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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 a rich vertebrate fauna from several sites within Bed II, Olduvai Gorge, Tanzania. Study of these as well as recently re-organized collections from Mary Leakey's 1972 HWK EE excavations here provides a synthetic view of the faunal community of Olduvai during Middle Bed II at ~1.7–1.4 Ma, an interval that captures the local transition from Oldowan to Acheulean technology. We expand the faunal list for this interval, name a new bovid species, clarify 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 an alkaline lake. Fish diversity is low and dominated by cichlids, which indicates strongly saline conditions. The taphonomy of the fish assemblages supports reconstructions of fluctuating lake levels with mass die-offs in evaporating pools. The mammals are dominated by grazing bovids and equids. Habitats remained consistently dry and open throughout the entire Bed II sequence, with no major turnover or paleoecological changes taking place. Rather, wooded and wet habitats had already given way to drier and more open habitats by the top of Bed I, at 1.85–1.80 Ma. This ecological change is close to the age of the Oldowan-Acheulean transition in Kenya and Ethiopia, but precedes the local transition in Middle Bed II.

The Middle Bed II large mammal community is much richer in species and includes a much larger number of large-bodied species (>300 kg) than the modern Serengeti. This reflects the severity of Pleistocene extinctions on African large mammals, with the loss of large species fitting a pattern typical of defaunation or 'downsizing' by human disturbance. However, trophic network (food web) analyses show that the Middle Bed II community was robust, and comparisons with the Serengeti community indicate that the fundamental structure of food webs remained intact despite Pleistocene extinctions. The presence of a generalized meat-eating hominin in the Middle Bed II community would have increased competition among carnivores and vulnerability among herbivores, but the high generality and interconnectedness of the Middle Bed II food web suggests this community was buffered against extinctions caused by trophic interactions.

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1. Introduction

Fieldwork by the Olduvai Geochronology and Archaeology Project (OGAP) since 2008 has produced a large collection of vertebrate fauna from Middle Bed II at Olduvai Gorge, Tanzania. Most paleontological studies of the last 100 years at Olduvai have focused on Bed I and Lower Bed II, and comparatively little attention has been paid to the Middle and Upper parts of Bed II, which document the transition from Oldowan to Acheulean stone tool technologies (Stanistreet et al., 2018; de la Torre et al., 2012).

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 the Berlin expedition of 1913 (Reck, 1914). Geological work over the last 100 years (Leakey, 1978) has clarified the chronostratigraphy at Olduvai. Bed I is well dated to 2.0–1.8 Ma

(Deino, 2012). Bed II is divided into Lower, Middle, and Upper units (Leakey, 1971) that together span some 600,000 years (1.8–1.2 Ma; McHenry et al., 2016). We take Middle Bed II to include all levels from the base of the Lower Augitic Sandstone up to Tuff IIC (Stanistreet et al., 2018). The age of Middle Bed II is constrained to 1.76–1.3 Ma or 1.76–1.5 Ma based on the ages of Tuffs IIA (Curtis and Hay, 1972) and IID (Manega, 1993; Domínguez-Rodrigo et al., 2013). Our estimate for the undated Tuff IIC, which defines the top of Middle Bed II, is ~1.6–1.4 Ma. Tuff IIB bisects the sequence and is located just below a tuff dated to 1.66 Ma (Uribelarrea et al., 2017) that itself underlies the Bird Print Tuff (BPT; McHenry and Stanistreet, 2018; Díez-Martín et al., 2015). In this paper, we follow the stratigraphic model of Stanistreet et al. (2018) and McHenry and Stanistreet (2018), in which the transition from Oldowan to Acheulean stone tool technologies at Olduvai occurs in

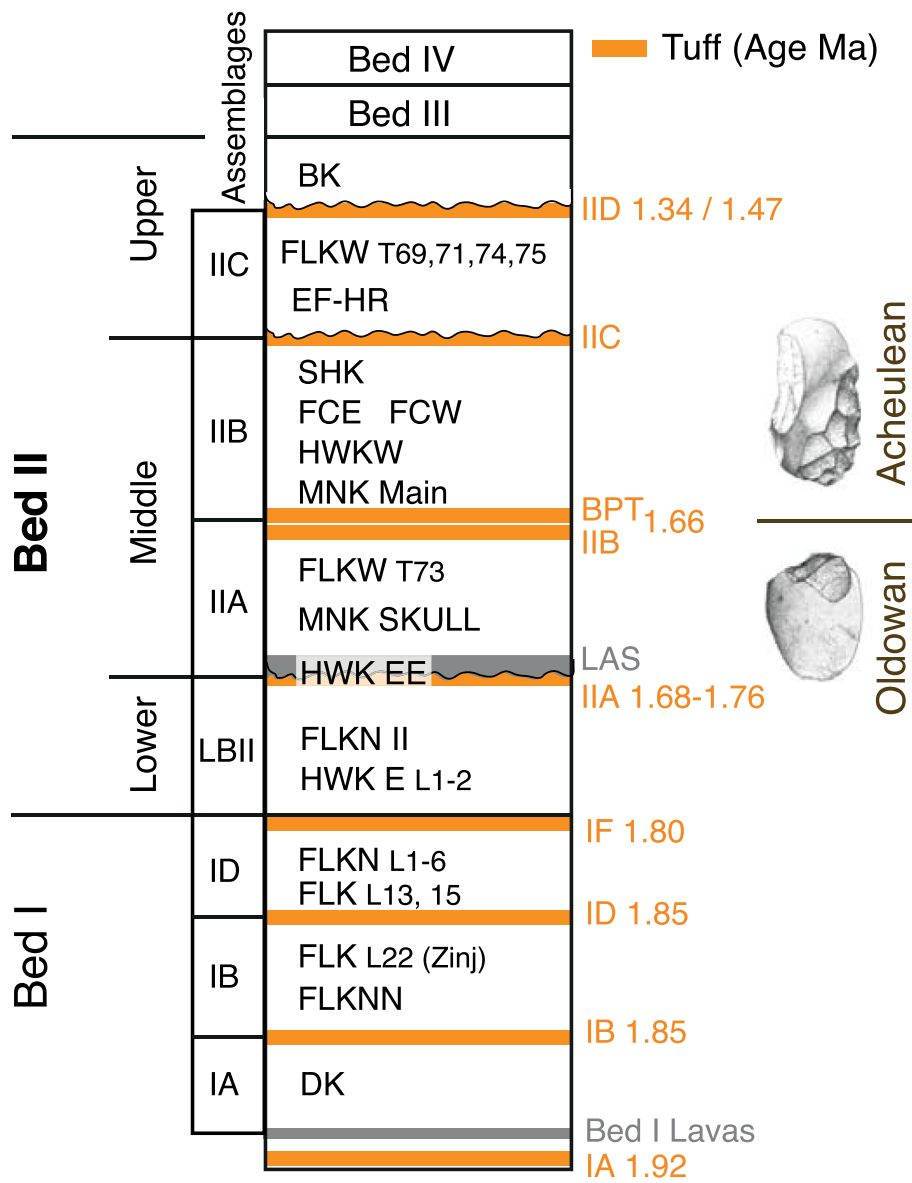


Figure 1. Simplified stratigraphy of Olduvai Gorge. This mainly follows previous stratigraphic schemes, though Bed II tuff ages and the placement of EF-HR above Tuff IIC are updated following OGAP findings. Site names within bracketing tuffs are alphabetical, not stratigraphic. Assemblage IIA comprises specimens from sites between Tuffs IIA and IIB and represents the Oldowan component of Middle Bed II. Assemblage IIB encompasses sites between Tuffs IIB and IIC and represents the Acheulean component of Middle Bed II. BPT = Bird Print Tuff, LAS = Lower Augitic Sandstone. Undulating lines represent unconformities. Geochronological ages follow Deino (2012), McHenry and Stanistreet (2018), and references therein.

the Middle Augitic Sandstone (around the level of Tuff IIB), rather than just above Tuff IIA (Uribelarrea et al., 2017).

Here we present the mammal and fish remains from the new Bed II collections recovered by OGAP, as well as the large collections from Mary Leakey's 1972 excavations at the site of HWK EE (Pante and de la Torre, 2018). It is common at Olduvai to find all four Beds exposed within close proximity at a single outcrop. This raises the concern that surface material collected by previous expeditions may be of uncertain stratigraphic origin. The new collections described here provide an opportunity for close examination of the fossil community of Bed II using samples from well-controlled archeological and geochronological contexts.

A central question within the Middle Bed II timeframe is whether the transition from Oldowan to Acheulean technology was driven by environmental changes. The coincidence of major transitions in human evolution with major changes in global climate has been a longstanding theme in paleoanthropological research (e.g., Vrba, 1985; deMenocal, 2011). Of relevance to the current time frame is the inception of Walker Circulation over the Pacific at around 1.8 Ma (Ravelo et al., 2004), which coincides with evolutionary changes in eastern African mammals (Vrba, 1995; Behrensmeyer et al., 1997; Bobe et al., 2007; Bibi and Kiessling, 2015) and the appearance of the earliest Acheulean in Ethiopia and Kenya at 1.75 Ma (Lepre et al., 2011; Beyene et al., 2013). We here ask whether the transition from Oldowan to Acheulean technologies at Olduvai at ~1.66 Ma was accompanied by important paleoecological or paleoenvironmental changes.

We first describe the fauna and then reconstruct the paleoecology of Middle Bed II times, comparing the Oldowan and Acheulean, here termed the IIA and IIB assemblages, respectively (Fig. 1). We also analyze the Middle Bed II large mammal community with respect to its modern equivalent, the Serengeti ecosystem. This includes a trophic network (food web) analysis to describe the properties of the Olduvai Bed II large mammal community and the role that early Pleistocene hominins might have played in it.

With the redefinition of the base of Middle Bed II (Stanistreet et al., 2018), the Lemuta levels at HWK EE now technically belong to the uppermost part of Lower Bed II. Nonetheless, to maintain compatibility with previous studies (and those in this volume; e.g., Uno et al., 2018), we refer to all levels between Tuffs IIA and IIC, including the entire HWK EE collection, as 'Middle Bed II.' Specimens from sites EF-HR and some trenches of FLK West are above Tuff IIC, and therefore part of Upper Bed II (de la Torre et al., 2018). Micromammals are practically absent from these collections and the small number found are not investigated here.

2. Materials and 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 Supplementary Online Material (SOM) Tables S1 a–g. Only the most significant specimens are referred to in the text. OGAP specimens are numbered as Site Trench-Level-Specimen; e.g., 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, an M and an S respectively follow the locality, before the level and specimen number (e.g., MNK M-L6B-151 stands for locality MNK, Main site, archeological unit L6B, specimen number 151).

Specimen numbers from the main trenches at HWK EE and EF-HR do not normally include a trench number (e.g., HWK EE L2-395 refers to site HWK EE, main trench, level 2, specimen number 395), but here 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 begin with HWK EE 1972 and then a specimen number. A few unnumbered Leakey specimens are here referred to by OGAP barcode numbers. Specimens housed at the Natural History Museum in London have the letter M prefixed with NHM. Dental metrics given in the text are abbreviated as AP (anteroposterior length), T (transverse width), and Ht (crown height). Basal horn core metrics are DAP (anteroposterior diameter) and DT (transverse diameter).

FLK West trenches 69, 71, 74, 75, and site EF-HR are located above Tuff IIC and in Upper Bed II. HWK EE specimens from OGAP archeological units L10, 12, 32–34, 43–46, and 51–52 and HWK EE Leakey specimens with numbers 1–27, 1036–1209, and 3562–4398 are from Lower Bed II as defined by Stanistreet et al. (2018— their Fig. 7). Otherwise, all specimens are from Middle Bed II.

Ungulate species richness (Proboscidea, Perissodactyla, Artiodactyla) was compiled for 15 eastern African fossil assemblages (in addition to Middle Bed II), all dated 7.5–1 Ma, with >300 identified ungulate specimens, and mainly from the Afar and Turkana Basins (SOM Table S2). These are the Lower Nawata, Upper Nawata, Upper Burgi, KBS, and Okote Members from the Turkana Database (Bobe et al., 2011), the Asa Koma and Kuseralee Members (Haile-Selassie and WoldeGabriel, 2009), the Daka Member (Gilbert and Asfaw, 2008), the Upper Laetolil Beds (Su and Harrison, 2015), and Members B, C, D, E, F, and G of the Shungura Formation (JRB, Omo Group Research Expedition project database). Ungulate species richness for 205 extant African game parks was taken from Rowan et al. (2016).

Correspondence analysis of bovid abundances uses dental specimen counts from the OGAP and HWK EE 1972 collections for Middle and Upper Bed II, and number of individual specimen (NISP) counts for Bed I and Lower Bed II from Kappelman (1984), which derive ultimately from Gentry and Gentry (1978a, b). We grouped Kappelman's data by assemblages based on the main dated tuff underlying them. Assemblage IA comprises site DK, IB, FLK NN levels 1–3 and FLK level 22 (*Zinjanthropus*), ID, FLK levels 13 and 15 and FLK N levels 1–6, and LBII (Lower Bed II), HWK E levels 1–2. Abundance data for large mammals for the food web analyses were based on the dental specimen counts and considered only mammals larger than 15 kg (prey) and 20 kg (predators). Taxa that were not definitely identified in the current collections but were previously recorded from Middle Bed II (e.g., *Diceros bicornis*) were given abundance counts of 1. Adult body mass ranges for extant taxa were taken from the literature (e.g., Kingdon, 1982, 1997; Kingdon and Hoffmann, 2013). Mass estimates for fossils were calculated using either metric (usually dental) regressions based on extant species (data from 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 *Equus grevyi*). For an approximation of neonate mass, we used 10% of the minimum adult body mass value (SOM Table S3). 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 abundance analyses, we divided all Alcelaphini teeth in the OGAP collection ($n = 268$) according to the ratios found by third molar classification analysis (*M. isaaci*, $n = 48$; two *Parmularius* spp. and *Damaliscus niro*, $n = 180$; the small alcelaphin, $n = 40$).

For trophic network analyses, predators were assigned a preferred prey body size range based on analogy with their nearest living relative, including assumptions of possible group hunting (which allows for larger prey capture). Middle Bed II hominins (*Homo habilis*, possibly *Homo erectus* and *Australopithecus boisei*) were 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). Though HWK EE taxa with cut marks include small bovids to proboscideans (Pante et al., 2018), we conservatively modeled hominin maximum prey size at an arbitrary cutoff of 400 kg (potentially underestimating the role of the hominin in the food web). Species presence and abundance 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 sizes, including allowing predators to prey on neonates of large species when they fit into their preferred body-size ranges. We used prey abundance to weight trophic links, as prey availability was probably a determinant of the strength of interactions. We calculated the following 10 food web structure parameters 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 distinguished out-degree (predator) and in-degree (prey) distributions; 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, rated 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.

To explore the role of a Middle Bed II hominin in its food web, we calculated the structure of the food web removing one carnivore species at a time, using the results as a null model against which to compare the effect that hominins 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 followed prey abundance (rare species disappearing first), vulnerability (prey with more predators disappearing first), or random extinction. We also 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 and to calculate the area below the secondary extinction curve ('robustness'). All analyses were performed in R (R Core Team, 2014).

3. Fish: results and discussion

3.1. The Middle Bed II fish

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, 1971). 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 Lower and Middle Bed II: FLK West, FC East, FC West, MNK-T5, MNK Main, and HWK EE (Table 1). 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 is 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 make up 5.7% of all elements; cichlid elements comprise 94.3%. The *Clarias* elements represent individuals estimated to be between <10 and 90 cm in total length—most were between 25 and 50 cm total length. *Clarias* are air breathers that can live outside of water for up to 18 h, allowing movement overland between water bodies. Today, they are ubiquitous in rivers and lakes throughout Africa, including *Clarias gariepinus*, which inhabits smaller eastern African lakes and rivers. The Olduvai Gorge *Clarias* bones are identical to those of *Clarias gariepinus*. *Clarias* are common in African fossil sites, in part due to their robust bones.

The cichlids represented at Olduvai Gorge are generally small, with estimated total length ranging from <5 to 32 cm—most were between 15 and 20 cm in 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

Table 1
Numbers and percentages of identified fish taxa from Bed II sites at Olduvai Gorge.

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

^a Mostly level 6.

^b Mostly levels 4 and 6.

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 streams or rivers that probably flowed into the eastern side of the lake (Hay, 1976).

3.2. Paleoecological implications of the Middle Bed II fish

The presence of only two fish taxa in paleo-Lake Olduvai is surprising given the large diversity of taxa in most African lakes today. The overwhelming dominance of fragile cichlid elements over robust *Clarias* elements (ratio of about 16:1, Table 1) is unusual and may point to lake chemistry. Paleo-Lake Olduvai was small, particularly in Middle and Upper Bed II, and high in salinity and alkalinity (Hay, 1976). Similar small African lakes today include 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 streams or rivers (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 are well represented at all sites, but *Clarias* bones are rare except in the MNK Main and FC West sites, where they make up about 67% and 38%, respectively, of all fish specimens (Table 1). Both sites were located in the Side Gorge, where stream channels were present (Hay, 1976), 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 MNK-T5 and HWK EE, the high number of cichlid individuals found in close proximity 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; Leakey, 1971; Hay, 1976). Similarly, 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. 2), while an earlier study from different levels at MNK Main 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 that carried the denser postcranial bones elsewhere, or of consumption of the bodies of the stranded fish by predators such as raptors and mammals (e.g., Kruuk, 1972; Ewer, 1973; 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

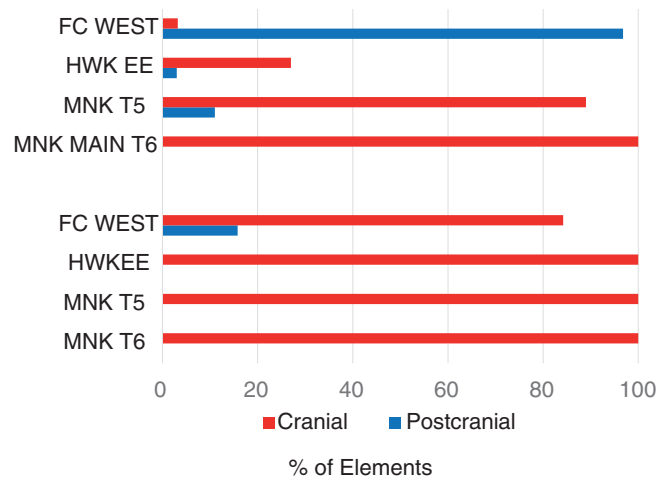


Figure 2. Percentage of cranial and postcranial elements of Cichlidae (above) and *Clarias* (below) at Olduvai Gorge sites.

et al., 2010), although fish consumption is yet to be conclusively documented at Olduvai.

A reversed scenario from that just discussed at MNK-T5 and HWK EE is present at FC West, where cichlid bones are dominated (99%) by postcranial elements (vertebrae and spines; Fig. 2). These are denser, and therefore heavier, 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 from which 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 occurred 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 IIB interval (Hay, 1976).

4. Large mammals: results and discussion

4.1. The Middle Bed II large mammals

Full details and systematic descriptions are given in Appendix A. The newly described fauna matches previous faunal lists for Middle Bed II (Table 2). A few taxa previously reported from this interval (Leakey, 1965, 1971; Gentry and Gentry, 1978b) are missing, among these *Syncerus acoelotus*, a small *Tragelaphus*, *Giraffa pygmaea*, *Panthera pardus*, and *Hyaena hyaena*. *Homo habilis* has previously been found in Middle Bed II, and both *H. erectus* and *A. boisei* are assumed to have been present, but no hominins have been conclusively identified from the new collections. A hartebeest-like antelope that was previously described as *Parmularius* aff. *rugosus* (Gentry and Gentry, 1978a) has now been named as *Parmularius maasaicus* sp. nov. 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 small felid (*Caracal/Leptailurus*), and *Deinotherium*, which was previously only recorded from Bed I and Lower Bed II.

Table 2

All large mammals recovered from Middle Bed II (assemblages IIA and IIB).

				IIA	IIB		
Artiodactyla	Bovidae	Aepycerotini	<i>Aepyceros melampus</i> *		X*		
			Alcelaphini	Alcelaphini small sp.	X	X	
			Alcelaphini 'sp. 3'		X*		
			<i>Connochaetes</i> sp.	X	X		
			<i>Damaliscus niro</i>	X	X		
			<i>Megalotragus isaaci</i>	X	X		
			<i>Parmularius angusticornis</i>	X	X		
			<i>Parmularius maasaicus</i> sp. nov.	X	X*		
			Antilopini	<i>Antidorcas recki</i>	X	X	
				' <i>Gazella</i> aff. <i>rufifrons</i> '	X	X*	
				Antilopini sp. large (or <i>Aepyceros</i>)	X		
			Bovini	<i>Pelorovis oldowayensis</i>	X	X	
				<i>Syncerus acoelotus</i> *		X*	
			Caprini	indet.	X	X*	
			Hippotragini	<i>Hippotragus gigas</i>	X	X*	
			'Neotragini'	indet.*		X*	
			Reduncini	<i>Kobus sigmodalis/ellipsiprymnus</i>	X	X	
				<i>Kobus kob</i> *		X*	
			Tragelaphini	<i>Tragelaphus strepsiceros</i>	X	X	
				Tragelaphini small sp.*		X*	
				cf. <i>Taurotragus</i> sp.		X	
			Giraffidae	Giraffini	<i>Giraffa gracilis</i>	X	
					<i>Giraffa pygmaea</i> *		X*
				Sivatheriini	<i>Sivatherium maurusium</i>	X	X
			Hippopotamidae		<i>Hippopotamus gorgops</i>	X	X
			Suidae		<i>Kolpochoerus limnetes</i>	X	cf.
					<i>Kolpochoerus paiceae</i>	cf.	X
		<i>Kolpochoerus majus</i>		X	X		
		<i>Metridiochoerus compactus</i>		X	X		
		<i>Equus oldowayensis</i>		X	X		
		<i>Eurygnathohippus</i> cf. <i>cornelianus</i>		X	X		
		<i>Ceratotherium simum/germanoaffricanum</i>		X	X		
			<i>Diceros bicornis</i> *		X*		
Carnivora	Canidae		<i>Prototocyon recki</i>		X		
	Hyaenidae		<i>Crocuta</i> cf. <i>ultra</i>	X	X		
			<i>Hyaena hyaena</i> *		X*		
			<i>Atilax</i> *		X*		
	Herpestidae		<i>Dinofelis</i> sp.*	X	X*		
	Felidae	Machairodontini	<i>Caracal/Leptailurus</i> sp.		X		
			<i>Panthera pardus</i> *		X*		
				<i>Pseudocivetta ingens</i>	cf.		
	Primates	Viverridae		<i>Theropithecus oswaldi</i>	X	X	
		Cercopithecidae		<i>Homo habilis</i> *	X*		
	Hominidae	Hominini	<i>Deinotherium bozasi</i>	X			
Proboscidea	Deinotheriidae		<i>Elephas recki</i>	X	X		
	Elephantidae						

*Indicates identification from a previous study.

4.2. Ecological continuity across the Oldowan-Acheulean transition at Olduvai

Both assemblages IIA (Oldowan) and IIB (Acheulean) are dominated by grazing ungulates, indicating the prevalence of open grassland habitats. Assemblage IIB has a more even distribution of grazers, with higher proportions of equids and *Hippopotamus gorgops*, which is three times more abundant than in IIA, and a lower proportion of Alcelaphini and Antilopini (Fig. 3), which may reflect a more even sampling of habitats, but these differences are not significant (paired Wilcoxon on all taxa with >5 specimens, $p = 0.39$). Hominin butchery clearly played a role in the formation of these assemblages (Pante et al., 2018) and may account for some of the differences.

To compare the environments represented by the IIA and IIB assemblages within the Bed I-II sequence, we used correspondence analysis of bovid tribal abundances (Greenacre and Vrba, 1984). Assemblages from Lower and Middle Bed I stand out by larger proportions of Tragelaphini and Reduncini, which indicate wooded and humid (flooded) grassland habitats, respectively (Fig. 4). In particular, assemblage IB, the interval from which the

OH 5 *Zinjanthropus* cranium derives, shows a dominance of wetland habitats, supporting previous geological, paleobotanical, isotopic, avian, and micromammal data for wetter conditions at this time (Kappelman, 1984; Fernández-Jalvo et al., 1998; Ashley and Driese, 2000; Hay and Kyser, 2001; Ashley, 2007; Blumenschine et al., 2012; Stanistreet, 2012; Magill et al., 2013; Prassack et al., 2018). In contrast, uppermost Bed I and all Bed II assemblages are dominated by open grassland habitats (Fig. 4), and these were probably semi-arid to arid, fitting reconstructions for alkaline and saline lake waters based on the fish. Assemblages IIA and IIB are very similar to each other, as well as to those of Lower Bed II (LBII) and Upper Bed II (IIC). This supports the findings of Kovarovic et al. (2013) for ecological continuity throughout the Bed II sequence. However, their study also argued for the importance of woodland habitats in Middle and Upper Bed II (their 'Upper Bed II') mainly based on an analysis of small mammals (rodents *Tatera*, *Thryonomys*, *Arvicanthis*, *Pedetes*, and monkey *Lophocebus*). While trees and bushes were certainly present on the landscape, the Middle Bed II large mammal community overwhelmingly indicates the dominance of open and dry grassland habitats. Tree cover must have been low and

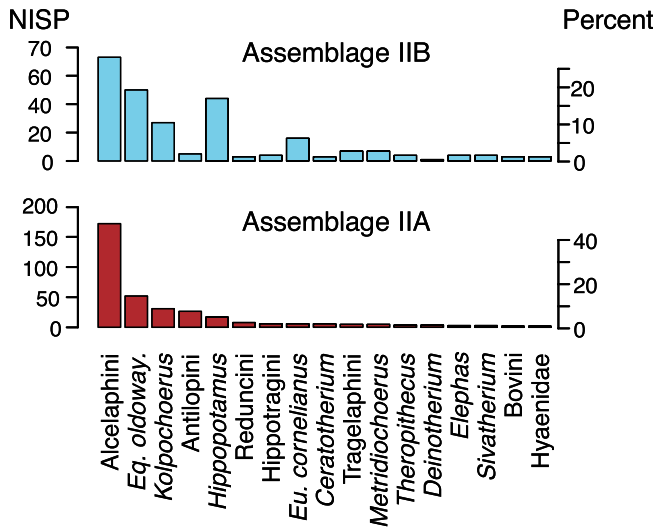


Figure 3. Relative abundance distributions of large mammals in the IIA and IIB assemblages. The IIB assemblage is more even, with a lower proportion of alcelaphins and a higher proportion of *Hippopotamus*, but the distributions are not significantly different. Taxa with less than five identified dental specimens are not shown. *Eq. oldoway.* = *Eq. oldowayensis*.

true woodlands practically absent. An analysis of the large assemblage of Middle Bed II birds (Prassack et al., 2018) supports indications for very low proportions of trees on the landscape. The birds, however, indicate a much greater wetland signal in

both Lower and Middle Bed II, with cormorants, an aninga, pelican, duck, and flamingo from HWK EE indicating the presence of well-watered environments with diverse species of fish (Prassack et al., 2018). This contrasts with the mammal and fish data presented here, suggesting different spatial scales of foraging and taphonomic accumulation operating on the mammal, fish, and avian assemblages.

The change toward drier, more open habitats took place in Bed I between 1.85 and 1.80 Ma (Fig. 4), prior to the local transition from Oldowan to Acheulean technologies within Middle Bed II at ~1.66 Ma. This environmental change is, however, closer to the time of the Oldowan-Acheulean transition in the Konso and Turkana basins to the north at 1.75 Ma (Lepre et al., 2011; Beyene et al., 2013), supporting the idea that Acheulean technology probably dispersed into the Olduvai region and did not develop in place there (de la Torre, 2016). The ecological change we observe in Bed I also matches a period of increased species richness (Behrensmeyer et al., 1997; Bobe et al., 2007; deMenocal, 2011; Bibi and Kiessling, 2015; Fortelius et al., 2016), C₄ grassland expansion (Feakins et al., 2005; Bonnefille, 2010; Levin et al., 2011), increased regional aridity (deMenocal, 2004), and increases in open habitat faunal indicators in both eastern and southern Africa (Reed, 1997). These changes may in turn be related to the development of Walker Circulation above the Pacific Ocean around 1.9 Ma (Ravelo et al., 2004), which would have resulted in precipitation decreases over large parts of Africa (Brierley and Fedorov, 2010). It will be interesting to further investigate all these possible causal links.

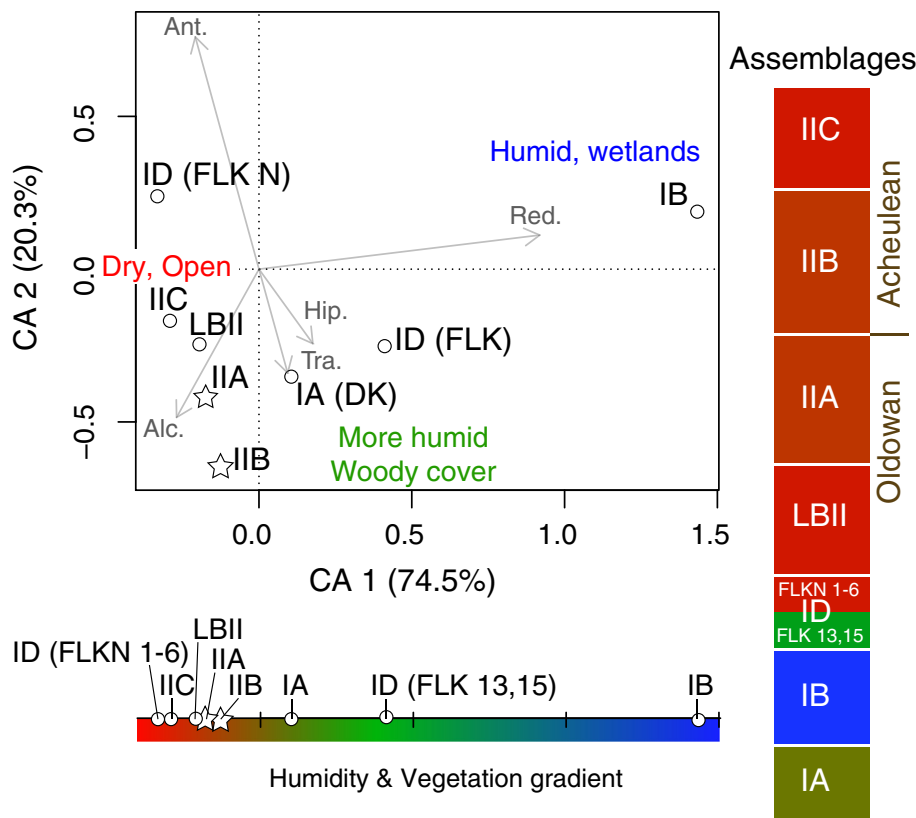


Figure 4. Correspondence analyses (CA) of Olduvai bovid abundances by assemblage. Alcelaphini (Alc., open habitats) and Reduncini (Red., humid habitats) represent the main endmembers of the first axis. More wooded and humid habitats in lower and middle Bed I (especially IB) give way to dry and open grasslands in interval ID. Habitats remain dominantly dry and open throughout Bed II, and no major environmental change accompanies the local Oldowan-Acheulean transition. Data for Bed I and Lower Bed II (LBII) from Kappelman (1984) and Gentry and Gentry (1978a, b). Hip = Hippotragini, Tra = Tragelaphini. Colors in the assemblage column match those of the CA 1 gradient axis at bottom.

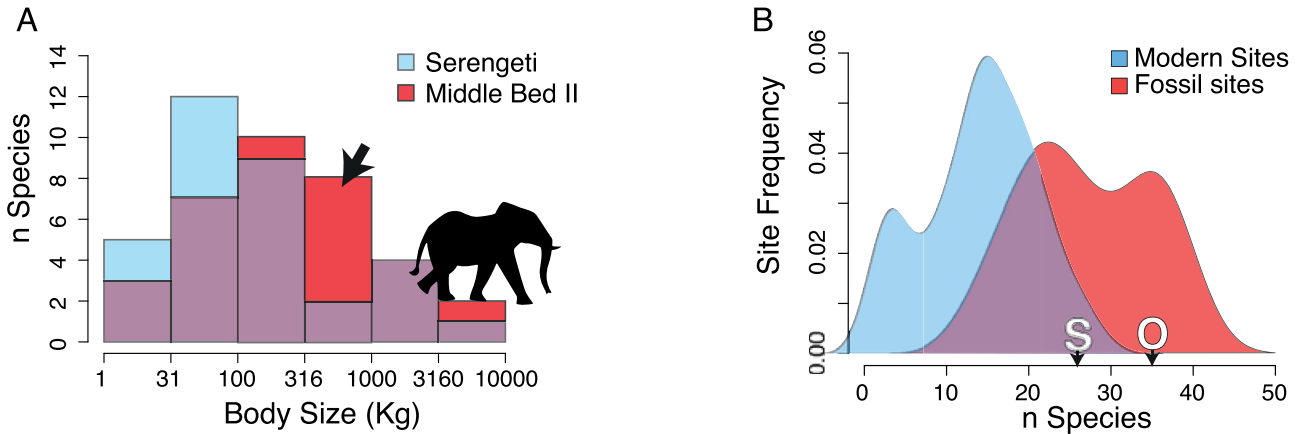


Figure 5. Body size distribution of fossil versus modern African large mammal communities. A) Middle Bed II and extant Serengeti large mammal community profiles. The fossil assemblage has more species, mostly in the ~300–1000 kg body size range (arrow). B) Density distribution of ungulate species richness at 200 modern African game parks and 16 well-studied eastern African fossil assemblages dated 7.5–1 Ma. Fossil assemblages consistently record high species richness. S = richness of Serengeti, O = Olduvai Bed II. Overlapping areas shown in purple in both A and B.

4.3. Middle Bed II versus the Serengeti: where have all the species gone?

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 actually richer in species than its extant analog, the greater Serengeti ecosystem. Most of the additional Pleistocene species diversity is to be found in the 300–1000 kg body size range, a size category that is totally depauperate today (Fig. 5A). Pleistocene species of this size include the suids *Kolpochoerus limnetes-paiceae* and *Metridiochoerus compactus*, *Giraffa stillei*, *Giraffa pygmaea*, and large bovids such as *Pelorovis oldowayensis* and *Megalotragus isaaci*. Middle Bed II is also richer in megaherbivores (>1000 kg), such as *Sivatherium maurisium* and *Deinotherium bozasi*, two species with no extant close relatives.

A comparison of species richness of eastern African fossil assemblages with modern African game parks shows that Plio-Pleistocene sites consistently record higher species richness (Fig. 5B). Higher fossil species richness is not caused by time-averaging, because in our dataset fossil richness is not correlated with maximal assemblage duration (Spearman's $p = 0.99$) and is in fact negatively correlated with assemblage age ($p = 0.04$). The raw differences are further accentuated by the fact that while the Serengeti census is at 100%, we can be sure we are underestimating

fossil richness, as fossil assemblages are typically just a subsample of the original community. The difference between extant and Pleistocene mammal community richness is therefore bound to be greater than what we observe here.

There are two main explanations proposed for the loss of so many large-bodied Pleistocene species. The first is that climatic changes, by decreasing primary productivity, drove the extinction of many large bodied species in the Middle and Late Pleistocene. Increasing aridity after 0.8 Ma seems a reasonable cause, and 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. Also in favor of more productive Pleistocene habitats, Leakey (1965:76) suggested that “optimum feeding conditions” existed in Middle Bed II times, based on several fossil species being mostly larger than their living equivalents (also Gentry and Gentry, 1978a).

A second, not mutually exclusive, explanation is that Pleistocene large mammals went extinct as a result of human disturbance. The community ‘downsizing’ pattern seen in Figure 5A matches extant and archeological communities affected by human hunting and environmental modification (Lyons et al., 2004; Dirzo et al., 2014; Young et al., 2016), whereby large species are more directly threatened by human activities, while small species are more affected by habitat loss. The implication is that, in the absence of

Table 3
Olduvai Middle Bed II (MBII) and Serengeti food web parameters.

	MBII	MBII with hominin	Impact of hominin (%)	Serengeti	Serengeti with hominin	Impact of hominin (%)
Connectance	0.56	0.6	7	0.65	0.7	8
Links per species	2.38	3	26	3.19	3.88	22
Linkage density	9.47	11.72	24	11.14	12.41	11
Nestedness	55.82	33.88	-39	32.96	28.11	-15
Generality	15.2	17.5	15	17	18.29	8
Vulnerability	2.82	3.62	29	3.92	4.92	26
Dietary overlap among carnivores	0.55	0.59	8	0.63	0.68	8
Shared predators among prey	0.51	0.63	23	0.65	0.73	12
Number of predators	5	6	20	6	7	17
Number of prey	27	29	7	26	26	0
Predator prey ratio	0.19	0.21	12	0.23	0.27	17

humans, the Serengeti would support an even greater number of species than it does today. Besides losses of large herbivores, Werdelin and Lewis (2013b) suggested that hominins may even have driven the extinction of large carnivores through competition by 2 Ma or earlier. There is a strong theoretical and empirical basis for the existence of hominin-carnivore competitive interactions in the early Pleistocene, particularly at Olduvai (e.g., Shipman and Walker, 1989; Blumenschine et al., 1994; Lewis, 1997; Egeland et al., 2004; Pante et al., 2012; Werdelin and Lewis, 2013b; Egeland, 2014; also Pante et al., 2018). In order to investigate the strength and stability of trophic links among herbivores, carnivores, and hominins in Middle Bed II, we turn to food web analysis.

4.4. The Middle Bed II food web (trophic network)

The structural properties of food webs reveal the trophic interconnectedness of communities. Changes in these properties over time can provide indications of community-level responses to past environmental changes (Yeakel et al., 2013; Nenzén et al., 2014; Pires et al., 2015). Here, we use network analysis to 1) describe the properties of the Middle Bed II large mammal food web and to compare it to the extant Serengeti; 2) explore the role that a meat-eating hominin might have played in the fossil community; and 3) quantify the resilience of the Middle Bed II carnivore and herbivore species to different extinction scenarios.

Our results (Table 3, Fig. 6) indicate that the Middle Bed II and Serengeti food webs have a similar underlying structure, with similar values for nestedness, generality, vulnerability, and predator-prey ratios and high connectance (>0.5). In comparison, large mammal food webs of the Iberian Pleistocene had low connectance (less than 0.2; Nenzén et al., 2014), and many extant food webs have connectance values of less than 0.4 (Dunne et al., 2002). High interconnectedness is the result of high species richness and a large number of prey available to a

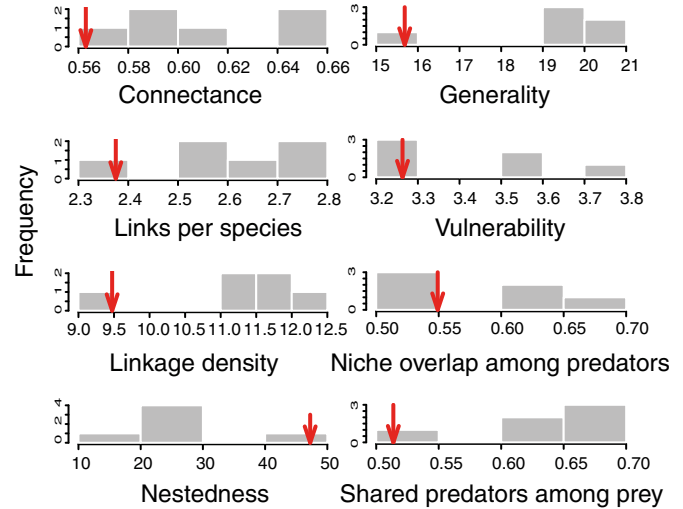


Figure 7. Distribution of the food web parameters after the removal of one predator at a time. Removal of the hominin results in large changes (red arrows) at the extremes of all parameters.

smaller number of generalized carnivores, likely a lingering effect of the early Pleistocene loss of much large carnivore diversity (Werdelin and Lewis, 2013b). The high similarity of the Middle Bed II and Serengeti food webs indicates that there has been no fundamental change in the trophic structure of these savanna communities despite the large number of large herbivores that went extinct in the Pleistocene. This contrasts with the situation in the Iberian Peninsula, where Pleistocene losses resulted in a fundamentally different trophic community (Nenzén et al., 2014).

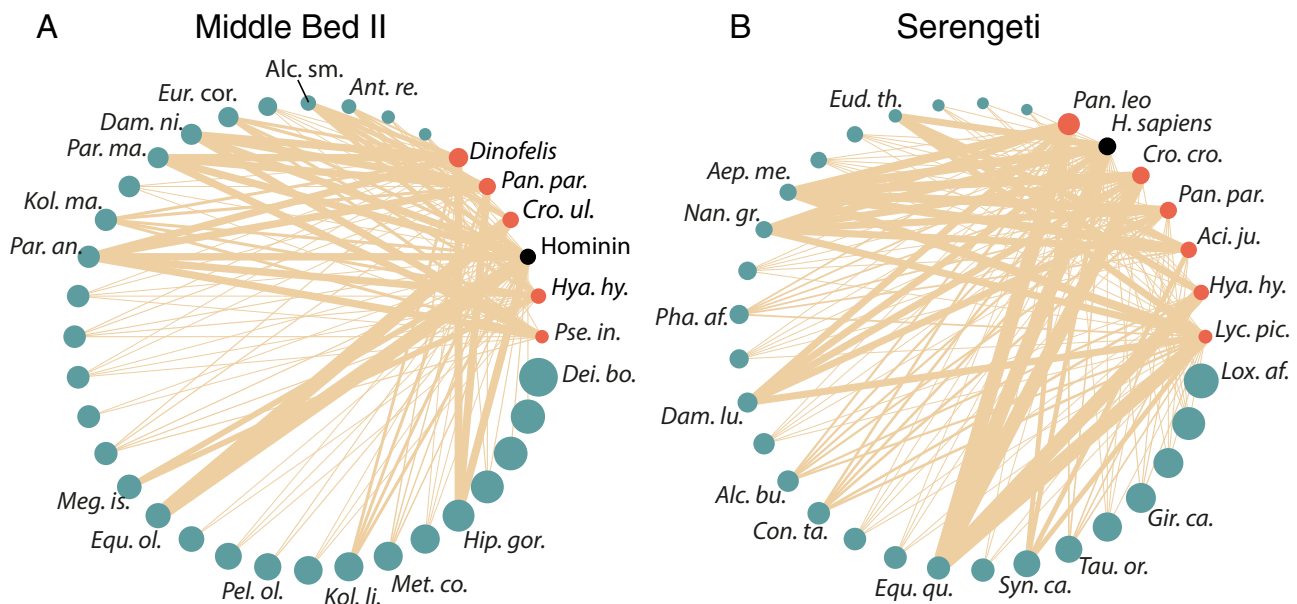


Figure 6. Olduvai Bed II (A) and Serengeti (B) food webs including a generalized meat-eating hominin. Prey in green, predators in red, hominin in black. Node sizes are proportional to species body mass and link width is weighted by prey abundance. Both webs have a similar, highly-interconnected trophic structure. Addition of the hominin increases connectance further, but also increases competition among predators and apparent competition among prey species. For full species names, see SOM Table S3.

Table 4

Robustness of Middle Bed II and Serengeti food webs (including hominins) to three extinction simulations removing prey species.

	Middle Bed II	Serengeti
Random extinction	0.96	0.93
Abundance driven extinction	0.97	1.00
Predator driven extinction	0.81	0.89

We find that a generalist meat-eating hominin would have had connections to almost every species in the community (Fig. 6), increasing competition among carnivores and greatly increasing vulnerability among herbivores (Table 3). Predator extinction simulations show that the removal of the hominin affects Olduvai food web structure much more so than the removal of any other predator species (Fig. 7). However, simulated extinctions of prey species also indicate that Serengeti and Middle Bed II food webs are highly resilient to secondary extinctions (Table 4), with only slight decreases in robustness even when key prey species are removed (those with high abundance or those with a larger number of predators). These results suggest, on the one hand, that the effects of competition by hominins on other predators may have been intense, particularly if concentrated against one or a few species (e.g., *Dinofelis*). At the same time, the high stability of the Middle Bed II trophic web suggests that this community—particularly the herbivores—may have been buffered against extinction from trophic pressures exerted by hominins.

5. Conclusions

The fish and mammal assemblages presented here provide 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 previous gaps between older and younger faunas (e.g., Beds I and IV) and provide a new comparative reference for contemporaneous faunas from other parts of Africa. 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 like Olduvai is perplexing and makes extant African faunas look depauperate in comparison. These fossil assemblages remain relevant to discussions of Pleistocene mammal extinctions and the continuing loss of species diversity in the Holocene.

Further work should focus on the faunal 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, should provide unparalleled insights into long-term community evolution at a single site leading to one of the world's most emblematic savanna ecosystems, the Serengeti.

Acknowledgments

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Appendix A: Systematic paleontology of the large mammals

All specimen numbers, anatomical and taxonomic determinations, as well as dental metrics, are given in [Supplementary Online Material \(SOM\) Table S1](#). 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: their fig. 8), with the exception of *Syncerus antiquus*, which is not known from Olduvai. The OGAP bovin teeth are on average larger than those of extant *Syncerus caffer* and within the range of *Pelorovis* (upper molars consistently longer than 30 mm). 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; Gentry and Gentry, 1978a).

Discussion Both *Syncerus acoelotus* and *P. oldowayensis* have been previously recorded from Middle Bed II (Gentry and Gentry, 1978a), 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 and 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. A1C). 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 *Tragelaphus oryx*.

Discussion Fossil greater kudu specimens are already well known from Olduvai. Gentry and Gentry (1978a) follow Leakey (1965) in recognizing two subspecies: *T. strepsiceros maryanus*, present in Bed I-early Middle Bed II, and *T. strepsiceros grandis*, from Middle Bed II to Bed IV. The latter was diagnosed as having a slightly larger size than extant individuals.

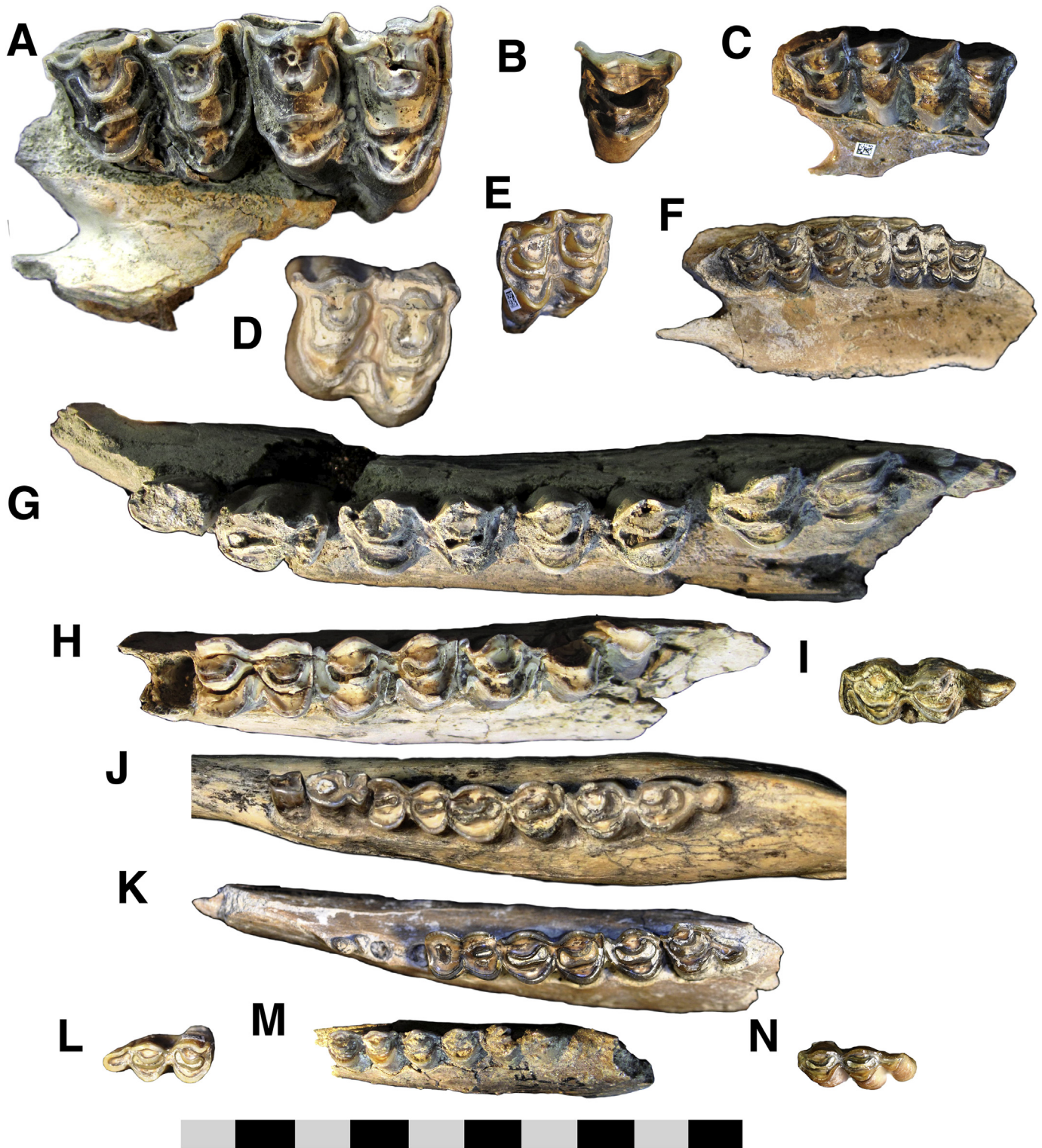


Figure A1. Bovid teeth. A) *Pelorovis oldowayensis*, HWK EE T27-L31-28. B) cf. *Taurotragus*, MNK T5-L10-2124. C) *Tragelaphus strepsiceros*, HWK EE 1972-3916. D) *Hippotragus gigas*, MNK M-L3-231. E) *Kobus sigmoidalis/ellipsiprymnus*, HWK EE L6-1911. F) Alcelaphini small sp., HWK EE T27-L32-608. G) *Megalotragus isaaci*, MNK T5-L10-1733 left mandible. H) *H. gigas*, FLKW T69-L22-596 left mandible. I) *K. sigmoidalis/ellipsiprymnus*, 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-N) Alcelaphini small sp.: L) HWK EE-L6-1740 right m3. M) HWK EE 1972-1156 left mandible. N) HWK EE L10-707 left m3. Scale bar = 10 cm.

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

Description MNK T5-L10-2124 (Fig. A1B) 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 eland species belong within the *Tragelaphus* clade. The name *Taurotragus* may be retained as a subgeneric clade uniting the two living species. 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 (Kingdon, 1982; Cerling et al., 2003). Enamel $\delta^{13}\text{C}$ from MNK T5-L10-2124 was measured at -2.8% , which indicates a high intake of C_4 vegetation (Uno et al., 2018). This contrasts with the normally C_3 -dominated diets of extant tragelaphins, but is common in the Plio-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 *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 is the presence of a very small unnamed species only slightly larger than a Thomson's gazelle and *M. isaaci*, a massive species larger than a wildebeest.

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. A2A, 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 *Parmularius altidens*, differing from it mainly in larger size and in the longer and more massive horn cores (Gentry and Gentry, 1978a). 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 and 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. A3A). Housed at Olduvai Gorge.

Referred specimens HWK EE 1972-2061, frontlet with both horn cores (Fig. A3B). 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 attributed to *Parmularius* aff. *rugosus* by Gentry and Gentry (1978a), 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 (Gentry and Gentry, 1978a:pl. 32 fig. 2); from Lower Bed II: HWK 1960.58, left horn core (Gentry and Gentry, 1978a:pl. 32 fig. 3); HWK 067/5523, right horn core; HWK (1960?)0.054, 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 (Leakey, 1965:pl. 88; Gentry and Gentry, 1978a).

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 and 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 *Beatragus 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 lacking the straight distal ends typical of *B. antiquus* and *Beatragus hunteri*.

The basal lateral divergence and upwards recurvature, along with the shape of the cross-section and tall pedicels, are reminiscent of the horn shape in living hartebeest (*Alcelaphus buselaphus*), especially subspecies *A. buselaphus cokei* or *A. buselaphus tora*. The

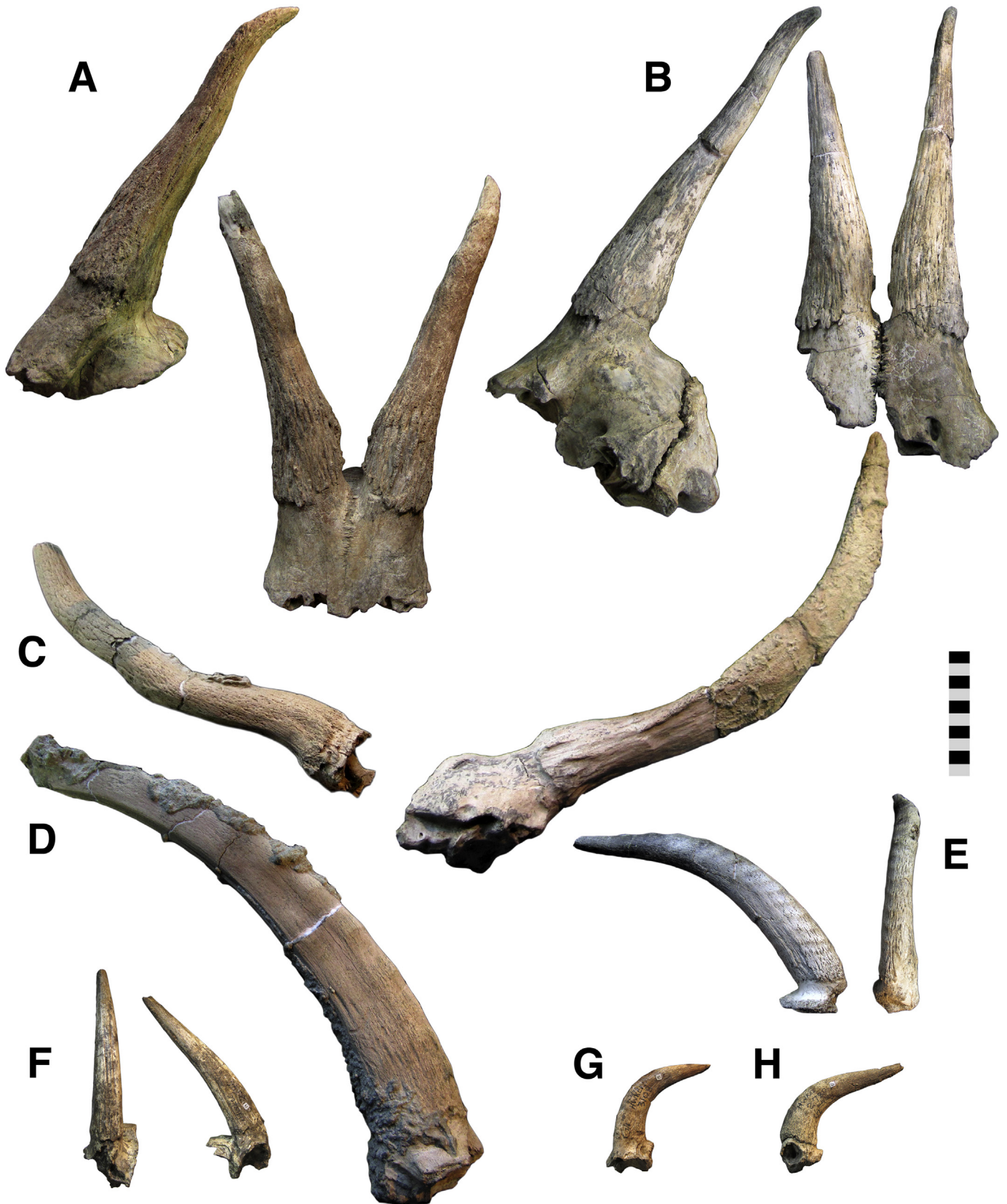


Figure A2. Bovid cranial and horn core remains. A, B) *Parmularius angusticornis*. A) HWK EE 1972-172, frontals with both horn cores in left lateral and anterior views. B) HWK EE M-L1-4052 (= L4-53), partial cranium with horn cores in left lateral and anterior views. C) *Megalotragus isaaci*, MNK M-L6B-151, 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.

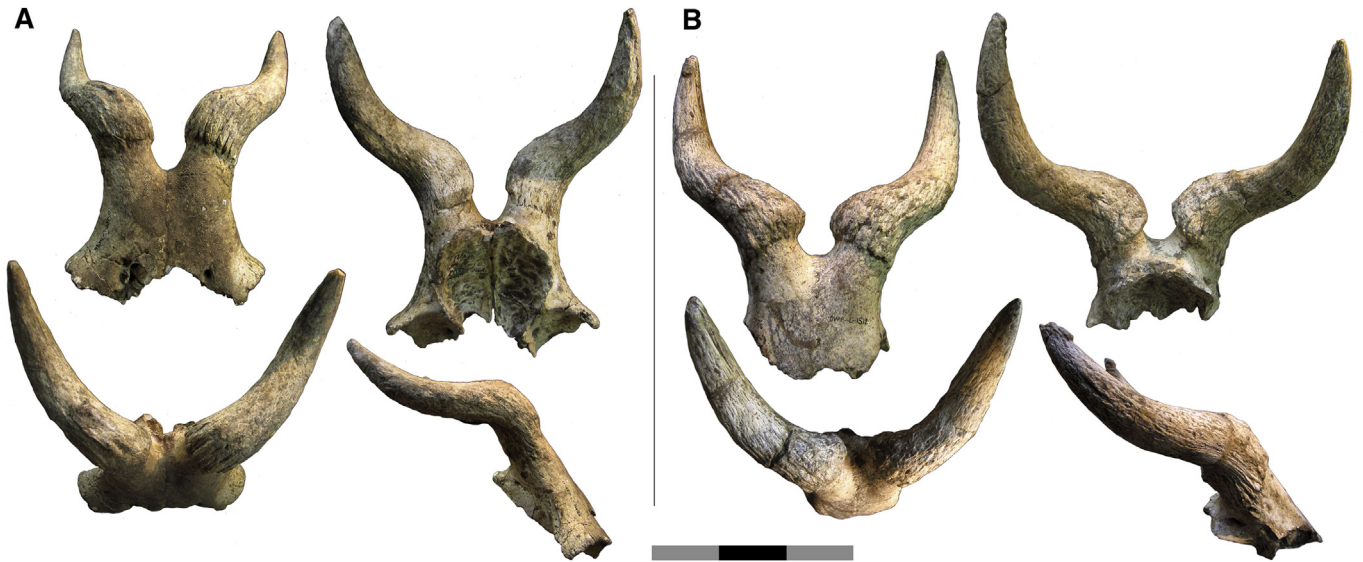


Figure A3. *Parmularius maasaicus* sp. nov. A) HWK EE 1972-2181, holotype frontlet with horn cores. B) HWK EE 1972-2061, frontlet with horn cores. Both in anterior (top left), posterior (top right), dorsal (bottom left), and right lateral (bottom right) views. Scale bar = 15 cm.

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 the hartebeest it is homonymous.

Description The main features of all specimens may be deduced from the diagnosis. Metrics are given in Table A1. 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 toward 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. A3A) but well developed in HWK EE-1972-2061 (Fig. A3B). 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 HWK EE 1972-954 could represent an adult female horn core. Gentry and

Gentry (1978a:pl. 32 fig. 2) illustrated an immature specimen (HWK East 1962.068/6649) which, in contrast to HWK EE 1972-954, lacks development of the basal curvature and swelling.

Discussion Gentry and Gentry (1978a) proposed that *P. aff. rugosus* (here *P. maasaicus*) 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 the horns of *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. *Numidocapra* (= *Rabaticeras*) *arambourgi* was previously proposed as an ancestor for the hartebeest (Gentry and Gentry, 1978a; Vrba, 1997; but see Gentry, 2010), but *P. maasaicus* may make a better candidate. Similarities in general shape of the horns in *P. maasaicus* and *A. buselaphus* 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 and Thomas, 1894
Damaliscus niro (Hopwood, 1936)

Table A1
 Measurements (mm) of horn cores and frontlets of *Parmularius maasaicus* sp. nov.

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+ (210e)	-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	—	—	—	—	—

Abbreviations: L, left; R, right; DAP, basal anteroposterior diameter; DT, basal transverse diameter; Dist., distance; Div., horn core divergence in anterior view; Incl., horn core inclination in lateral view; Dist. SOF, distance between the supraorbital foramina; e, estimated.

Description Two horn cores. MNK M-L6B-149, a complete right horn core (Fig. A2D), is larger in basal dimensions (72.4×51.8 mm) than any other Olduvai specimen recorded by Gentry and Gentry (1978a), but otherwise is a morphological match with the *D. niro* holotype (NHM M14561). 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 (45.1×33.4 mm) about the size of *Damaliscus 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 *Damaliscus agelaius*. It is a better match for some of the specimens distinguished by Gentry and Gentry (1978a) 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 and Gentry (1978a) 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 and Gentry (1978a) 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. A2C); 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 ($\sim 100^\circ$ in anterior view), weakly curving posterolaterally at their base, then gradually recurving anteromedially toward 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. A4) and simple occlusal morphology (Gentry and Gentry, 1978a; Faith et al., 2011). The single complete mandible confirms the loss of the second premolar in this species.

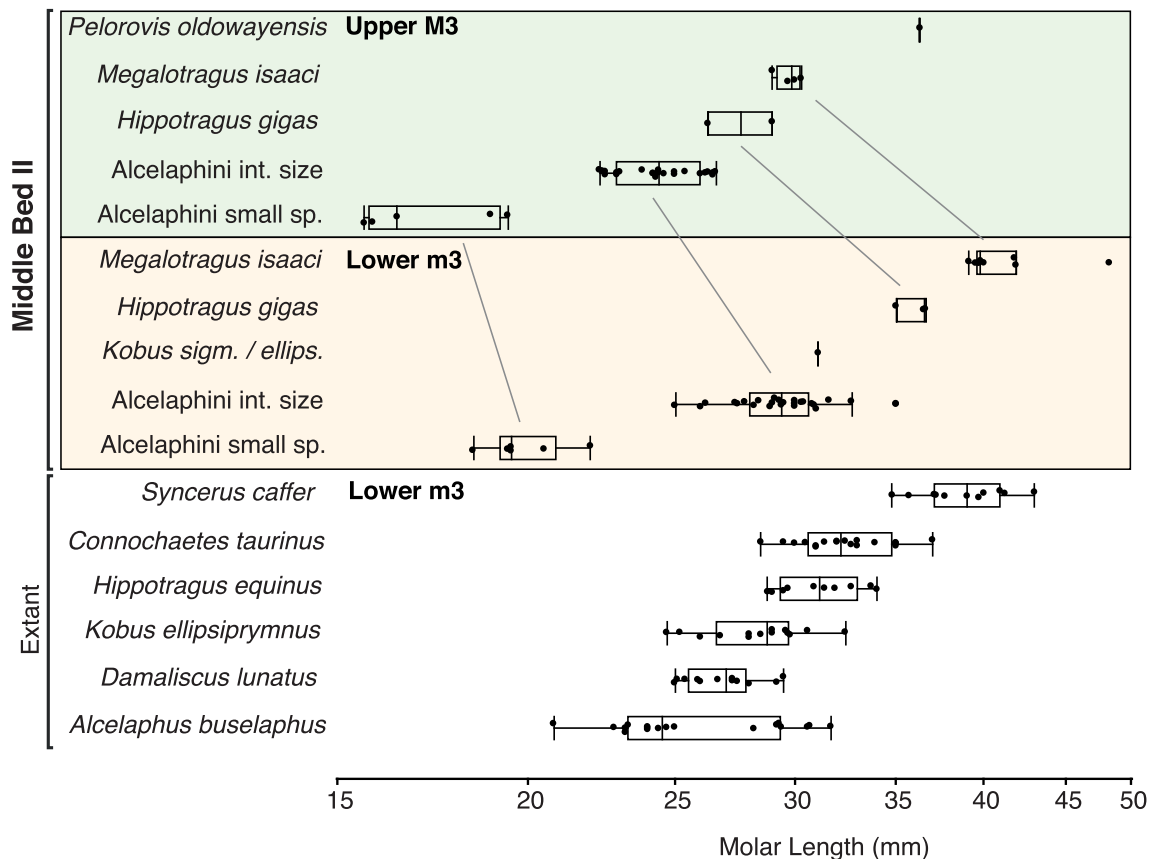


Figure A4. Distribution of third molar lengths in bovid species reveals body size (niche) partitioning. Lower m3 length in extant (lower panel) and fossil Middle Bed II (central panel) bovids. Upper M3 length in Middle Bed II bovids in top panel. Note the clearer size separation in the sympatric fossil community (the extant data [Janis, 1990] is pan-African). Note the large size of *Megalotragus isaaci* and even larger *Pelorovis*. The unnamed small alcelaphin occupies a size range smaller than any extant alcelaphin. X-axis is log scaled. Whiskers reach the furthest point within $1.5 \times$ the interquartile range from the box.

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 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, 1991a) or Members G–L of the Shungura Formation (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) 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 between 30 and 36 mm, which falls within the range of *Connochaetes taurinus* (Faith et al., 2011:fig. 5). Dental rows of *M. kattwinkeli* are in fact similar in size to those of *Rusingoryx atopocranium*, which by all accounts appears to be referable to *Megalotragus* (Harris, 1991a; Vrba, 1997; O'Brien et al., 2016). 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, *M. 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 (1978a). 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).

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 *Connochaetes gentryi* or *Connochaetes 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 preparation). 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. A1,F 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. A1F); HWK EE 1972-1156, left mandible with m1-3 (Fig. A1M); MNK S-L10-5, left maxilla with M1-2.

This is a small alcelaphin, with teeth slightly smaller than those of extant *D. pygargus* or the late Pleistocene *Damaliscus 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 and Gentry (1978a) state that mandibles mainly from Bed I retain a small p2, perhaps representing an earlier form of the same species. Gentry (1985) described a small alcelaphin from Members D–G of the Shungura Formation (~2.5–2.0 Ma), which is of similar size to the Olduvai species but already lacked lower second premolars. Lack of metaconid-paraconid fusion on p4 in the current specimens is similar to the other Olduvai specimens and different 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 × T × Ht = 16.4 × 11.4 × 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 Faith, pers. comm.). Older small alcelaphins include an unnamed species from Hadar (Alcelaphini sp. B in Geraads et al., 2012) and *Parmularius parvicornis* from Laetoli 2011 (Gentry, 2011).

Alcelaphini indet. (teeth)

Isolated alcelaphin teeth were sorted into three gross size categories, representing *M. isaaci* on the large end (Fig. A1G), the small alcelaphin species on the small end (Fig. A1,F L–N), and an intermediate category (here Alcelaphini indet.) that potentially includes species such *P. angusticornis*, *P. maasaicus*, *D. niro*, and possibly *Connochaetes* (Fig. A1J,K, see Materials and 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 Figure A4.

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 (*A. buselaphus*) to wildebeest (*C. taurinus*).

Antilopini Gray, 1821

Antidorcas Sundevall, 1847

Antidorcas recki (Schwarz, 1932)

Description Five horn cores (all from HWK EE) are assigned to this species (Fig. A2G, 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 *A. 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 the extant springbok, *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 quite abundant at Olduvai, including remains of a herd from SHK in Middle Bed II (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. A2F), and HWK EE 1972-1211. Horn cores are mediolaterally compressed, with the lateral surface noticeably flatter than the medial surface, bearing 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 and Gentry (1978a), 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, 1978a), which is similar but has more upright horn bases, with less flattening of the lateral wall, and heteronymous torsion (lyration) in longer-horned specimens. ‘*Gazella*’ aff. *rufifrons* horns are also very similar to those of larger individuals of ‘*Gazella*’ *praethomsonii* and to those of extant *Eudorcas thomsonii*, but less mediolaterally compressed.

Discussion The taxonomy of fossil gazelles is challenging, and the recent revision of extant African gazelle taxonomic nomenclature (genera *Eudorcas* and *Nanger*) means that many fossils assigned to ‘*Gazella*’ are not necessarily closely related to the extant

representatives of that genus. 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, though *Eudorcas* may be a better genus designation. This species, ‘*Gazella*’ *praethomsonii*, and Gentry’s ‘*Gazella* sp. 3’ must have been a closely related group, from which the extant *E. thomsonii* and *Eudorcas 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 extant *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 styliids 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 *A. melampus* from Lower Bed I (THC), possibly the upper part of Middle Bed II (SHK), and Upper Bed II (BK), 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 dubious (Gentry, 2010).

This larger antilopin separates nicely from *A. recki* on the dietary spectrum as well (enamel stable carbon isotopes), with the former browsing and mixed-feeding and the latter grazing, in contrast to extant springbok, which are browsers (Uno et al., 2018).

Bovidae incertae sedis

?Antilopini gen. et sp. indet.

Description HWK EE M-L1-1860 (Fig. A2E) is a left horn core that would be on the large side for an antilopin (DAP × DT: 42.4 × 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), *A. recki*, and *N. granti*, and among Alcelaphini with some specimens of *D. niro* and Olduvai horns assigned to ‘Alcelaphini sp. 4’ by Gentry and Gentry (1978a).

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 *A. 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 *N. 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 and Gentry (1978a) doubtfully referred to as *D. niro* under the designation ‘Type A’ (‘*Gazellae* indet.’ in part, Leakey, 1965:pl. 86) or *D. cf. niro* from Turkana (Harris, 1991a). 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 (1978a) 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 specimen of uncertain taxonomic identity represents a medium-sized bovid with horn cores 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 and Blaine, 1914

Kobus A. Smith, 1840

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

Description HWK EE 1972-4356 is a basal fragment of a left horn core that may be reduncin. It is large with 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 evidence of sinuses at the base. These features are suggestive of the *K. sigmoidalis-ellipsiprymnus* (waterbuck) lineage. Identification is not secure, however, as the surface texture, though greatly eroded, does not seem rugose enough for Reduncini, the basal horn core seems to project too far upwards, and the liration appears too developed 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 *K. sigmoidalis* can overlap smaller *Hippotragus* individuals. HWK EE 1972-1123 is a lower third molar that was previously attributed to *K. sigmoidalis* by Gentry and Gentry (1978a). A few more molars are here attributed to this lineage based on size similar to extant waterbuck (Figs. A11, A4). Given the lack of diagnostic material, namely horn cores, it is not possible to securely identify the large Middle Bed II kob as either *K. sigmoidalis* or *Kobus ellipsiprymnus*.

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*. Gentry and Gentry (1978a) assigned a few Middle Bed II specimens to *K. kob*, including a female skull with partial skeleton from site MNK.

Discussion At Olduvai, *K. sigmoidalis* has previously been reported mainly from Bed I, namely at sites between Tuffs IB and ID including the *Zinjanthropus* site, while *K. ellipsiprymnus* is known from a handful of specimens mainly from Bed III (Gentry and Gentry, 1978a). Reduncins are primary indicators of humid conditions with wet grass availability, and their rarity in Bed II indicates a significant lack of freshwater input on the Olduvai landscape at this time. This matches evidence from the fish (above) for an evaporative and saline lake. In contrast to the situation at Olduvai, reduncins are common at contemporaneous sites in the Turkana Basin (Bobé et al., 2007).

Hippotragini Retzius and Lovén, 1845

Hippotragus gigas Leakey, 1965

Description A handful of dental specimens are attributable to *H. gigas*, 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. Tooth size is comparable with or even slightly larger than the largest individuals of extant roan, *Hippotragus equinus* (Fig. A4). The best specimen is FLKW T69-L22-596 (Fig. A1H), a partial mandible with m1–3 (length m1–3: 83.5 mm), the 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: their figs. 12 and 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. A4). There is also the possibility of confusion of isolated molars of *H. gigas* with those of the bovin *S. 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 upper 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 (*Hippotragus niger*) 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 extant takin, *Budorcas taxicolor*.

Discussion With the exception of the Ethiopian walia (*Capra walie*), caprins are today absent from sub-Saharan Africa. The fossil record, however, establishes their presence through much of the Pliocene and Pleistocene (Bibi, 2011; e.g., Bibi et al., 2012), until the Holocene in South Africa (Brink, 1999; Faith, 2013). Gentry and Gentry (1978a) and Leakey (1965) 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 *Budorcas churcheri* from Hadar (Gentry, 1996). HWK EE M-L0-172 might record the same species. Unfortunately, this was a surface find, and its preservation differs slightly from specimens found in situ at HWK EE. Bed III is widely exposed and steeply inclined above the HWK EE site level, and the exact provenance of this tooth is not certain.

Giraffidae Gray, 1821

Sivatherium Cautley and Falconer, 1835

Sivatherium maurusium Pomel, 1893

Description Referred dental specimens include HWK EE 1972-377 and HWK EE 1972-634 (Fig. A5B), both right mandibles preserving p2-m3. These are massive giraffid teeth that are within the metric ranges of *S. 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) 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, *Sivatherium 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 gracilis Arambourg 1947

Description HWK EE M-L4-339 is a right upper P3 or P4 (AP × T: 19.7 × 24.3 mm) with a low crown that matches *Giraffa* rather than *Sivatherium*. This tooth bears a posterolateral spur extending from

the posterior protocone into the central fossette, a character Harris (1976a) noted in *Giraffa* (but not in *Okapia*) and that Geraads et al. (2013) noted as distinguishing *G. gracilis* from *Giraffa stillei*.

This specimen falls at the smaller end of the size range of *Giraffa camelopardalis* and is smaller than *Giraffa jumae* (Singer and Bone, 1960; Harris, 1976a). It is probably too large for *Giraffa pygmaea*, though no upper premolar measurements are available from 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. pygmaea* would have been about 14–16 mm long, which is shorter than in the current specimen. HWK EE M-L4-339 is smaller than specimens of *G. gracilis* from Koobi Fora (Harris, 1976a), but similar in size to the P4 in the lectotype of *G. gracilis* from the Shungura Formation (Arambourg, 1947; Geraads et al., 2013).

Discussion *G. gracilis* was established by Arambourg (1947) based on material from the Shungura Formation in Ethiopia and has since been described from Olduvai and Koobi Fora. *G. gracilis* and *G. pygmaea* have both been recorded previously from Olduvai Beds I and II (Leakey, 1965; Harris, 1976a; Harris et al., 2010).

Harris et al. (2010) treated *G. gracilis* as a junior synonym of *G. stillei*, best known from Laetoli and Hadar, but Geraads et al. (2013) maintained the distinction, recognizing a *G. stillei-gracilis* lineage leading to the extant giraffe.

Giraffa cf. *jumae* Leakey 1965

Description EF-HR T2-L2-1410 is a lower p2 (AP × T: 17.7 × 12.1 mm) from Upper Bed II that falls within the size range of both extant *G. camelopardalis* and a specimen of *G. jumae* from Rawe (Harris, 1976a). It is larger than Upper Laetoli specimens referred by Robinson (2011) to *G. stillei*, but similar to specimens he referred to *Giraffa* aff. *jumae*. It might also fit within the size range of *G. gracilis* from the Shungura Formation (J. Rowan, pers. comm.). Size overlap among these fossil species precludes any confident assignment for this specimen.

Discussion A well-preserved cranium of *G. jumae* was previously described from EF-HR by Leakey (1970), and EF-HR T2-L2-1410 might belong to the same species.

Hippopotamidae Gray, 1821

Hippopotamus Linnaeus, 1758

Hippopotamus gorgops Dietrich, 1926

Description Numerous teeth (Fig. A5D) 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 *Hippopotamus 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). 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 second species (even larger than *H. gorgops*) or a degree of intraspecific variation that is unparalleled in the extant hippopotamus.

Discussion *Hippopotamus gorgops* was first described based 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 Upper Bed II and Bed III (sites BK and JK; Coryndon, 1970; Harris, 1991b; Weston and Boisserie, 2010), but no remains of it have come to light in the new OGAP collections.

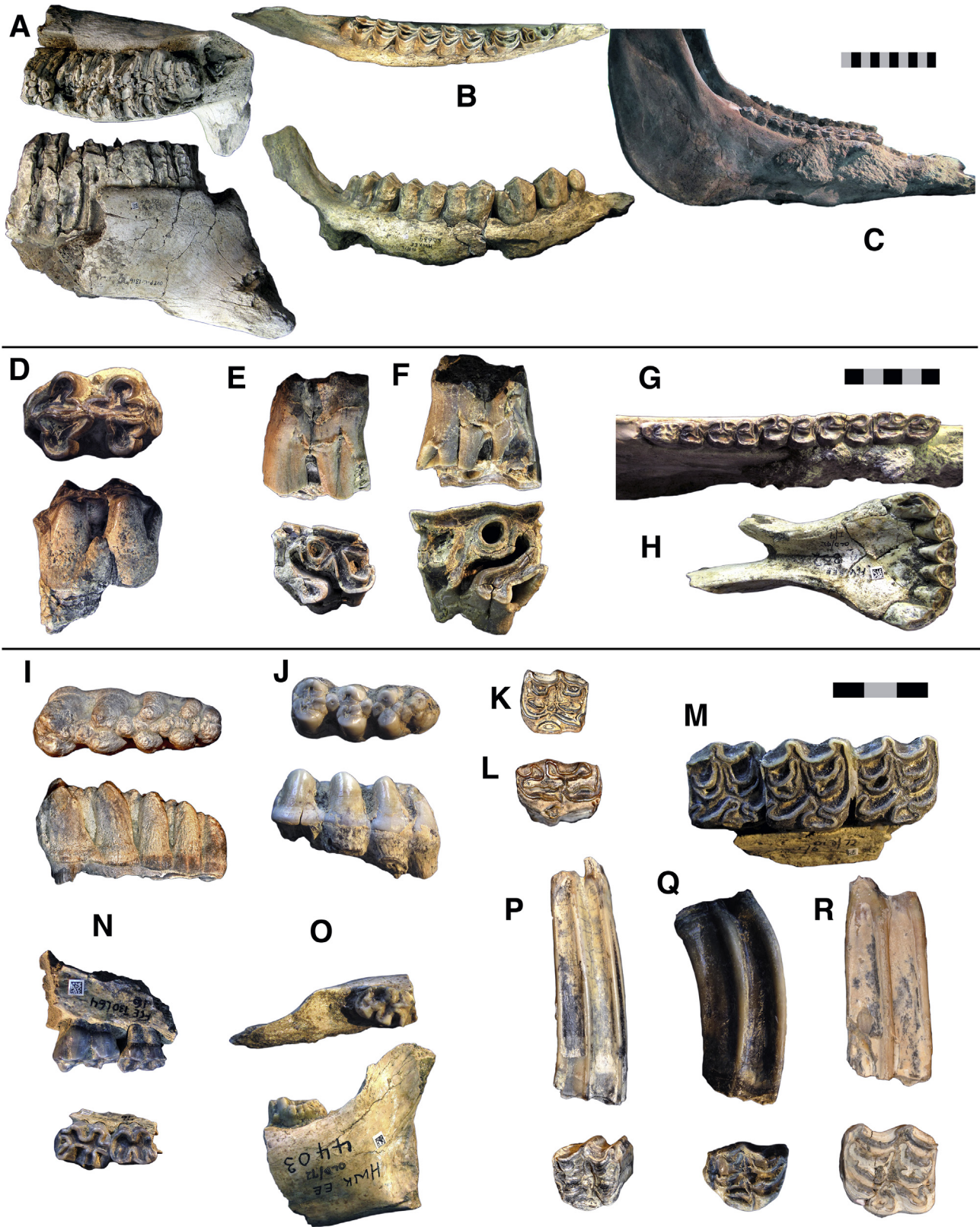


Figure A5. Teeth of large herbivores (non-bovids). A) *Elephas recki*, HWK EE 1972-1210, left mandible with m2 or m3. B) *Sivatherium maurusium*, HWK EE 1972-634, right mandible with p2-m3. C) *Equus oldowayensis*, HWK EE M-L10-1575, left and right mandibles with p2-m2. D) *Hippopotamus gorgops*, HWK 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) *Kolpochoerus 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, right 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. Scale bars = 10 cm in A, 5 cm in B, and 3 cm in C.

Suidae Gray, 1821

Olduvai Bed II suids have a convoluted taxonomic history, a useful summary of which is provided by Kovarovic et al. (2013: their Appendix A). Uncertainties regarding the taxonomy and stratigraphic provenience of previously described material limit our ability to make precise comparisons here. The new collection preserves specimens that belong to the suid genera *Kolpochoerus* and *Metridiochoerus*. *Kolpochoerus* is represented by two lineages that predominate in the Pleistocene African fossil record: *Kolpochoerus majus* and *Kolpochoerus limnetes* (and its more derived descendant usually named *Kolpochoerus olduvaiensis*, but here named *Kolpochoerus paiceae*, see 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*.

In our Middle Bed II sample, *Kolpochoerus* is more abundant than *Metridiochoerus*, which is similar to the situation in the Konso Formation at ~1.6 Ma in Ethiopia (Suwa et al., 2003, 2014) and the opposite of the situation in the KBS and Okote Members of the Koobi Fora Formation (Patterson et al., 2017). Presumably these differences reflect environmental factors, but too little is known of suid paleoecology to provide an accurate interpretation. Stable carbon isotopes from various African sites indicate that the suid species present at Olduvai fed predominantly on C₄ plants, likely grasses (Harris and Cerling, 2002; van der Merwe, 2013; Souron, 2017; Uno et al., 2018). 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; Uno et al., 2018). The paleoenvironmental implications of this are not clear, however, as the abundance of *Kolpochoerus* does not seem to be correlated with other woodland or wet grassland indicator taxa (e.g., *Giraffa* or *reduncin* bovids).

Kolpochoerus Van Hoepen and Van Hoepen, 1932

Kolpochoerus limnetes (Hopwood, 1926)

Description Two specimens are confidently assigned to *Kolpochoerus limnetes*. HWK EE 1972–4186 (Fig. A5J) 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. HWK EE 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 *Kolpochoerus limnetes* in contrast to recent publications that prefer the name *Kolpochoerus heseloni* (e.g., Bishop, 2010). The holotype of *Sus limnetes* Hopwood, 1926 is a right upper M3 (NHM M 12614) that comes from the Kairo 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 ~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*. However, he chose to use the specific name *K. heseloni* for the latter (Leakey, 1943), as he had some doubts regarding the stratigraphic provenience of the *S. limnetes* holotype 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 HWK EE, from between Tuffs IIA and IIB.

Kolpochoerus paiceae (Broom, 1931)

Description Three specimens are assigned with certainty to *Kolpochoerus paiceae*. FCW M-L10-194 (Fig. A5I) 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 *Kolpochoerus 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 mesiodistal length (Souron, 2012: their Fig. 2.17). The name *K. olduvaiensis* has thereafter been widely used for eastern African specimens with third molars more elongated than those of *K. limnetes* (e.g., Gilbert, 2008a; Bishop, 2010; 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; Souron, 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*. Among the four specimens tentatively assigned to *K. cf. limnetes*, two 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*. HWK EE 1972-4349 is a complete left upper M3. FCE T67-L12-23 is a

complete right upper M1. HWK EE M-L10-69 is a near complete right lower ml. FCW T62-L54-54 is a right mandibular corpus 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 *Kolpochoerus phillipi* (Suwa et al., 2014; Souron et al., 2015) and became extinct close to the end of the Pleistocene (Souron, 2012; Faith, 2014). 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 craniomandibular 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 Hopwood, 1926

Metridiochoerus compactus (van Hoepen, 1932)

Description Three specimens are assigned to *Metridiochoerus compactus* (although completely ruling out a very late stage of *Metridiochoerus andrewsi* is difficult). FCW T65-L79-2 is a nearly complete left lower m3. Dimensions and morphology are a match with *M. compactus*. HWK EE 1972-2065 is a complete right upper M3 partly enclosed in maxillary bone. MNK T5-L10-3028 is a right fragmentary mandibular corpus 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 ~1.6 Ma and ~1.3 Ma (Suwa et al., 2014).

Discussion There is the possibility of confusion between *M. compactus* and *Metridiochoerus 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 penecontemporaneous 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 here 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 (Leakey, 1942, 1958; Harris and White, 1979; Bishop,

2010; Kovarovic et al., 2013). An edentulous mandibular symphysis, HWK EE 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 belong to a large papionin, with high crowns and columnar cusps indicative of *Theropithecus*. These include FCE T30-L64-16, a left maxillary fragment with M1–2 (Fig. A5N), and HWK EE 1972-4403, a right mandible fragment with m3 (Fig. A5O). Size is larger than *Theropithecus brumpti* and matches *Theropithecus oswaldi* from Koobi Fora (Jablonski and Leakey, 2008). The molar fragment HWK EE 1972 (no number, 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 comparable to a *T. oswaldi* humerus from Koobi Fora (Jablonski and Leakey, 2008).

Discussion *T. oswaldi* was a large-sized terrestrial papionin 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 *H. habilis* partial skull OH 13 from the MNK Skull site (Leakey et al., 1964). The contemporaneous presence of *H. 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, *A. boisei* was there too, as evidenced by remains from Bed I (Leakey, 1959) and Upper Bed II (Domínguez-Rodrigo et al., 2013). Despite abundant stone tools, hominins are among the rarest large mammals in the community. They probably never reached high densities, comparable perhaps with the low densities of large carnivores.

PERISSODACTYLA Owen, 1848

Rhinocerotidae Owen, 1838

Ceratotherium Gray, 1868

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

Description A few dental specimens are attributable to *Ceratotherium* (Fig. A5E, F). They are of similar size to teeth of *Dicerus* 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, uppers with a more curved proto-loph, 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), though 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. A5E), the parastyle groove may not have been so pronounced,

unlike the state in *C. simum* (Hernesniemi et al., 2011). However, the protoloph curve quite smoothly toward 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 ‘*Rhinoceros simus germano-africanum*’ was named by Hilzheimer (1925) based on a lost skull from Olduvai. This has sometimes been treated as a separate species, *C. germanoaffricanum*, or 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., 2018). The black rhinoceros, *D. bicornis*, has previously been documented from Lower, Middle, and Upper Bed II (Leakey, 1971; Geraads, 2010). It is 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 (1982) described the oldest African ass (*Equus africanus/Equus 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. A5C, G). Teeth assigned to this species are large, similar to the size of extant *Equus grevyi*. Upper cheek teeth (Fig. A5M, 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 lingua-flexids, 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 *Equus koobiforensis* and the contemporaneous southern African species *Equus capensis* (Bernor et al., 2010). It has been proposed as an ancestor to the extant *Equus 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 *Eq. oldowayensis* and relatively higher-crowned (Fig. A5 K, L, P). Upper teeth with protocone isolated, oval in shape, typically rounded buccally and flattened lingually; infundibular plications often complex; pli caballin present and often large. Lower teeth with tall and large ectostylids; ecto- and lingua-flexids often quite shallow; parastylid typically long and reaching the 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 *Eurygnathohippus cornelianus* ‘sensu lato,’ as described in Bernor et al. (2010). This species is best diagnosed by hypertrophied lower central incisors i1 and i2, and reduced i3 (Bernor et al., 2010), elements that are not preserved among the OGAP remains. Hooijer (1975) reported lower and upper cheek tooth crown heights of 70–80 mm for ‘hipparion’ material from Upper Bed II (mainly BK, SHK, JK). EF-HR T2-L2-1946, a left upper P4 or M1 of *Eq. oldowayensis*, has an unworn crown height of 72.5 mm. FLK T69-L26-204 is a right lower m1 in early wear with a preserved crown height of 81.0 mm. This is about the same absolute height as teeth of *Eq. oldowayensis* (SOM File 1), but the significantly smaller size of *Eu. cornelianus* means it had relatively greater hypsodonty. Presumably, *Eu. cornelianus* had a more abrasive diet than the larger *Eq. oldowayensis*, a conclusion this is supported by tooth wear data (Uno et al., 2018).

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. A5A). 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 ~ 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 *E. recki*, as expected for the age of Middle Bed II (Beden, 1980; Sanders et al., 2010). 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; Sanders et al., 2010). 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, 1965, 1971: appendix B), Leakey (1965) 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 carnivoran assemblage from 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*, *Panthera pardus*, *Hyaena hyaena*, and *Atilax* from the current assemblage is certainly a question of sampling intensity. Petter (1973) previously described lion (including ‘*Panthera crassidens*’) from Lower and Upper Bed II (FLKN and BK), and striped hyena, leopard, and marsh mongoose 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, 2013a). 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 (1928) from Reck’s ‘Graben X’ (‘Excavation 10’) of unknown stratigraphic provenience. Three mandible fragments from Bed II were later referred by Ewer (in Leakey, 1965) and there exists an unpublished specimen (LW, pers. obs.), but it is not clear where in Bed II all these were found. Similarly, an upper M1 from Bed II referred to *Aonyx* is also of unclear stratigraphic position. We exclude these two taxa from the Middle Bed II faunal list (Table 1) for now.

Canidae Fischer, 1817

Prototocyon Pohle, 1928

Prototocyon recki Pohle, 1928

Material FCW T63-L62-240, left distal humerus (Fig. A6A). Distal width = c. 13 mm, max AP = 10.1 mm, min trochlear AP = 6.4 mm. MNK T5-L9-1159a (b-g are birds), distal metatarsal fragment (Fig. A6B). Distal width is 4.2 mm.



Figure A6. Carnivoran postcrania. A-B) *Prototocyon recki*. 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. E) *Caracal/Leptailurus*, MNK T5-L12-482, right humerus. Scale bars = 3 cm in A, 1 cm in B, and 10 cm in C-E.

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 Deghani, 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
Crocota Erxleben, 1777
Crocota cf. *Crocota ultra* Ewer, 1954

Description HWK EE 1972–400, left humerus shaft and distal end (Fig. A6D). HWK EE M-L6-1444, left lower m1. HWK EE M-L4-102, left lower m1. HWK EE M-L4-294, right scapula (Fig. A6C).

Discussion Analyses of *Crocota* (LW, unpublished data) reveal a clear size separation between the older *Crocota dietrichi* and *Crocota ultra*, except at Olduvai. The Olduvai *Crocota* material described by Petter (1973) as *Crocota 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 length ~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, 2013a; their Fig. 7.6a). The Olduvai *Crocota* is here provisionally referred to *Crocota* 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 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*, leads 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. A6E).

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.

Supplementary Online Material

Supplementary online material related to this article can be found at <https://doi.org/10.1016/j.jhevol.2017.10.009>.

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