinus*) based on a metatarsal from site EF-HR (Upper Bed II). Postcranial remains were not examined in the current study, but we tentatively find no evidence for a second, smaller species among the *Equus* dental remains. Further work on the Bed II equid material may yet refine the taxonomy or turn up a greater equid diversity. In the descriptions that follow, tooth position identifications (e.g. P4/M1, m1/m2) are tentative.

Equini Gray, 1821

Equus Linnaeus, 1758

Equus oldowayensis Hopwood, 1937

Description – Numerous dental specimens, the best among these being HWK EE M-L10-1575, articulated left and right mandibles with p2-m2 (Fig. 6C, G). Teeth assigned to this species are large, similar to the size of extant *E. grevyi*. Upper cheek teeth (Fig. 6M, Q, R) have a protocone that is typically elongate and often lingually concave, fusing to the hypocone by middle wear; with simpler plications of the central enamel cavities than in *Eurygnathohippus*; pli caballin present but small. Lower cheek teeth have deep ecto- and linguaflexids, a short parastylid that does not normally reach the lingual edge, and lack ectostylids.

Discussion – This large equid is the main *Equus* species recorded from the eastern African Pleistocene, first described on material from Olduvai by Hopwood (1937), and is the most common equid at Plio-Pleistocene sites in eastern Africa (Bernor et al., 2010 and therein). It is apparently very similar to (and perhaps synonymous with) the earlier *E. koobiforensis*, and the contemporaneous southern African species *E. capensis* (Bernor et al., 2010). It has been proposed as an ancestor to the extant *E. grevyi* (Churcher and Richardson, 1978).

Hipparionini Quinn, 1955

Eurygnathohippus van Hoepen, 1930

Eurygnathohippus cornelianus van Hoepen, 1930

Description – Teeth assigned to this species are smaller than those of *Equus oldowayensis* but are noticeably high-crowned, even more so than the much larger *Equus* (Fig. 6K, L, P). Upper teeth with protocone isolated, oval in shape, typically rounded buccally and flattened lingually; infundibular plications can be very complex; pli caballin present and often large. Lowers with tall and large ectostylids; ecto- and linguaflexids usually not deep, often quite shallow; parastylid typically long and reaching lingual edge.

Discussion – The 'hipparion' from Olduvai has a convoluted taxonomic history, and may represent more than one species (Armour-Chelu et al., 2006). We here refer all remains of the Middle Bed II hipparionin to *Eu. cornelianus* 'sensu latu', as described in Bernor et al. (2010). This species is best diagnosed by hypertrophied central incisors i1 and i2, and reduced i3 (Bernor et al., 2010), elements that unfortunately are not present among the OGAP remains. Hooijer (1975) reported maximal crown heights of 75 mm for equid material from BK II. Specimens from Middle Bed II exceed even those heights: FLK T69-L26-204 is a right lower m1 in early wear with a preserved crown height of 81.0 mm. For comparison, EF-HR T2-L2-1946, a left upper P4 or M1 of *Eq. oldowayensis*, has an unworn crown height of 72.5 mm. Whatever dietary differences separated the two Olduvai equids, these were clearly not determined solely by the body size differences (we estimate ~100-150 kg for the hipparionin and 350-450 kg for the equin - see Supplementary Table 2). Rather, the smaller equid, with its much higher crowned teeth, must have also had a more abrasive diet.

PROBOSCIDEA Illiger, 1811

Elephantidae Gray, 1821

Elephas Linnaeus, 1758

Elephas recki (Dietrich, 1915)

Description – A few dental specimens, best among these being HWK EE 1972-1210, a left mandibular fragment with part of m2 or m3 (Fig. 6A). Ten preserved plates have a total length of about 173 mm; enamel thickness measured at different points on the worn occlusal plate edges ranges from around 2.1-3.5 mm; maximum preserved crown height is c. 110 mm. In this and other specimens, the closely arranged enamel

plates, thin enamel, absence of free accessory conules, and tall crowns all indicate an advanced *Elephas recki*, as expected for the age of Middle Bed II (Beden, 1980). It is not possible to assign this fragmentary material more precisely to one of the chronological stages of this species.

Discussion – This is a common and widespread elephant in the eastern African Plio-Pleistocene. Later forms are characterized by teeth that are more hypsodont, with a greater number of plates that are spaced more closely together, thinner enamel that is more complexly folded, and accessory conules that are incorporated into the main enamel loops. Middle Bed II may record a transition between *E. recki atavus* (present in Bed I and Lower Bed II) and *E. recki ileretensis* (Upper Bed II) (Beden, 1980). The fragmentary specimens reported on here may belong to either subspecies.

Deinotheriidae Bonaparte, 1845

Deinotherium Kaup, 1829

Deinotherium bozasi Arambourg, 1934

Description – Several small enamel fragments, all from HWK EE (both Leakey and OGAP collections). None preserve any significant tooth morphology, but are identified as deinothere based on the characteristic structure and texture of the enamel, which is thick, only weakly curved with a smooth external surface, and is strongly striated in cross-section.

Discussion – *Deinotherium bozasi* is the only deinothere recognized from late Miocene to Pleistocene deposits in Africa; their last record in the continent is at about 1 Ma (Sanders et al., 2010). This species was previously recorded from Bed I and Lower Bed II (Leakey, 1967; Leakey, 1971a: appendix b), Leakey (1967) writing that it was not found at any higher levels. These new specimens therefore appear to constitute a new record for Middle Bed II.

CARNIVORA Bowdich, 1821

Overall, the carnivore assemblage from Olduvai, Middle Bed II, is modern in aspect, although *Dinofelis* and *Pseudocivetta* represent morphotypes that are no longer present in the eastern African fauna. The absence of *Panthera leo*, *P. pardus*, and *H. hyaena* from the current assemblage is certainly a question of sampling

intensity. Petter (1973) previously described lion (including '*P. crassidens*') from Lower and Upper Bed II (FLKN and BK), and striped hyena and leopard from Middle Bed II (MNK). The same can also, but with less justification, be said of medium-sized canids of the genus *Lupulella* (jackals) as these tend to be rare in the fossil record and their presence at Olduvai Middle Bed II is not assured.

Conspicuous by their absence are the derived Machairodontinae, *Megantereon* and *Homotherium*. The former was almost certainly extinct in Africa by Middle Bed II time and the latter was, at the very least, exceedingly rare. In the extensive assemblage from the Okote Member, Koobi Fora Formation, *Homotherium* is represented by only two associated postcranial elements, whereas in similar-sized assemblages from earlier Koobi Fora Formation Members it is a common taxon (Werdelin and Lewis, 2013).

Also absent from Olduvai Middle Bed II are aquatic carnivorans. Several species of otter are known from sites in the Koobi Fora Formation of about this time and their absence from the present assemblage may be an environmental signal, despite the small sample size.

Xenocyon falconeri (= *Canis africanus*) was described by Pohle from Reck's 'Graben X' ('Excavation 10') of unknown stratigraphic provenience. Three mandible fragments from Bed II were later referred by Ewer (in Leakey, 1965b), and there exists an unpublished specimen (L.W. pers. obs.), but it is not clear where in Bed II all these were found. We therefore exclude *X. falconeri* from the Middle Bed II faunal list for now.

Canidae Fischer, 1817

Prototocyon Pohle, 1928

Prototocyon recki Pohle, 1928

Material – FCW T63-L62-240, left distal humerus (Fig. 7A). Distal width: c13; max AP: 10.1, min troch AP: 6.4. MNK T5-L9-1159a (b-g are birds), distal metatarsal fragment (Fig. 7B). Distal width 4.2 mm.

Discussion – This species is known only from Olduvai, and previously only from Bed I, though bat-eared fox has tentatively been identified at Laetoli (Werdelin and Dehghani, 2011). The generic distinction between *Prototocyon* and the extant *Otocyon* is doubtful, but regardless, these records push the temporal range of this fossil bat-eared fox into Middle Bed II.

Hyaenidae Gray, 1821

Crocuta Erxleben, 1777

Crocuta cf. *C. ultra* Ewer, 1954

Description – HWK EE 1972-400, left humerus shaft and distal end (Fig. 6D). HWK EE M-L6-1444, left lower m1. HWK EE M-L4-102, left lower m1. HWK EE M-L4-294, right scapula (Fig. 6C).

Discussion – Analyses of *Crocuta* (L.W. unpublished data) reveal a clear size separation between the older *C. dietrichi* and *C. ultra*, except at Olduvai. The Olduvai *Crocuta* material described by Petter (Petter, 1973) as *C. crocuta ultra*, spans the size gap between these two species as identified at sites in the Turkana and Afar Basins (Werdelin and Lewis, 2013a). The new dental material here confirms that – HWK EE M-L6-1444 is large (m1, length ~29 mm) while HWK EE M-L4-102 is small (m1, ~25.7 mm). From the comparable measurements, the scapula is almost identical in size with a partial scapula of *C. dietrichi* from the Upper Burgi Member, Koobi Fora (Werdelin and Lewis, 2013b fig. 7.6a). The Olduvai *Crocuta* is here provisionally referred to *Crocuta* cf. *C. ultra*, but may alternately be a late occurring population of *C. dietrichi*. Today the spotted hyaena *C. crocuta*, a possible descendant of *C. ultra* (but see Sheng et al., 2014), is common in the Olduvai/Serengeti area.

Felidae Fischer, 1817

Machairodontinae Gill, 1872

Dinofelis Zdansky, 1924

Dinofelis sp.

Description – HWK EE M-L4-2215 is a mesial fragment of a lower p3.

Discussion – Petter (1973) referred a single specimen from Lower Bed II (FLKN) to '*Machairodus* sp.', and a specimen from Middle Bed II (MNK) to '*Metailurus* sp.' The latter taxon is otherwise confined to the Miocene and this, together with the overlap in size between large *Metailurus* and small *Dinofelis* lead us to reassign the Olduvai '*Metailurus*' to *Dinofelis*. *Dinofelis* sp. is represented in Bed I, but only by postcranial elements (Werdelin and Lewis, 2001).

Caracal Gray, 1843 or *Leptailurus* Severtzow, 1858

Caracal sp. or *Leptailurus* sp.

Description – MNK T5-L12-482, humerus shaft and distal end (Fig. 7E).

Discussion – The caracal and serval are medium-sized felids of very similar size and skeletal morphology. The fossil record of these taxa is not adequate for a generic attribution of isolated elements.

Viverridae Gray, 1821

Pseudocivetta Petter, 1967

cf. *Pseudocivetta ingens* Petter, 1967

Description – HWK EE M-L2-491, distal fragment of a lower premolar. Appears to be a viverrid, and possibly *Pseudocivetta ingens* based on large size.

Discussion – *Pseudocivetta* was originally described from Olduvai, but has since been recovered from sites in the Turkana Basin as well (Werdelin and Lewis, 2013a). Most material is fragmentary and the affinities, ecomorphology and diet of the sole species, *P. ingens*, are still obscure, though Morales and Pickford (2011) suggest that it belongs in the Paradoxurinae.

Summary of the Middle Bed II Large Mammals

The newly described fauna matches previous faunal lists for Middle Bed II (Table 1). A few taxa previously reported from this interval (Gentry and Gentry, 1978c; Leakey, 1965a; Leakey, 1971a) are missing, among these being *Syncerus acoelotus*, a small *Tragelaphus*, *Beatragus antiquus*, *Giraffa pygmaeus* and *G. jumae* among the large herbivores, and *Panthera leo*, *P. pardus*, and *H. hyaena* among the large carnivores. A hartebeest-like antelope that was previously described has now been named as *Parmularius maasaicus* sp. nov. *Homo habilis* has previously been found in Middle Bed II, and both *H. erectus* and *Australopithecus boisei* are assumed to have been present, but no hominins have been conclusively identified from the new collections. At least a couple of records are new to the Middle Bed II fauna at Olduvai. These include the canid *Prototocyon recki*, previously only reported from Bed I and only doubtfully distinguished from the extant bat-eared fox, a possible caracal, and *Deinotherium*, which was previously only recorded from Bed I and Lower Bed II.

Fossil Fish from Middle Bed II Sites

Material

Fossil fish elements were first recovered from Olduvai Gorge sites by Louis and Mary Leakey and their team in the 1950s and 1960s (e.g. Leakey, 1971b). These remains were later analyzed and published (Greenwood and Todd, 1970; Stewart, 1994, 1996). The fish reported here are those more recently collected by OGAP. A total of 768 elements identifiable to family or lower rank were recovered from six sites located in Middle Bed II: FLK West, FC East, FC West, MNK-T5 and MNK Main, and HWK EE (Table 4). Fewer than five elements were identified at each of FC East and FLK West, and these sites will not be discussed further. The taxonomic diversity of the Olduvai Gorge fish was very low, with only two taxa identified – *Clarias* (a large catfish) and Cichlidae (perch-like fish known as cichlids or tilapia) (Table 1). *Clarias* elements made up 5.7% of all elements; cichlid elements comprised 94.3%. The *Clarias* elements at Olduvai Gorge represented individuals estimated to be between <10 cm and 90 cm total length; most were between 25 and 50 cm total length. *Clarias* are air breathers which can live outside of water for up to 18 hours, allowing movement overland between water bodies. Today, they are ubiquitous in rivers and lakes throughout Africa, including *C. gariepinus* which inhabits smaller eastern African lakes and rivers. The Olduvai Gorge *Clarias* bones are identical to those of *C. gariepinus*. *Clarias* are common in African fossil sites, in part due to their robust bones.

The cichlids represented at Olduvai Gorge were generally small, with estimated total length ranging from <5 cm to 32 cm; most were between 15 and 20 cm total length. Today cichlids are highly abundant and diverse, with upwards of 1600 species known in Africa alone (Nelson, 2006). Given the similarity of bones between the many cichlid genera and species, their elements are usually identified at the level of family. However, the small size of the fish, and a distinctive character on their opercula (gill cover) absent in larger cichlid taxa, suggests that most of the Olduvai Gorge cichlids belonged to the tribe Haplochromini, which today includes hundreds of the smaller cichlid species of the African Great Lakes. The haplochromine and *Clarias* individuals that inhabited paleo-Lake Olduvai during Bed II were likely derived from stream(s) or river(s), which probably flowed into the eastern side of the lake (Hay, 1976a).

Paleoecological Implications of the Middle Bed II Fish

Despite the limited taxonomic diversity of fish in the Olduvai Gorge sites, several unusual ecological patterns were observed. The presence of only two fish taxa in paleo-Lake Olduvai is surprising given the

large diversity of taxa in most African lakes. Further, the overwhelming dominance of fragile cichlid elements over robust *Clarias* elements (ratio of about 16:1, Table 3) is unusual. These skewed proportions may point to lake chemistry. Paleo-lake Olduvai was small, particularly in middle and upper Bed II, and high in salinity and alkalinity (Hay, 1976a). Several small African lakes today have similar water chemistry, including Lakes Manyara, Natron, Chilwa, Singida and Magadi. Lakes Singida and Magadi are the most saline, and contain only cichlids, which inhabit the central, open lake. Lakes Manyara, Natron and Chilwa have cichlids in the open lake, but also smaller *Clarias* populations in the fresher lake margins or in the mouths of inflowing stream(s) or river(s) (Beadle, 1981; L  v  que, 1997). Cichlids are generally highly tolerant of saline and alkaline lake water (e.g. Beveridge and McAndrew, 2000), unlike most other African freshwater taxa; *Clarias* is also tolerant of reasonably high salinity. At the Olduvai Gorge sites, cichlid elements were well represented at all sites, but *Clarias* bones were rare except in the MNK Main and FC West sites, where they make up about 67% and 38% respectively of all elements (Table 3). Both of these sites were located in the Side Gorge, where stream channels were present (Hay, 1976a), presumably with fresher water. The greater abundance of *Clarias* bones at FC West may be explained by the presence of less saline (fresher) waters than at other sites, while at MNK Main the numbers of *Clarias* bones may represent fish stranded during receding waters in the dry season, or a lag deposit.

Another ecological enigma among the Olduvai Gorge fish is the cichlid mortality pattern. At the MNK-T5 and HWK EE sites, the high number of cichlid individuals found in the same level(s) indicates that these fish died at the same time in reasonably large numbers. Given the frequency of these clusters of perfectly preserved cichlid bones throughout the MNK-T5 and HWK EE site deposits, this pattern of mortality was likely a recurring seasonal event among fish. Today in eastern Africa, cichlids have often been observed stranded in marginal lake or stream waters, due to either sudden fluctuations in water levels, or to receding lake levels near the end of the dry season (e.g. Coe, 1966; Hay, 1976a; Leakey, 1971b). Similar to today's cichlids, the MNK-T5 and HWK EE cichlids may have been stranded by receding waters at the end of the dry season. The carcasses were then covered by sediments brought in by floodwater when the rains began. Quick burial enabled excellent preservation of the bones.

A surprising 90% of the MNK-T5 and HWK EE site cichlid bones were made up of cranial elements (Fig. 8), while an earlier study from different levels at the MNK Main site found cichlid cranial and postcranial elements equally well preserved (Stewart, 1994). The almost complete absence of postcranial bones at MNK-T5 and HWK EE may have been the result of water movement which moved the denser postcranial bones elsewhere, or of consumption of the bodies of the stranded fish by predators, such as

raptors and terrestrial mammals (e.g. Ewer, 1973; Kruuk, 1972; Stewart et al., 1999). Evidence of cut marks on fishbones at about 1.9 Ma indicates that hominins were eating fish in eastern Africa at this time (Braun et al., 2010), although fish consumption is yet to be conclusively documented at Olduvai.

A reversed scenario from that just discussed at the MNK-T5 and HWK EE sites is present at the FC West site. The FC West cichlid bones are dominated (99%) by postcranial elements (vertebrae and spines) (Fig. 8), which are denser, and therefore heavier by area, than cranial elements. Numerous *Clarias* elements were also recovered from FC West, and most of these are dense cranial bone and spine fragments. The denser structure of both the cichlid and *Clarias* FC West bones, and the much lower proportions of more fragile cranial elements, suggest that these bones were part of a 'lag' deposit - where the lighter material has been winnowed out by stream or river action, leaving the denser material clustered together. This dominance of denser postcranial bones among both *Clarias* and cichlids occurs in several different levels at FC West, suggesting that stream or river deposition recurred at FC West over time. Several stream channels were mapped in the Side Gorge, where FC West was located, throughout the deposition of the Tuff II B interval (Hay, 1976a:85).

In sum, the fish diversity in the Olduvai Gorge sites was low, but provides new ecological data about paleo-lake Olduvai. Only *Clarias* (catfish) and Cichlidae were present in the lake as both are more tolerant than other taxa of highly saline and alkaline waters, which were characteristic of paleo-lake Olduvai. Numerous cichlid elements were recovered together in large numbers in the Olduvai sites, suggesting recurrent catastrophic death events. Based on present-day observations, the Olduvai cichlids were likely stranded *en masse* in response to receding lake levels in the dry season. Cichlids inhabit shallow littoral waters, and so were vulnerable to receding lake levels. Surprisingly, in contrast to an earlier study, few postcranial elements were recovered from these strandings. This suggests either water movement transporting the less dense cranial elements elsewhere, or predation by raptors or mammals, potentially including hominins. Finally, it was suggested that the FC West site levels represent lag deposits, based on the dominance of dense, mainly postcranial cichlid bones and fragmented, dense *Clarias* bones, which were not found in the assemblages at other sites.

Paleoecological Implications of the Middle Bed II Large Mammals

No Major Environmental Change within Middle Bed II

We examined bovid tribal abundance data as a proxy for paleoenvironments (Greenacre and Vrba, 1984), comparing assemblages of Bed I, Middle Bed II between tuffs IIA and IIB (assemblage IIA) and tuffs IIB

and IIC (assemblage IIB), and Upper Bed II (above tuff IIC). Correspondence analyses (Fig. 9) indicate that the compositions of the Middle and Upper Bed II assemblages are very similar to each other (dominated by *Alcelaphini*), but differed greatly from those of Bed I, which has greater proportions of *Reduncini*. When Bed I is divided into Lower, Middle, and Upper assemblages (using data from Kappelman, 1984; Shipman and Harris, 1988), it is specifically Middle Bed I (sites between tuffs IB and ID, both dated to ~1.85 Ma) that stands out by a large proportion of *Reduncini*, signaling a temporary but significant increase in wetland habitats. Geological, paleobotanical, isotopic, and micromammal data also indicate a wetter phase during Middle Bed I (Kappelman, 1984 and references therein), which appears to match at least a single humid episode in which paleo-lake Olduvai expanded (Ashley, 2007; Ashley and Driese, 2000; Trauth et al., 2005).

Otherwise, the bovid record provides no evidence for a major environmental change taking place in association with the archaeological shift from Oldowan technologies in assemblage IIA to Acheulean technology in assemblage IIB.

No Major Faunal Turnover in Lower and Middle Bed II

Leakey (1967: 75-76) and Gentry & Gentry (1978c: 59-60) discussed a faunal turnover event between Lower and Middle Bed II. Leakey did not provide details and treated Middle and Upper Bed II as a single assemblage ('upper'). Gentry & Gentry considered the bovid changes in detail and noted several species or sub-species replacements between Lower and Middle Bed II. It is difficult to precisely assess the magnitude of this turnover without larger sample sizes (particularly for Lower Bed II), but we consider these changes to have been minor in relation to the entire large mammal assemblage. As for turnover within Middle Bed II, a comparison of species abundances between assemblages IIA and IIB (using all species represented by a minimum of 5 dental specimens) indicates differences between these two assemblages are also non-significant (paired signed rank Wilcoxon, $p = 0.94$).

Middle Bed II is Species Rich and Top-Heavy

Though fossil assemblages might be expected to be less diverse than analogous extant communities due to preservation biases, the Middle Bed II large mammal fauna is more species-rich than its extant analog, the greater Serengeti ecosystem. Most of the additional Pleistocene species diversity is to be found in the 100-1000 kg mean body size range (Fig. 10A): among the 'macroherbivores' *sensu* Owen-Smith (2013). These include the suids *Kolpochoerus* and *Metridiochoerus* spp., *Giraffa stillei* and *G. pygmaea*, and

bovids such as *Pelorovis oldowayensis* and *Megalotragus isaaci*. Middle Bed II is also richer in megaherbivores (>1000 kg), such as *Sivatherium* and *Deinotherium*, two species with no extant analogs.

Body mass frequency distributions for Middle Bed II and Serengeti are both unimodal and right skewed (Fig. 10A). Unimodal right-skewed distributions are usually typical of continental-scale communities, while biome and local scales show a more symmetric or uniform distribution pattern (Brown and Maurer, 1989; Brown and Nicoletto, 1991; Kozłowski and Gawelczyk, 2002). However, our analysis is missing mammals <10 kg, which are poorly represented in Bed II, and presumably their addition would shift the distribution towards greater symmetry.

Regardless, the Middle Bed II community is more 'top-heavy' and has a heavier mode than the extant Serengeti. The differences are magnified when relative abundance is taken into account (Fig. 10B-C). There is no relationship between mean body mass and abundance in the Middle Bed II assemblage (using dental abundance, spearman's rho < 0.14 and $p = 0.38$). The greater diversity of large species (100-10,000 kg mean body mass) and the lower diversity of medium-sized species (10-100 kg) in the Middle Bed II assemblage cannot, therefore, be explained by taphonomic bias favoring fossilization and recovery of larger species. Furthermore, our taxonomic sample is unlikely to be inflated by temporal or spatial averaging as most taxa can be found in the IIA interval (1.71-1.66 Ma), and many taxa in the Middle Bed II fauna are long-lived lineages commonly found together at numerous other sites.

There are two main explanations proposed for the absence today of so many large-bodied Pleistocene species: climate change or human influence. In the case of Middle Bed II, hypotheses can be framed as follows: 1) Climatic conditions, through their effects on vegetation and productivity, supported more and larger species in Bed II times. A heavier 'fitness optimum' for the community (Brown et al., 1993) is further supported by the observation that some species in Middle Bed II are on average larger than their conspecifics or close relatives today (Gentry and Gentry, 1978a; Leakey, 1965a). Waterbuck, *Hippotragus*, *Equus*, and previously reported *T. strepsiceros*, are all the large end or larger than their living equivalents, and Leakey (1965a: 76) put this to the existence of "optimum feeding conditions" in the past relative to today. Increasing aridity coupled with high-amplitude Pleistocene climatic cycles after 0.8 Ma seem a reasonable culprit, such as the occurrence of several very dry episodes during the late Pleistocene (Scholz et al., 2007). As Faith (2014) has pointed out, the majority of megafaunal extinctions in Africa were of grazing and open-habitat species, potentially confounding the search for a common cause of extinction with other continents. Faith (2014) favors a view in which strong climatic

fluctuations over the last 1 Ma led to the gradual extinction of specialized grazers, leaving more generalized (and mostly smaller-bodied) species as survivors.

Alternately, 2) the loss of Pleistocene African megafauna may be a case of the 'downsizing effect', a pattern whereby the largest species in a community are the first to go when faced with human disturbance. This pattern has been recorded in both extant and archaeological communities faced with human hunting and environmental modification (Dirzo et al., 2014; Lyons et al., 2004; Young et al., 2016). Downsizing is believed to result from the fact that large-bodied species are more likely to be threatened by human hunting, while habitat loss will more often affect smaller species. In this case, the extant Serengeti would represent a 'defaunated' community that is far below its potential species richness. The implication is that, in the absence of humans, the Serengeti would support a much larger number of species than it does today. The 'human' hypothesis for Pleistocene extinctions in Africa and North America has largely fallen out of favor. However, it is difficult to discount entirely. Werdelin and Lewis (2013c) have recently suggested that hominins may have driven the extinction of large carnivores through competition by 2 Ma or even earlier. In this scenario, later extinctions of megaherbivores would be due to a trophic cascade causing long-term restructuring of the mammal community. This is difficult to test directly, but there is a strong theoretical and empirical basis for the existence of hominin-carnivore competitive interactions in the early Pleistocene (e.g. Blumenschine et al., 1994; Lewis, 1997; Shipman and Walker, 1989; Werdelin and Lewis, 2013c), including Olduvai specimens that exhibit both hominin and carnivore feeding traces (Egeland, 2014; Egeland et al., 2004; Pante et al., 2012) (also Pante, et al. this volume, "The carnivorous feeding behavior of early *Homo*").

Middle Bed II and extant Serengeti Trophic Webs

Food web properties reveal structural patterns underlying trophic relationships of different communities, and can provide indications of how mammal communities responded to past climate changes (Nenzén et al., 2014; Pires et al., 2015; Yeakel et al., 2013). Here, we use network analysis in order to 1) describe the properties of the Middle Bed II large mammal food web and compare it to the extant Serengeti; 2) explore the role that an early *Homo* species – e.g. *H. habilis*, a likely scavenger, or *H. erectus*, a generalized predator – might have played in the fossil community; and 3) quantify the resilience of the Middle Bed II and the Serengeti large mammal communities to different extinction scenarios.

Our results indicate that 1) Middle Bed II and Serengeti have similar foodweb structure, and 2) early hominins acted as a key node in the foodweb, connecting almost all the species in the Middle Bed II

community (Fig. 11). As a consequence, hominins – generalist and opportunistic carnivores – would have significantly increased competition among carnivores and vulnerability among herbivores. We also find that the Middle Bed II food web structure is extremely similar to that of the extant Serengeti (Table 4, Fig 11). Both webs have similar connectance, nestedness, generality, and vulnerability values and similar predator-prey ratios. Connectance values in both webs are very high (over 0.5). For comparison, European Pleistocene mammal food webs have low connectance (less than 0.2, Nenzén et al., 2014), and many extant food webs have connectance values less than 0.4 (Dunne, 2002). This means that – assuming our assumptions about predator prey range are realistic – large mammal species in Olduvai and Serengeti are more interlinked than species in many other communities. However, when taking into account prey density to weight the trophic interactions, results change, and connectance usually drops, and thus, strength of the interactions, and not only the basic architecture of the food webs, can be essential to understand food web dynamics across long time scales (Ings, 2009).

As a generalist species, the presence of *Homo* increases the number of links in the food web, increases nestedness and competition (dietary overlap) among predators, and increases vulnerability (apparent competition) among herbivores (by sharing more predators). The removal of *Homo* affects Olduvai food web structure more so than the removal of other predators. Food web parameters without early *Homo* are in the margins of the distribution of a null model which removed one predator at a time (Fig 12). Removal of *Homo* results in significant changes (outlier values) in three parameters: decreased link density, decreased generality and vulnerability (apparent competition among prey species).

Both Serengeti and Middle Bed II food webs are very resilient to extinction (>0.8 robustness values across all experiments). Interestingly, extinction processes based on species abundance or random extinctions cause very few secondary extinctions. Even when key prey are removed (the ones with more predators), robustness decreases only slightly. High generality values for both Middle Bed II and Serengeti food webs mean secondary extinctions of predators are unlikely to be caused by the extinction of prey species.

Conclusions

The fish and mammal assemblages presented here have provided a synthetic view of the faunal community that existed at Olduvai in Middle Bed II times, or between about 1.7 and ~1.4 Ma. These fill in previous gaps between faunas in older and younger intervals (e.g. Beds I and IV) and provide a new comparative reference for contemporaneous faunas from other parts of eastern Africa, such as the Turkana Basin. The Middle Bed II assemblage provides further information on the coevolution of

African savanna faunas and vegetation in the context of increasing Plio-Pleistocene aridity. The sheer diversity of species, including many large-bodied species, at Neogene and Pleistocene African sites is still perplexing and makes extant African faunas look depauperate in comparison. These assemblages, including that of Middle Bed II presented here, despite their antiquity are relevant to discussions of Pleistocene large mammal extinctions and the loss of species diversity coming into the Holocene.

Further work should focus on the communities of Upper Bed II, and Beds III and IV. Lack of information on these has impeded a long-term view of evolution at Olduvai, despite over a century of work there. This, in conjunction with improving local and regional paleoclimatic records (e.g. paleo-lake cores) should provide unparalleled insight into long-term community evolution at a single locality leading to one of the world's most emblematic savanna ecosystems, the Serengeti.

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Figure Captions

Figure 1. Simplified stratigraphy of Olduvai Gorge. This mainly follows previous stratigraphic schemes, though Bed II tuff ages and the placement of EF-HR above Tuff IIC are updated following OGAP findings. Site names within bracketing tuffs are alphabetical, not stratigraphic.

Figure 2. Bovid teeth. **A**, *Pelorovis oldowayensis*, HWK EE T27-L31-28. **B**, cf. *Taurotragus*, MNK T5-L10-2124. **C**, *Tragelaphus strepsiceros*, HWK EE 1972-3916. **D**, *Hippotragus gigas*, MNK M-L3-231. **E**, *Kobus sigmoidalis*, HWK EE L6-1911. **F**, Alcelaphini small sp., HWK EE T27-L32-608. **G**, *Megalotragus isaaci*, MNK T5-L10-1733 left mandible. **H**, *H. gigas*, FLKW T69-L22-596 left mandible. **I**, *K. sigmoidalis*,

HWK EE M-L10-564 left m3. **J-K**, Alcelaphini intermediate size: **J**, HWK EE L10-2400 left mandible; **K**, HWK EE L10-2566 right mandible (mirrored). **L**, Alcelaphini small sp., HWK EE-L6-1740 right m3. **M**, Alcelaphini small sp., HWK EE 1972-1156 left mandible. **N**, Alcelaphini small sp., HWK EE L10-707 left m3.

Figure 3. Bovid cranial and horn core remains. **A-B**, *Parmularius angusticornis*. **A**, HWK EE 1972-172, frontals with both horn cores in left lateral and anterior views. **B**, HWK EE M-L1-4052 (= L4-53), partial cranium with horn cores in left lateral and anterior views. **C**, *Megalotragus isaaci*, MNK M-L6B-151, right horn core, and MNK M-L6B-152 left frontlet with complete horn core, both almost certainly the same individual, both in anterior view. **D**, *Damaliscus niro*, MNK M-L6B-149, right horn core in lateral view. **E**, ? Antilopini, HWK EE M-L1-1860, left horn core in medial and anterior views. **F**, *Gazella* aff. *rufifrons*, HWK EE 1972-2396, right horn core with frontlet in anterior and lateral views. **G-H**, *Antidorcas recki*, left horn cores in lateral view. **G**, HWK EE 1972-3108. **H**, HWK EE 1972-2780. Scale bar 10 cm.

Figure 4. *Parmularius maasaicus* sp. nov. **A**, HWK EE 1972-2181, holotype frontlet with horn cores. **B**, HWK EE 1972-2061, frontlet with horn cores. Both in anterior (top left), posterior (top right), dorsal (bottom left), and right lateral (bottom right) views. Scale bar 15 cm.

Figure 5. Tooth size ranges in extant and fossil bovid taxa indicates body size (niche) partitioning. Lower m3 length in extant (below) and fossil Middle Bed II (middle) bovids. Upper M3 length in fossil taxa up top. Note that fossil species are generally larger than their extant relatives. The fossil alcelaphin *Megalotragus isaaci* was of similar size to a cape buffalo, and the bovin *Pelorovis oldowayensis* was much larger still. The unnamed small alcelaphin occupies a size range smaller than any extant alcelaphin. Extant data from Janis (1990). Note x-axis log scale.

Figure 6. Teeth of large herbivores (non-bovids). **A**, *Elephas recki*, HWK EE 1972-1210, left mandible with m2 or m3. **B**, *Sivatherium maurusium*, HWK EE 1972-634, right mandible with p2-m3. **C**, *Equus oldowayensis*, HWK EE M-L10-1575, left and right mandibles with p2-m2. **D**, *Hippopotamus gorgops*, HWK EE M-L10-1522, right lower m2. **E**, *Ceratotherium* HWK EE 1972-4172, left upper M1 or M2. **F**, *Ceratotherium*, HWK EE T27-L32-186, right upper M1 or M2. **G**, *Eq. oldowayensis* HWK EE M-L10-1575 (as in C). **H**, *Eq. oldowayensis* HWK EE 1972-2852, anterior mandible with right and left i1-3. **I**,

Kolpochoerus paiceae, FCW M-L10-194, left lower m3. **J**, *K. limnetes* HWK EE 1972-4186, right lower m3. **K**, *Eurygnathohippus cornelianus*, HWK EE M-L2-146, left upper M1 or M2. **L**, *Eu. cornelianus*, HWK EE M-L6-463, right lower m1 or m2. **M**, *Eq. oldowayensis* HWK EE 1972-2464, right maxilla with P4-M2. **N**, *Theropithecus oswaldi*, FCE T30-L64-16, left maxilla with M1-2. **O**, *T. oswaldi*, HWK EE 1972-4403, left mandible with partial m3. **P**, *Eu. cornelianus*, FCE T31-L80-1131, right upper M1 or M2. **Q**, *Eq. oldowayensis*, HWK EE 1972-1063, right upper M3. **R**, *Eq. oldowayensis*, HWK EE M-L10-2171, left upper P3 or P4.

Figure 7. Carnivore postcrania. A-B, *Prototocyon*. **A**, FCW T63-L62-240, left distal humerus. **B**, MNK T5-L9-1159a, distal metatarsal. **C-D, *Crocuta* sp..** **C**, HWK EE M-L4-294, right scapula. **D**, HWK EE 1972-400, left humerus. **D**, *Caracal/Leptailurus*, MNK T5-L12-482, right humerus.

Figure 8. Numbers and percentages of cranial and postcranial Cichlidae and Clarias elements at Olduvai Gorge sites.

Figure 9. Correspondence analyses of Olduvai bovid abundances by assemblage. Alcelaphini (open habitats) and Reduncini (humid habitats) represent the main endmembers of the first axis in all plots. Regardless of the data type used, it can be seen that all Middle Bed II assemblages are very similar to each other and also to those of Lower and Upper Bed I and Lower Bed II. This implies insignificant habitat differences (or changes) on the landscape-scale at these times. The only stratigraphic interval that stands out is that of Middle Bed I, which is abundant in Reduncini, suggesting an episode of wetland habitat expansion at that time.

Figure 10. Distribution of body size for the Middle Bed II and extant Serengeti large mammal communities. **A**, by species richness. **B**, by relative abundance (number of dental specimens), and **C**, by relative biomass (abundance x mass). The Middle Bed II community has a much greater diversity and abundance of larger-bodied species (>~300 Kg) than the extant Serengeti. The extant Serengeti community has a higher richness and abundance of smaller species (< 100 Kg) than during Middle Bed II times.

Figure 11. Olduvai Bed II and Serengeti food webs. Prey in green and predators in red (*Homo* sp. in brown). Node sizes are proportional to species body mass, and link width is weighted by prey abundance.

Figure 12. Distribution of the food web parameters after the removal of one predator at a time. Values for the removal of *Homo* sp. in red.

Table Captions

Table 1. List of all large mammals recovered from Middle Bed II. Asterisk indicates identification from a previous study.

Artiodactyla	Bovidae	Aepycerotini	<i>Aepyceros melampus</i> *	
		Alcelaphini	Alcelaphini small sp. Alcelaphini 'sp. 3'* <i>Connochaetes</i> sp. <i>Damaliscus niro</i> <i>Megalotragus isaaci</i> <i>Parmularius angusticornis</i> <i>Parmularius masaicus</i> sp. nov.	
		Antilopini	<i>Antidorcas recki</i> <i>Gazella</i> aff. <i>rufifrons</i> Antilopini sp.	
		Bovini	<i>Pelorovis oldowayensis</i> <i>Syncerus acoelotus</i> *	
		Hippotragini	<i>Hippotragus gigas</i>	
		Reduncini	<i>Kobus sigmoidalis</i> / <i>ellipsiprymnus</i> <i>Kobus kob</i> *	
		Tragelaphini	<i>Tragelaphus strepsiceros</i> Tragelaphini small sp.* cf. <i>Taurotragus</i> sp.	
		Giraffidae	Giraffini	<i>Giraffa jumae</i> <i>Giraffa stillei</i> <i>Giraffa pygmaea</i>
			Sivatheriini	<i>Sivatherium maurusium</i>
			Hippopotamidae	<i>Hippopotamus gorgops</i> Hippopotamidae small sp.*
	Suidae	<i>Kolpochoerus limnetes</i> <i>Kolpochoerus olduvaiensis</i> <i>Kolpochoerus majus</i> <i>Metridiochoerus andrewsi</i> <i>Metridiochoerus compactus</i> <i>Metridiochoerus hopwoodi</i> <i>Metridiochoerus modestus</i> *		
Perrisodactyla	Equidae	<i>Equus oldowayensis</i> <i>Eurygnathohippus</i> cf. <i>cornelianus</i>		
	Rhinocerotidae	<i>Ceratotherium simum/germanoaffricanum</i> <i>Diceros bicornis</i> *		
Carnivora	Canidae	<i>Prototocyon</i> sp. <i>Xenocyon falconeri</i> *		
	Hyaenidae	<i>Crocuta</i> cf. <i>ultra</i> <i>Hyaena hyaena</i> *		
	Felidae	Machairodontini	<i>Dinofelis</i> sp.	
		Felini	<i>Caracal / Leptailurus</i> sp. <i>Panthera leo</i> <i>Panthera pardus</i>	
		Viverridae	<i>Pseudocivetta ingens</i>	

Primates	Cercopithecidae		<i>Theropithecus oswaldi</i>
	Hominidae	Hominini	<i>Homo habilis</i> *
Proboscidea	Deinotheriidae		<i>Deinotherium bozasi</i>
	Elephantidae		<i>Elephas recki</i>

Table 2. Measurements of *Parmularius maasaicus* sp. nov. Dist. refers to distance; div. to divergence of the horn cores to each other (measured in anterior view); incl. to inclination (measured in lateral view as the angle between the posterior horn core and the posterior frontals / parietals); and SOF to the supraorbital foramina.

Specimen	DAP	DT	Length	Torsion	Dist. across bases	Dist. between bases	Dist. across dorsal orbit	Div. above base	Incl. against frontal	Fronto-parietal angle	Dist. SOF
HWK EE 1972-2181	38.9L 37.4R	44.2L 44.5R	165+ (170)L 170R	~45°	104.5	23.9	149.9	80°	90°	100°	58.6
HWK EE 1972-2061	51.9L 51.2R	56.6L 58.0R	220L 200+(21 0e)	~45°	108.8	20.5	-	100°	85°	100°	60e
HWK EE 1972-285	35.7	45.3	175	~45°	107e	26e	-	110°e	75°	120°	-
HWK EE 1972-954	24.0	32.2	170	~45°	-	-	-	-	-	-	-
HWK EE M-L4-7	38.6	43.4	165	~45°	95e	22e	-	-	-	-	-

Table 3. Numbers and percentages of identified fish taxa from Bed II sites at Olduvai Gorge. *

indicates that most elements come from levels 4 and 6. + indicates most elements from level 6.

Sites	<i>Clarias</i> sp.		Cichlidae		Total
	n	%	n	%	n
FC East- T31	1	50	1	50	2
FC West	19	38	31	62	50
FLK West-T69-L22	0	0	3	100	3
HWKEE- T1 Main*	1	2.6	37	97.4	38
MNK- T5 –Level 8	0	0	4	100	4
MNK- T5 –Level 9	7	1.9	364	98.1	371
MNK- T5 –Level 10	4	1.4	275	98.6	279
MNK-T5- Level 12	0	0	3	100	3
MNK Main-T6+	12	66.7	6	33.3	18
Total	44	5.7	724	94.3	768

Table 4. Olduvai Middle Bed II and Serengeti food web parameters.

	Middle Bed II	Serengeti
Connectance	0.58	0.65
Links per species	3.31	3.19
Linkage density	12.5	11.1
Nestedness	31.8	33.6
Weighted nestedness	0.5	0.22
Generality	18	17
Vulnerability	4.06	3.92
Dietary overlap among carnivores	0.54	0.63
Predator overlap among prey (shared predators)	0.64	0.64
Predator prey ratio	0.22	0.23

Table 5. Robustness of the food webs to three extinction processes.

	Middle Bed II	Serengeti
Random extinction	0.95	0.96
Abundance driven extinction	0.97	0.97
Predator driven extinction	0.8	0.87

Supplementary Materials

Supplementary File 1. Excel spreadsheets with all specimens reported here, including metrics.

Supplementary File 2. Table of body mass and abundance data used for the food web modeling.

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Figure 1

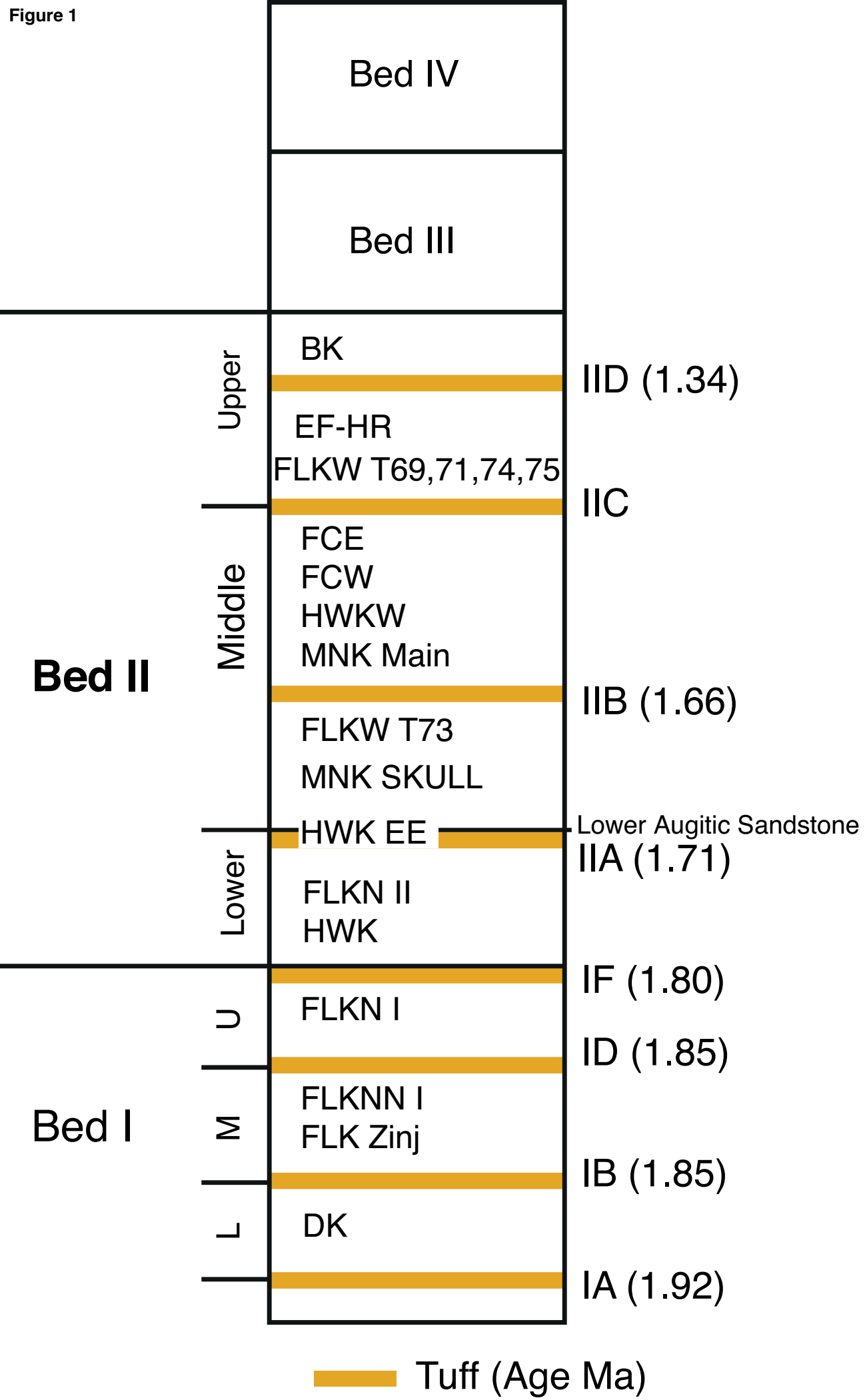


Figure 2
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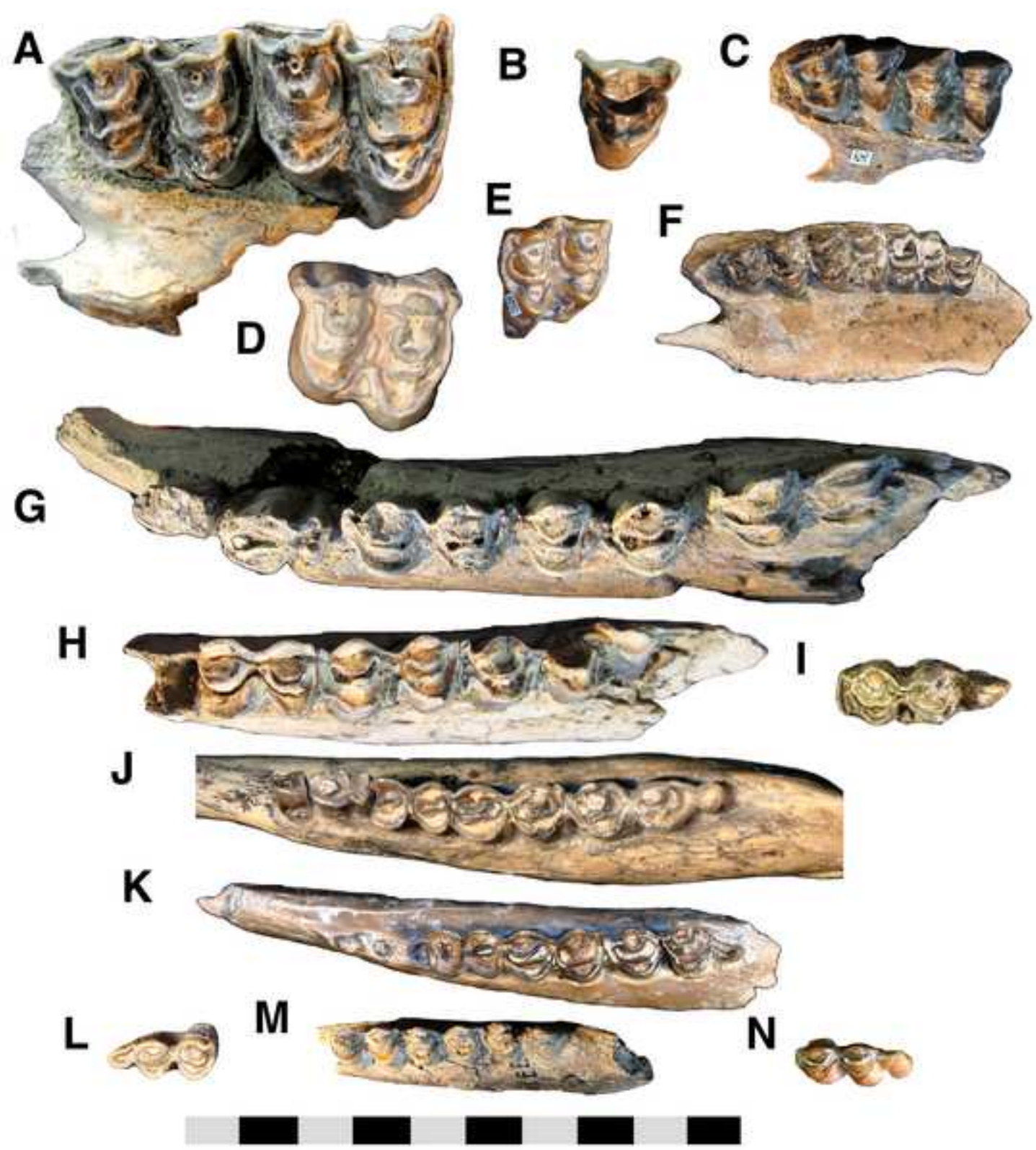


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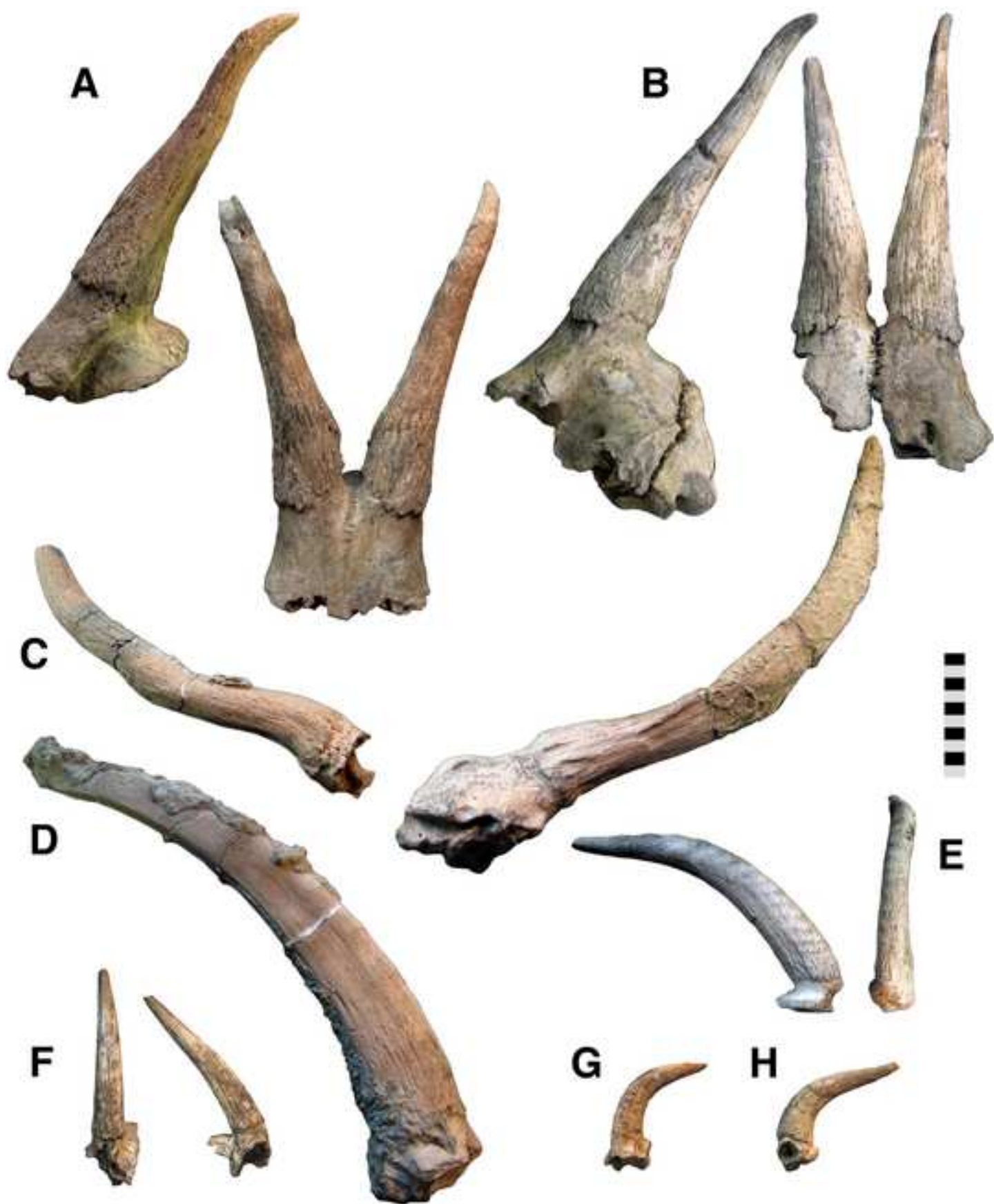


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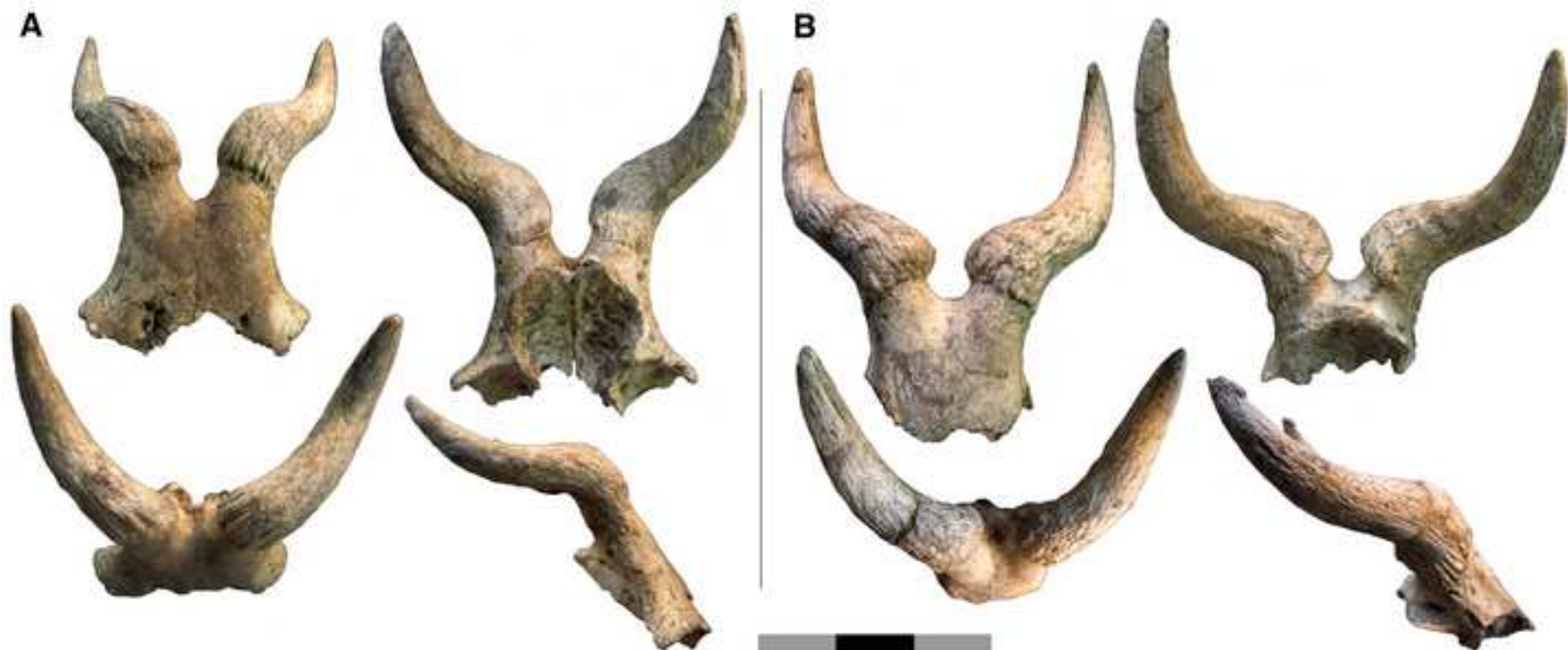


Figure 5

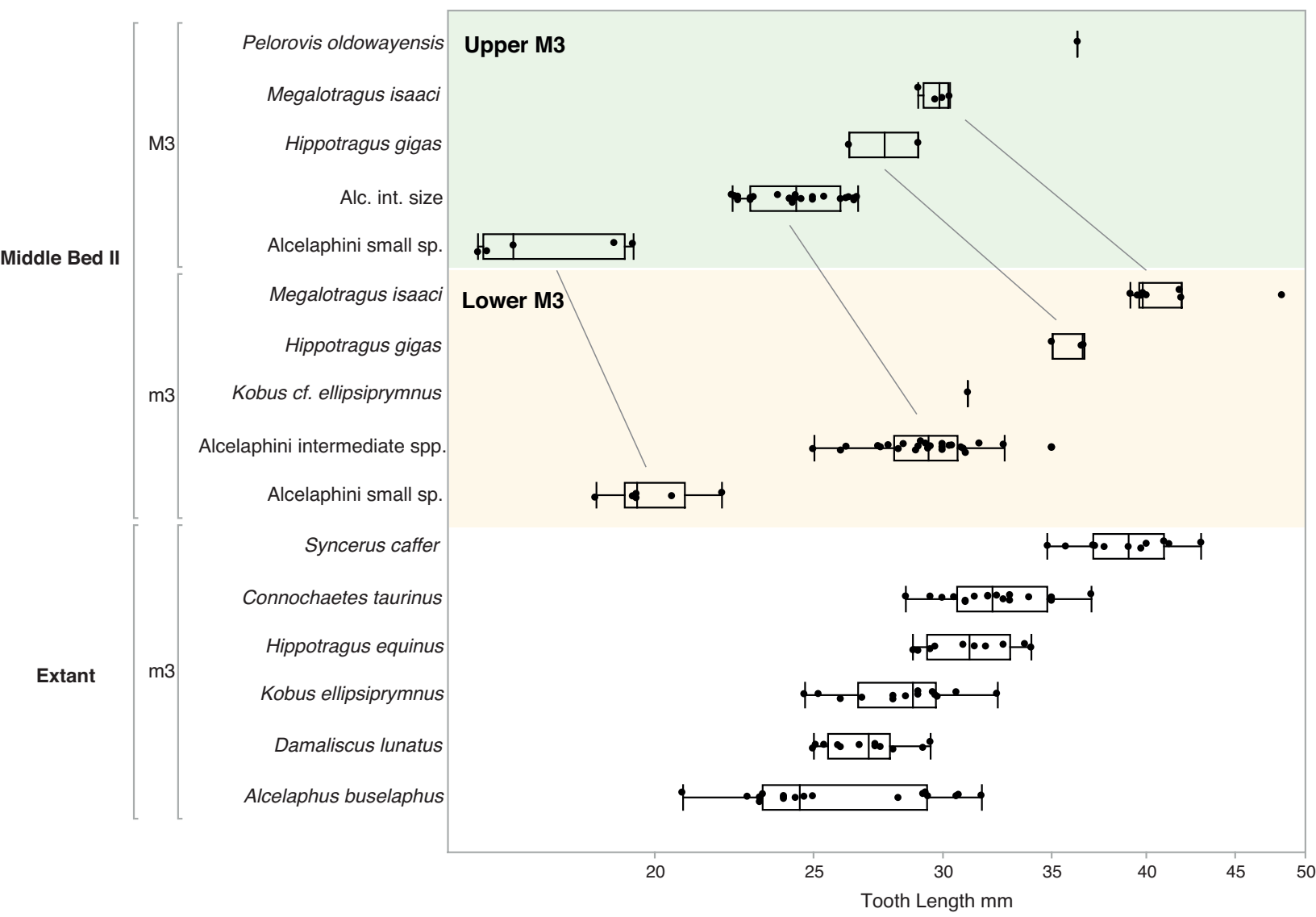


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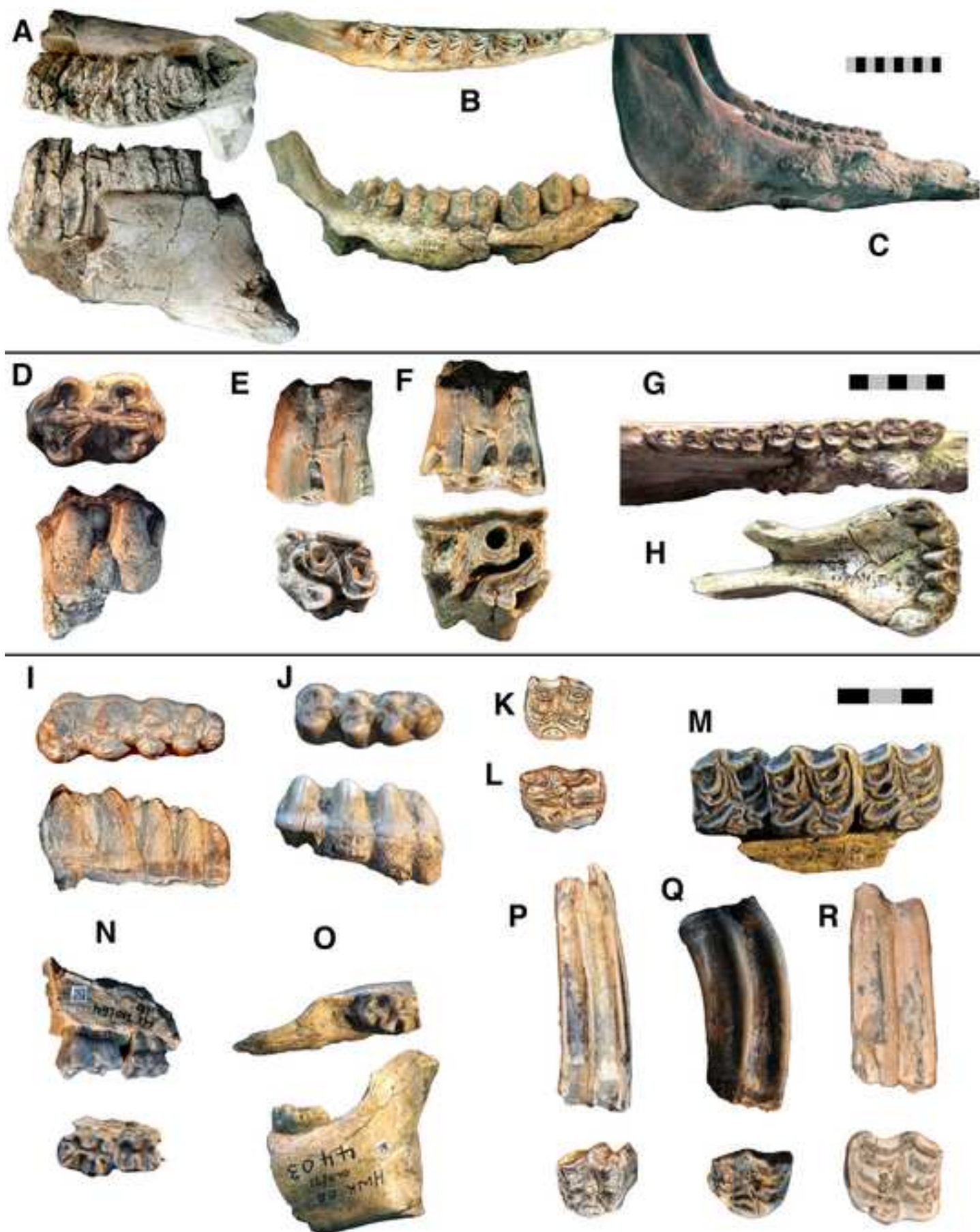


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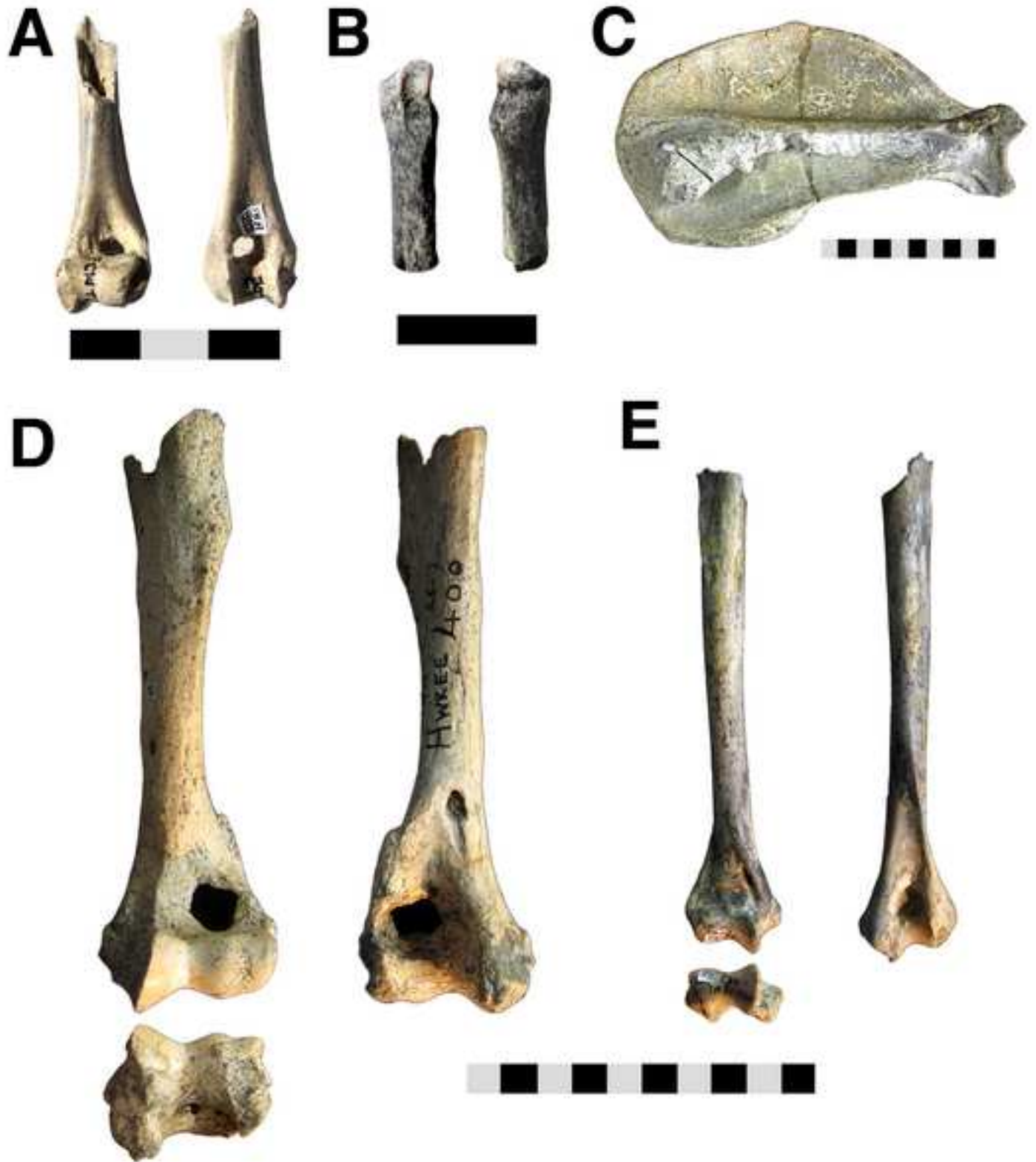


Figure 8

OLDUVAI
GORGE
SITES:

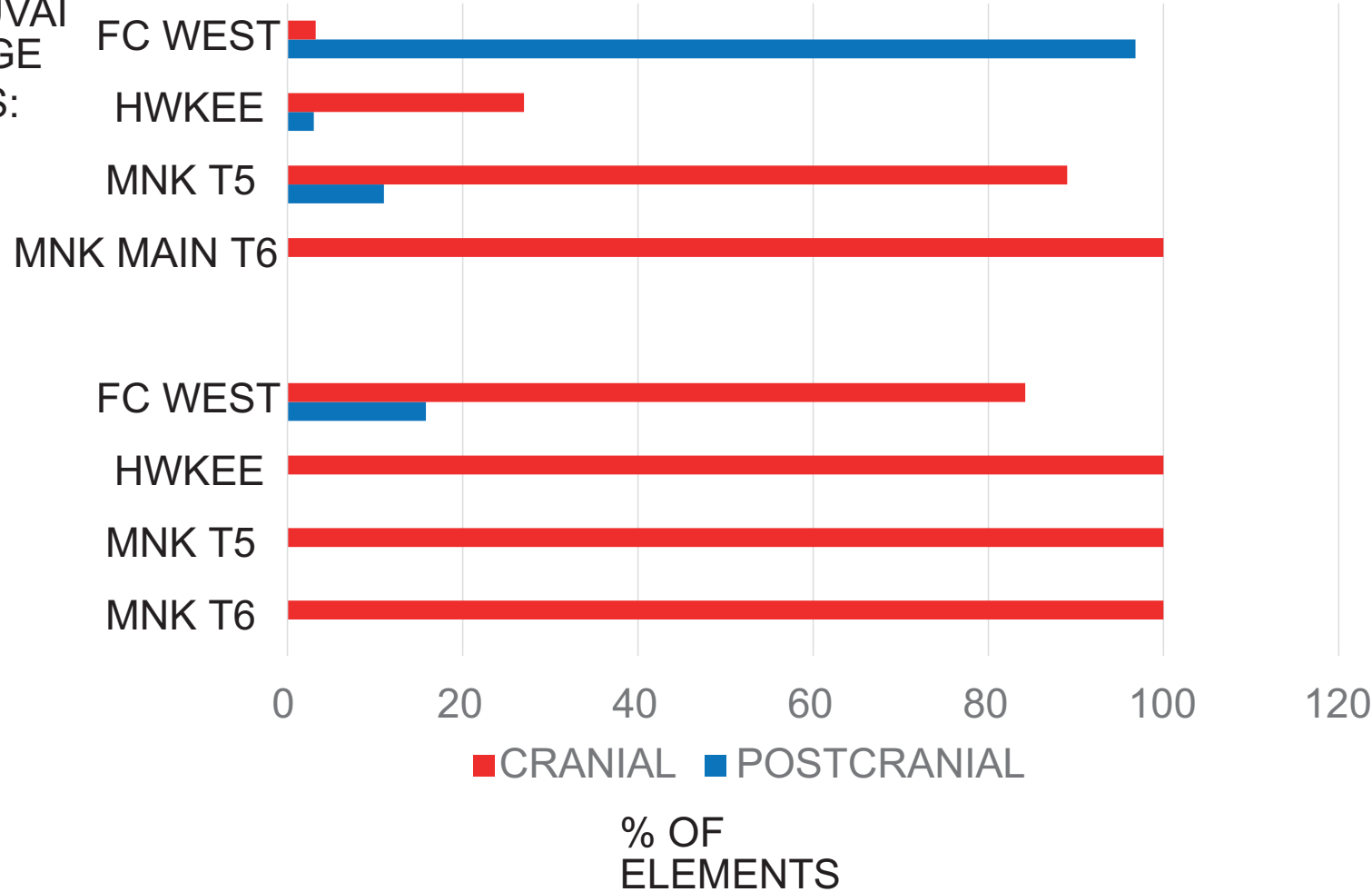
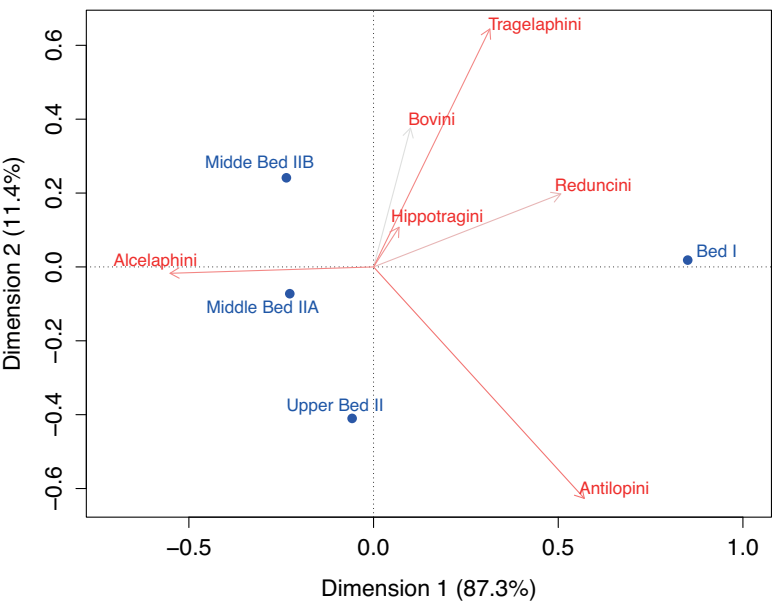
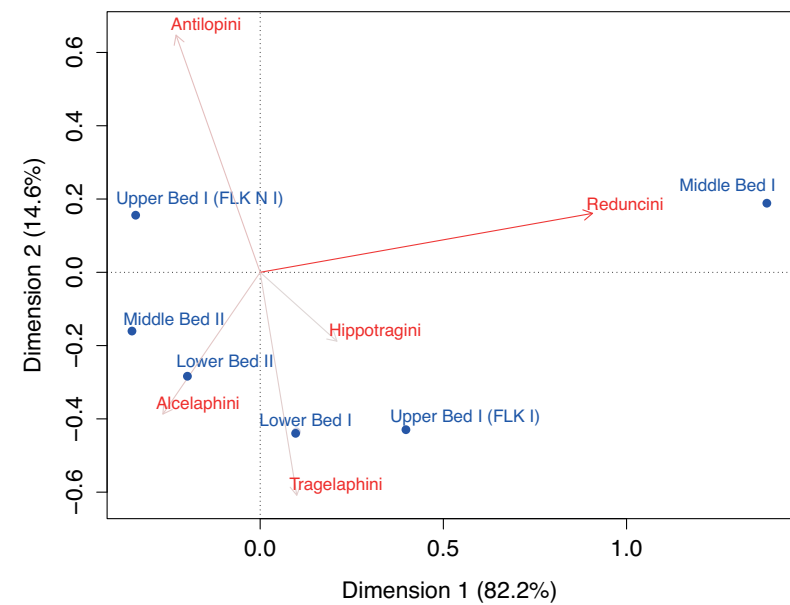


Figure 9

This study Dental NISP Data



Kappelman (1984) NISP Data



Shipman & Harris (1986) MNI Data

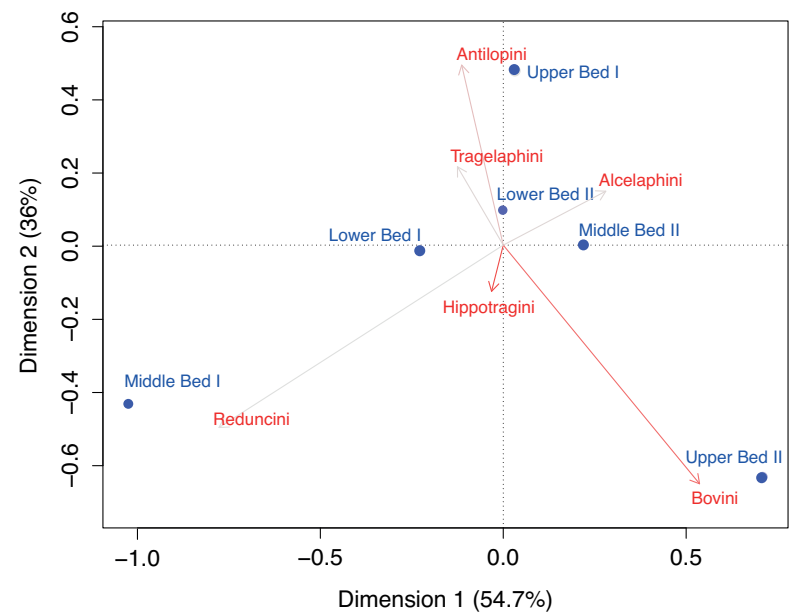
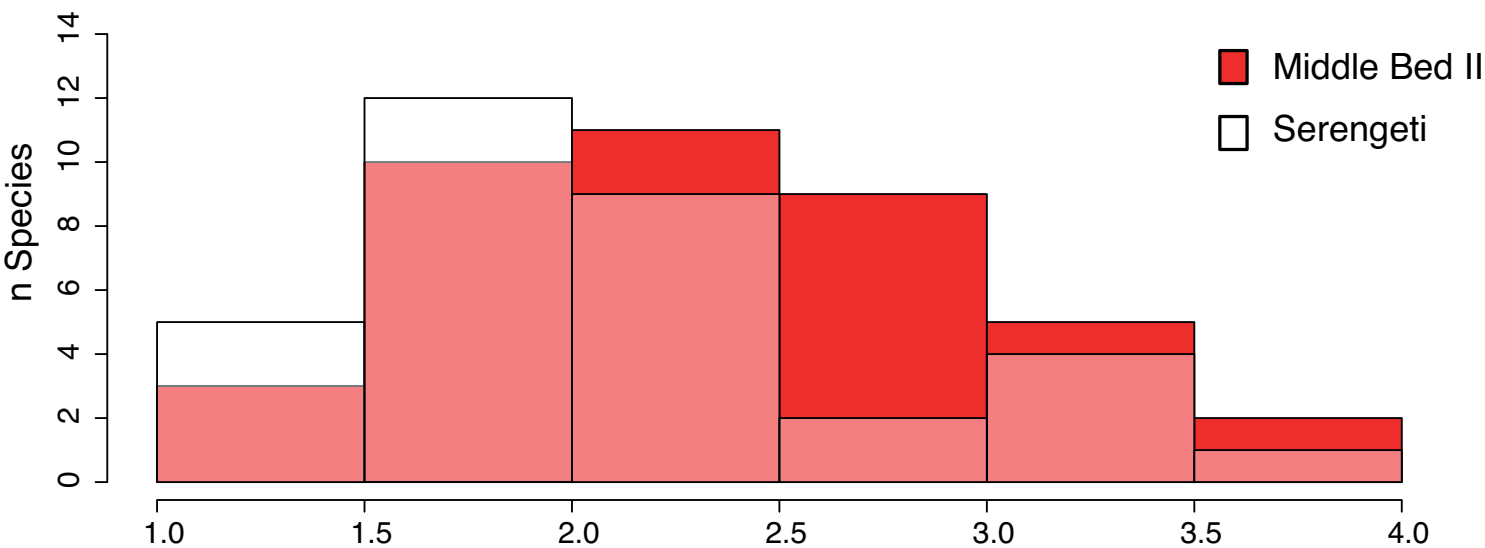
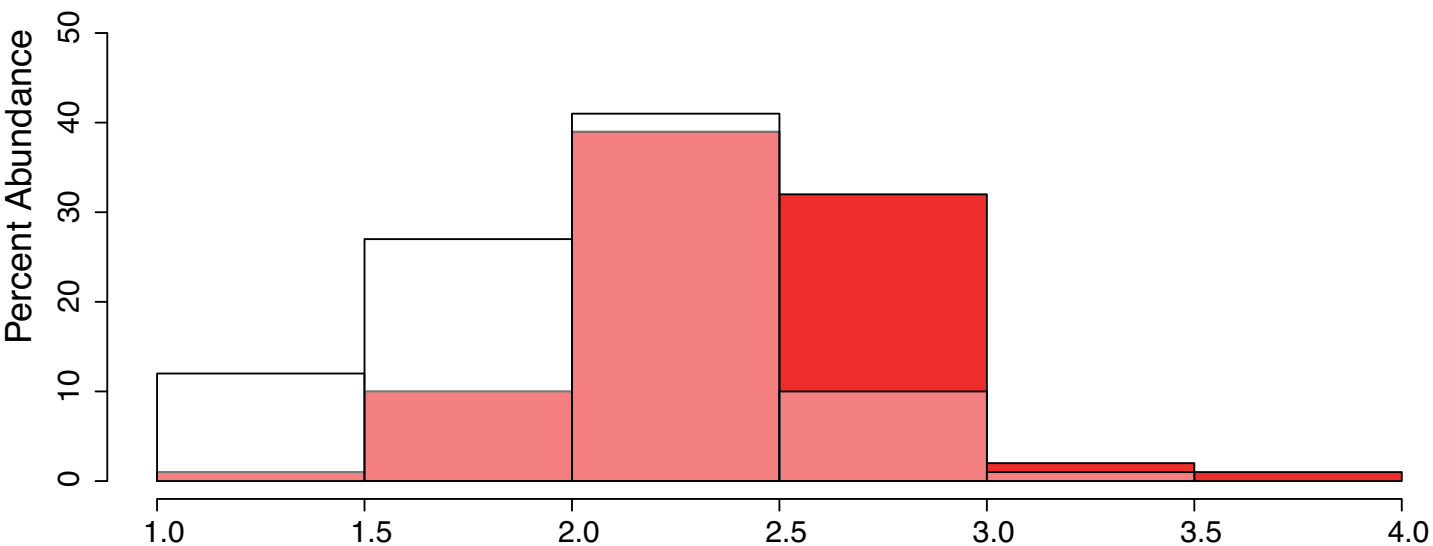


Figure 10

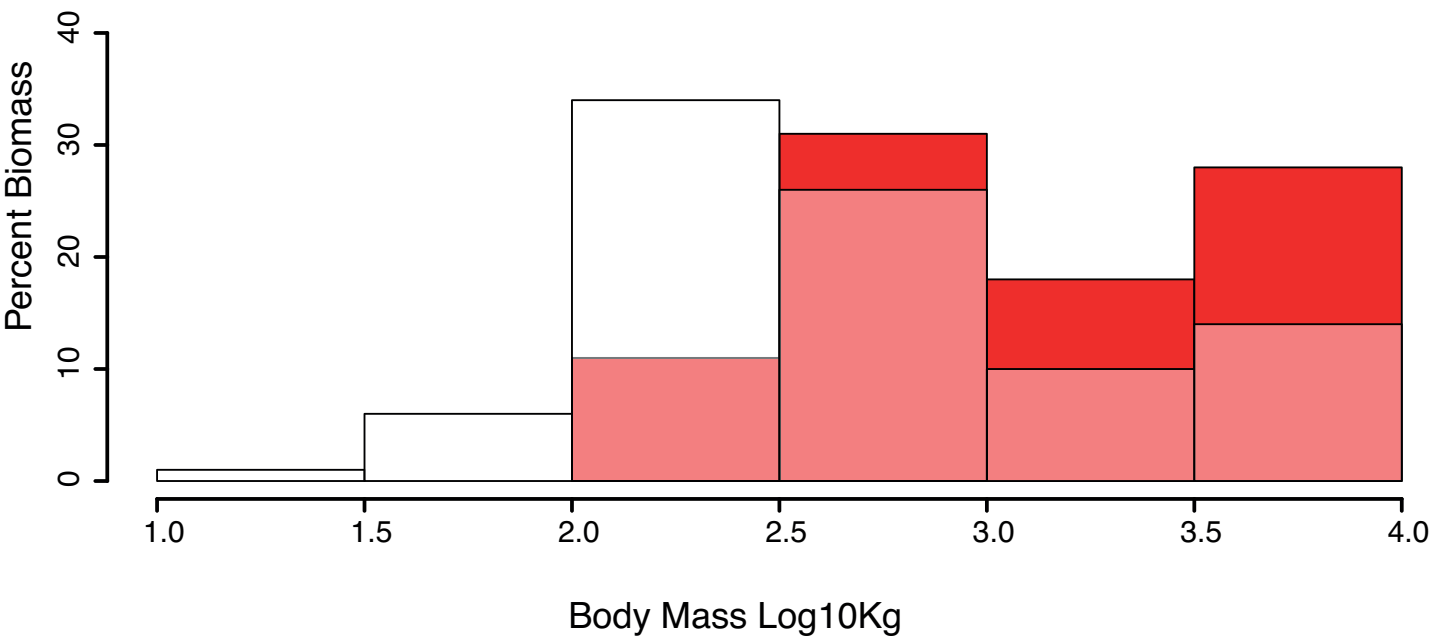
Body Size Distribution by Species Richness



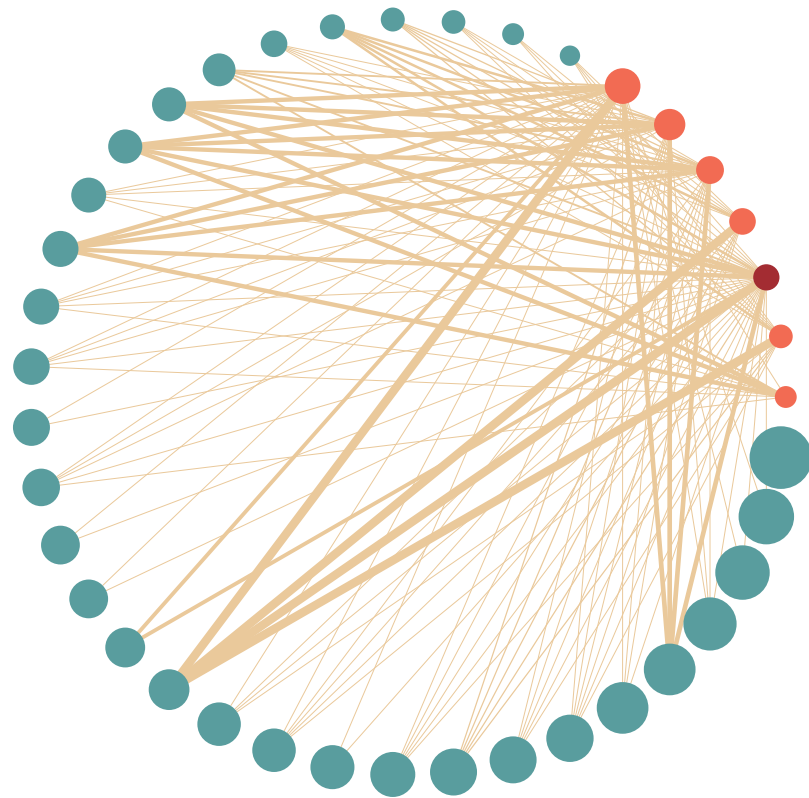
Body Size Distribution by Abundance



Body Size Distribution by Biomass (Abundance x Mass)



Olduvai Bed II



Serengeti

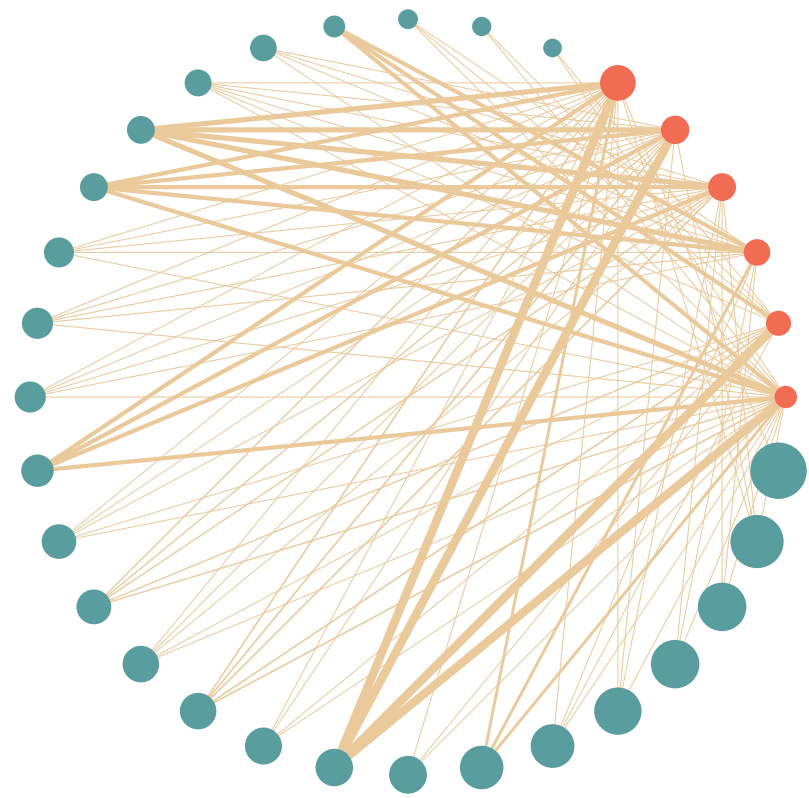
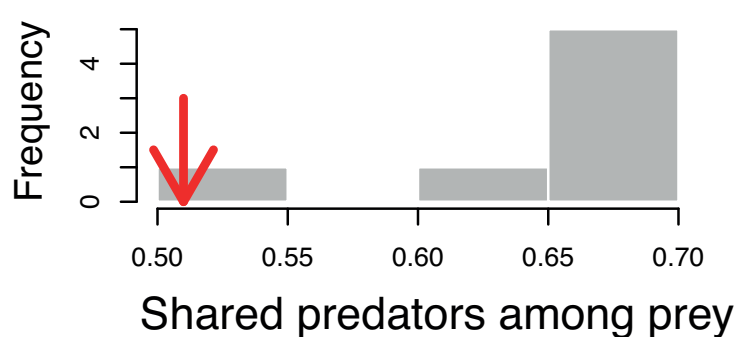
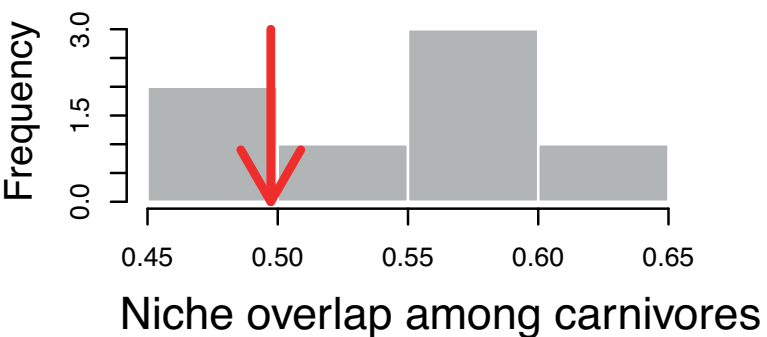
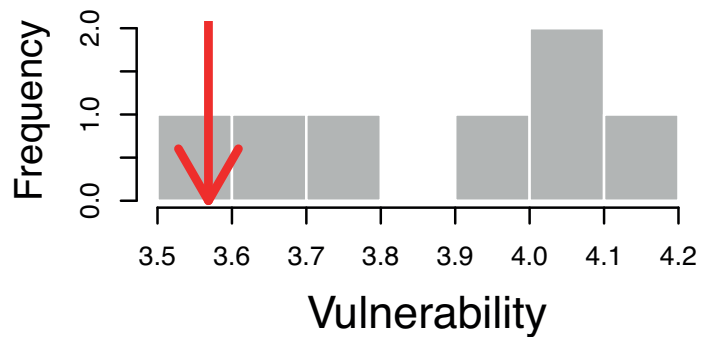
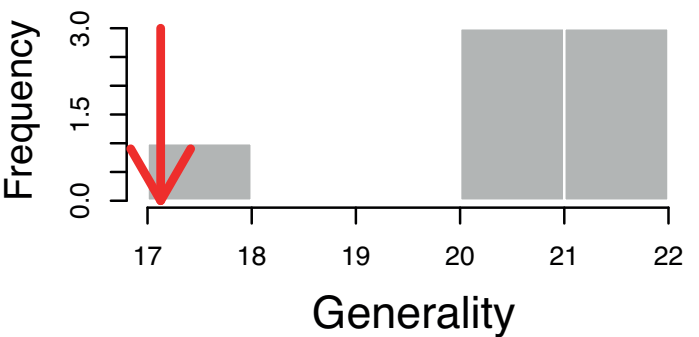
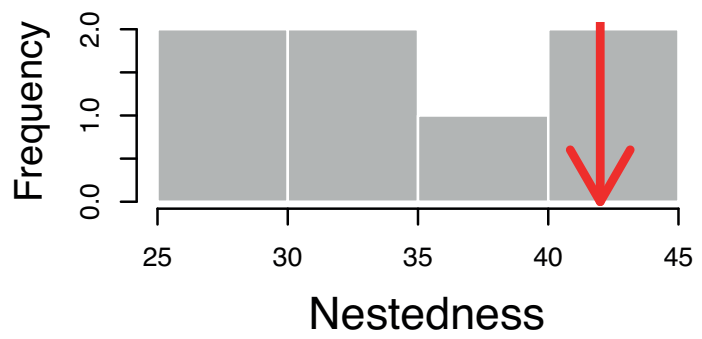
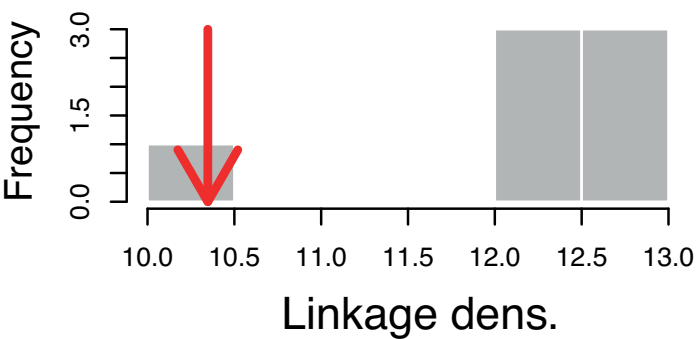
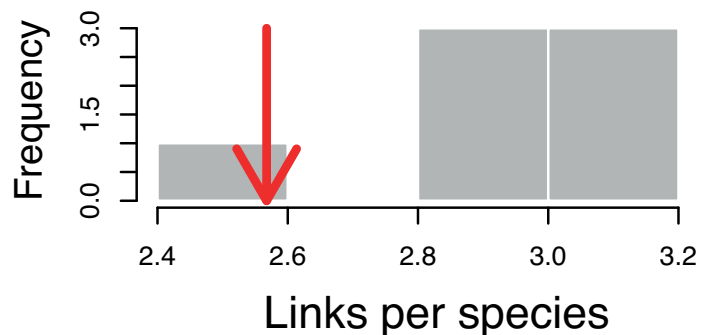
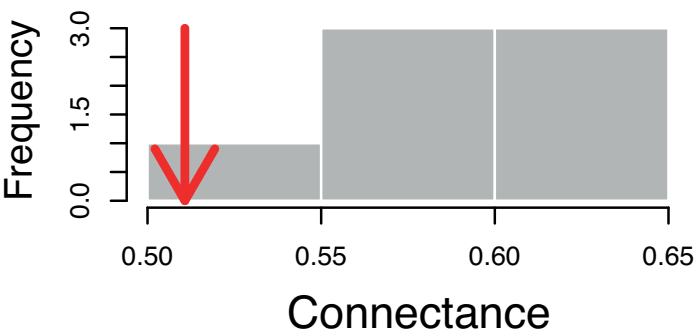


Figure 12



Supplementary Table 1

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Supplementary Table 2

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