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Plio-Pleistocene mammals from Mille-Logya, Ethiopia, and the post-Hadar faunal change

Running title : Faunal change at Mille-Logya, Ethiopia

DENIS GERAADS,^{1*} DENNE REED,² W. ANDREW BARR,³ RENÉ BOBE,^{4, 5} PETER STAMOS,⁶
ZERESSENAY ALEMSEGED⁶

¹ CR2P, Muséum National d'Histoire Naturelle, CNRS, Sorbonne Université, CP 38, 8 rue Buffon, 75231, PARIS Cedex 05, France.

² Department of Anthropology, University of Texas at Austin, Austin, TX 78712, USA.

³ Center for the Advanced Study of Human Paleobiology. Department of Anthropology, The George Washington University, Washington, DC 20052, USA.

⁴ Primate Models for Behavioural Evolution Lab, Institute of Cognitive & Evolutionary Anthropology, School of Anthropology, University of Oxford, Oxford, UK.

⁵ Gorongosa National Park, Sofala, Mozambique

⁶ Department of Organismal Biology and Anatomy, University of Chicago, Chicago, IL 60637, USA.

*Corresponding author

ABSTRACT : We describe the non-primate mammalian fauna from the late Pliocene to earliest Pleistocene deposits of Mille-Logya in the Lower Awash Valley, Ethiopia, dated to c. 2.9 – 2.4 Ma, and divided into three successive units; Gafura, Seraitu, and Uraitele. We identify 41 mammalian taxa (including rodents), the most diverse group being the Bovidae, with 17 taxa. While the Gafura assemblage still resembles those from the earlier Hadar Formation, the younger Seraitu assemblage documents a major turnover. While there is little change in the species present across this interval, the relative abundances of various taxa change dramatically, with suids being largely replaced by open-country bovids (Alcelaphini and Antilopini). We interpret this faunal change as reflective of an environmental shift, contemporaneous with the replacement of *Australopithecus afarensis* by *Homo* in the area.

KEYWORDS : Pliocene, Pleistocene, Ethiopia, Mammalia, faunal change

Introduction

Human evolution is marked by several major milestones starting with the divergence from our closest living primate relatives at c. 7.5 Ma, which initiated our lineage, to the speciation event at c. >300 ka that gave rise to *Homo sapiens* (Püschel *et al.*, 2021). Between these events is another key evolutionary milestone, the cladogenetic events that occurred between c. 3-2 Ma, which gave rise to the *Paranthropus* clade on one hand and the *Homo* clade on the other (Strait & Grine, 2004; Strait *et al.*, 1997; Villmoare, 2018). This Plio-Pleistocene transition has also been one of the most controversial periods, characterized by debates regarding some of the key events in human evolution linked to 1) changes in human material culture and tool use that for

many are a hallmark of the human condition (Antón & Josh Snodgrass, 2012; Braun *et al.*, 2019; Leakey *et al.*, 1964; Semaw *et al.*, 1997), 2) ongoing debates surrounding the climatic, environmental and tectonic factors causally underlying this transition (Antón *et al.*, 2014; deMenocal & Bloemendal, 1995; Vrba, 1985), and 3) many of the systematic and taxonomic debates surrounding hominid species delimitation, adaptation, the role of genera (and other higher taxa) in human evolution (Leakey *et al.*, 1964; Villmoare, 2018; Wood, 1992) and hominin paleobiogeography.

These conceptual issues are further exacerbated by a gap in the East African fossil record between 3 and 2 Ma. Specifically, this time period follows the 2.9 Ma unconformity and disruption of sediment deposition in the Hadar Formation and precedes the most fossiliferous deposits of the Koobi Fora Formation starting around 2.0 Ma.

The Mille-Logya Project (MLP) research area contains fossiliferous sediments representing this interval and our efforts are geared toward systematic collection of faunal, archaeological and geological data relevant to the broader evolutionary and environmental context of this key time period.

The MLP site is located between the towns of Mille and Logya in the Lower Awash River Valley, in the Afar region of northeastern Ethiopia (Fig 1). An earlier study synthesizing the field work and preliminary analysis (Alemseged *et al.*, 2020) concluded that the deposits at MLP represent lacustrine exposures dating to between c. 3.0 and 2.4 Ma with fossil assemblages that document a significant faunal change associated with more open conditions, and to the emergence or arrival of an early species of *Homo*.

Building on this earlier analysis, the current work details the systematic paleontology of the mammalian fauna at MLP, excluding Primates, which will be described elsewhere. The aim of this work is to provide details of the species discovered and how they compare to earlier faunas of the Hadar Formation argued to be the precursor to faunas at MLP. Our analysis supports earlier interpretations of a change in large mammal faunal composition and relative abundance at MLP compared to the faunas of the Hadar Formation and corroborates the hypothesis of environmental change associated with this faunal shift.

Materials and Methods

The c. 2200 fossil specimens included in this analysis were collected over six field seasons conducted between 2014 and 2020, using a standardized surface survey methodology (Reed *et al.* 2015). Most specimens were surface finds, but a few, as noted in the text, were excavated *in situ*. Systematic screening for small and micro-vertebrates has not yet been conducted, and this paper focuses on the larger vertebrate fossils recovered from surface survey.

Preservation at MLP is uneven and concentrated in specific, named regions. Many fossils were recovered from fields of fractured basalt cobbles that contributed to the heavy breakage in the assemblage. In contrast *in situ* specimens are very well preserved and relatively complete. All fossil specimens are accessioned at the National Museum of Ethiopia, a division of the Authority for Research and Conservation of Cultural Heritage (ARCCCH), Addis Ababa. Fossils are identified by catalog number in the text followed by a letter in brackets indicating its faunal unit and associated geochronological age: [G] – Gafura (older than 2.9 Ma), [S] – Seraitu (2.9 to c. 2.5 Ma), [U] – Uraitele (c. 2.5 to 2.4 Ma). Fossils not assigned to a unit are followed by [M] - MLP and have ages between 3-2.4 Ma.

The following abbreviations are used throughout: Fm = Formation; Mb = Member; ant. = anterior; art. = articular; dist. = distal; max. = maximum; prox. = proximal; H = height; L =

length; W = width; AP = anteroposterior. All measurements are in millimeters unless otherwise indicated.

Systematic Palaeontology

Proboscidea

Elephantidae

Elephas recki Dietrich, 1915

Elephant tooth plates are frequently encountered, but there are few complete teeth (measurements: Suppl. Table 1). MLP-1786[S] and MLP-2158[G] are upper DP2s; they have only 3 plates, instead of 4 plates as seen in a tooth from Omo 213, a locality from sub-Member B10 of the Shungura Formation, dated to c. 2.9 Ma (Beden, 1979). They are much smaller than this tooth and other teeth from Omo, but some teeth from Koobi Fora referred to *E. recki atavus* by Beden (1983) are comparable in size. MLP-1379[S] is an upper DP3 with only 5x plates (following Beden [1979], x means a plate that is not fully formed), instead of 6 as in Omo 213, which is about as large. All DP3s from later levels at Omo also have more than 5x plates.

MLP-2416[S] and MLP-2361[G] are lower dp2s, the latter incomplete; MLP-2416 is small and has only 3x plates. MLP-2399[U] is a lower dp3 that also has fewer plates than the Omo teeth. Deciduous teeth of *E. recki* have seldom been illustrated but, from their plate number, those from MLP, whatever their origin in the succession, definitely point to a correlation with the lowermost part of the Shungura Fm, within which no significant trend can be observed (Beden, 1979, 1983).

MLP-2524[U] is a complete, almost unworn M2. Unfortunately, there is no significant change in the metrics of this tooth from the earliest subspecies *E. recki brumpti* to the successive forms *E. recki shungurensis* and *E. recki atavus* (Beden, 1979, 1983, 1987). MLP-2524 is slightly narrower than the teeth from Shungura Mb B, and more like those from Shungura Mb C, but it is not less hypsodont and has only one plate less than KNM-ER 719 from the Upper Burgi Mb. Thus, this tooth provides no biochronological information.

MLP-1529[U] is a little-worn M3. At this wear stage, the anterior plates are widely spaced, with rather thick enamel and few folds. The tooth is more hypsodont but has fewer plates than in complete teeth of *E. recki shungurensis*, but KNM-ER 16456 from the Lokalelei Mb, assigned to *E. recki brumpti* by Harris *et al.* (1988) is about as high. Again, these somewhat contradictory characters do not have biochronological significance.

MLP-1725[S] is a mandible with partial left and complete right partly erupted m3. The symphysis is short, as in other *Elephas*. The anterior plates are slightly worn and show rather strong enamel folding and distinct median pillars, especially posteriorly. Neither the length of the tooth nor the number of plates can be estimated.

MLP-474[S] is a mandible with a much-worn m3 preserving only its distal part; what remains of the tooth is narrow, but it may have been broader anteriorly. The thick enamel and widely spaced plates give it a primitive look, but we believe it can be assigned to *E. recki* as well; though it also resembles teeth in *E. recki shungurensis* (Beden, 1987, fig.14A).

MLP-556[U] (Fig. 2E) is a lower molar, probably m3, but wear has erased the anterior plates; the remaining ones are somewhat chevron-shaped. It is not possible to assign it to a particular stage or sub-species.

All elephant remains from MLP can be assigned to *E. recki*, but their dental morphology does not allow a firm attribution to any subspecies in this species, although it seems that the deciduous teeth provide more reliable information about the evolutionary stage than the permanent ones. This is probably because the successive stages are certainly harder to characterize than originally assumed by Beden (1979, 1983, 1987).

Deinotheriidae

Deinotherium bozasi Arambourg, 1934

Deinotherium has not been found in the Gafura unit, but fragments of cheek-teeth are encountered at Uraitele, where an almost complete cranium MLP-2797[U] has also been found *in situ*. Together with KNM-ER 1087 (Harris 1983) and an unpublished skull from Hadar, it is one of the few known crania of this species, but it remains to be fully prepared, and its surface preservation is not excellent, making detailed comparisons difficult. The best-preserved tooth is the left P3 (L=92; W=86.7), which is also the most diagnostic tooth in deinotheres, as was shown by Arambourg (1947). He observed that, in this species, the lingual cups are fully separated from the labial ones, in contrast to the earlier *D. giganteum*. The protocone of the MLP-2797 P3 (Fig. 2H), bears a mesiolabial crest, which does not extend to the paracone; the hypocone fully lacks the labial crest which is strong in the Miocene forms. The lingual cusps are also fully separated, but there is some variation in this regard in *D. bozasi*, as teeth from Omo (Fig. 2I-K) may show a hint of connection (Omo 75-69-3153), or even a full connection (L596-20). MLP-2263[U] is an upper molar, whose dimensions (L = 105; W = 101.5) are similar to those of Koobi Fora specimens (Harris 1983).

Deinotherium is well-known to be a pure browser, and its presence testifies to the existence of significant forested patches, as its very large body size required massive quantities of forage to maintain (Sanders *et al.*, 2010).

Tubulidentata

Orycteropus sp.

MLP-1548[S] is a mandibular fragment bearing the third molar. In ventral aspect, the typical tubular dentine is clearly visible. The tooth is ovoid, decreasing in width distally, is only slightly longer than broad (c. 10 x 9 mm), and not at all bilobed. MLP-1548 is distinctly smaller than the holotype of *O. djourabensis* Lehmann *et al.*, 2005, whose m3 is distinctly bilobed (Lehmann, 2008), but the outline of m3 is strongly variable in upper Miocene forms (Bonis *et al.*, 1994). Thus, the MLP mandible is too incomplete to allow assignment to either the living species *O. afer* or to the extinct *O. crassidens* (if the two forms are really distinct).

Perissodactyla

Rhinocerotidae

Diceros sp.

A few teeth show that this genus is definitely present, although rare. MLP-382[S] (Fig. 2G) is a p2 (L =32.2, W =23.8) with a much-reduced paralophid, thus unlike living *Ceratotherium simum* and much more like *Diceros*, but the posterior valley is deeper than in modern *D. bicornis*. MLP-1710[S] is an m1 or m2 (L = 59, W = 40). Its large size and oblique hypolophid show that it is a molar, but the paralophid is distinctly shorter lingually

than in fossil and living *Ceratotherium*. It is larger than molars of the living *Diceros bicornis* (Guérin, 1980, Table 6).

Guérin (1985) showed that some extinct specimens of *Diceros* from Omo were larger than the living species, suggesting that taxonomic distinction might be needed. We concur with his opinion but no species name is available for this Plio-Pleistocene species, and we prefer not to propose species identification.

Ceratotherium mauritanicum (Pomel, 1888)

Systematics and nomenclature of Pliocene African rhinos long remained confused, but it is now clear that the ancestor of the modern *C. simum*, which has often been called *C. praecox*, should be called *C. mauritanicum*, as the species *praecox* is in fact a *Diceros* (Geraads, 2005, 2010, 2020). A few teeth and probably most of the rhino postcranials document this species at MLP. MLP-2192[U] is a very worn upper premolar, probably P4 (L = c.40; W = 60); it is more like *Ceratotherium* in its lingually expanded protocone, small hypocone with an anterolingual expansion, and tall posterior cingulum closing the postfossette. It resembles Koobi Fora specimens that Geraads (2005) assigned to *C. mauritanicum*. MLP-950[S] is a DP2-DP4 series (DP4 L = 57.8; W = 49.6; Fig. 2F). Deciduous teeth of early *Diceros* and *Ceratotherium* are not easy to tell apart, but the large size, the strong crista fusing with the crochet in early wear, and the large postfossette on DP2 are unlike *Diceros*. These teeth are a good match for definite *C. mauritanicum* from Ahl al Oughlam in Morocco, at c. 2.5 Ma (Geraads *et al.*, 1998). MLP-1638[S] are teeth and skull fragments, and MLP-701[G] is a mandibular piece, certainly of *Ceratotherium*.

An astragalus MLP-1181[S] (max. H = 95.3; medial H = 87.7; dist. artic. W = 83; max W = 99+) is probably attributable to *Ceratotherium*, based on its size similarity to Hadar specimens (most of which are definitely *Ceratotherium*). Other specimens cannot be identified to genus, but the calcanei at least are larger than in living *Diceros*, and are probably attributable to *Ceratotherium*. These are: scaphoid MLP-2077[S] (APD = 81.7, max. W = 57.3); Mc III MLP-1203[S] (L > 160; prox W = c.64); calcaneum MLP-1509[S] (L = 136, H of tuber 76.5); calcaneum MLP-2044[S] (L = 135, H of tuber 74); third phalanx MLP-1779[S] (max W c. 75).

It is well-known that *Diceros* is a mixed-feeder or browser, whereas *Ceratotherium* is a grazer, so that they could provide paleoecological information, but there are too few specimens here to estimate their relative abundances. *Ceratotherium* is present in all units, but the few specimens definitely identifiable to *Diceros* are from the Seraitu unit.

Equidae

'*Eurygnathohippus*' cf. *hasumense* Eisenmann, 1983

Hipparions appear in the Old World at the middle / late Miocene boundary and survived until the earliest Middle Pleistocene in Africa. A large number of taxa have been named, but robust distinctions are mostly based upon cranial remains, which are absent at MLP, so reliable identifications cannot be made. We will therefore restrict the comparison to the Hadar material, which has been partly described (Eisenmann, 1976, 1983; Bernor *et al.*, 2005, 2010).

Eisenmann (1983) followed by Bernor *et al.* (2005, 2010) referred most of the Hadar hipparion material to *Hipparion* (or *Eurygnathohippus* – see below for a discussion of this issue) *hasumense*, a species defined at Koobi Fora. Eisenmann (1976) also named *H. afarensis*, based upon a cranium from the Kada Hadar Mb and mandible from the Denen Dora Mb, but the latter specimen was transferred to *H. hasumense* by Eisenmann & Geraads (2007). Taking into account the slight cranial and dental differences, and the apparent homogeneity of the limb-bone sample, Bernor & Armour-Chelu (1997) and Bernor *et al.* (2005, 2010) were

skeptical about the presence of two distinct lineages at Hadar, '*E. afarensis*' being possibly descended from '*E. hasumense*', if really distinct at species level.

Dental remains, from all three MLP units, consist of a large number of isolated teeth or partial teeth, but associated sets are rare. MLP-1022[S] is a set of left and right i1s, plus i2 and i3; they are deeply grooved labially. The third incisor is not reduced, in contrast to Pleistocene hipparions of the *E. cornelianus* group. The most complete specimen is the upper tooth series MLP-1592[S] (Fig. 2A). The teeth slowly decrease in size from P3 to M2, the protocones are of moderate size, larger on P4, the 'pli caballin' is small, and there are long folds in the fossettes, especially in the anterior one. These features do not differ from the incompletely published material from Hadar (Eisenmann, 1976, 1983). The most remarkable feature of the lower teeth is the small size of the ectostylid on many teeth, although it may be strong on some others; it is fully absent on the molars of the partial mandible MLP-785[S] (Fig. 2B). The pli caballinid is seemingly constant, but weak.

Equid postcranials are relatively common at MLP; there are, for instance, eight astragali and 10 metapodials, including two complete metatarsals, which makes the MLP sample quite significant in eastern Africa. By contrast to bovids, hipparion postcranials have received some taxonomic interest recently, offering basis for comparison of the MLP ones, although limited to metrics.

The two complete metatarsals (Figs. 1C-D) are shorter, but slightly less slender than the Hadar ones (Bernor *et al.*, 2005; Suppl. Fig. 1). Partial specimens confirm the smaller size of the MLP form: even if all distal ends are metatarsals, they are smaller than at Hadar (Suppl. Fig. 2). Interestingly, Bernor *et al.* (2005) observed that a specimen from the Kada Hadar Mb is smaller than earlier ones at Hadar, and it is likely that this trend towards size reduction continued after Hadar times. Furthermore, the smallest two MLP distal ends are from the Uraitele unit (Suppl. Table 2), suggesting that this process of size reduction continued within the MLP time range. The few first phalanges are within the Hadar size range, which is rather large. The two phalanges MLP-1286[S] that are certainly of the same individual differ significantly in their length (Suppl. Table 3), in contrast to the standard Höwenegg *Hippotherium primigenium*, but as in '*Eurygnathohippus*' *hasumense* from Hadar AL-155-6 (Bernor *et al.*, 1997, 2005).

Identification of hipparions without good cranial material is always a challenge, but there is no strong reason for separating the MLP form) from the Hadar '*E. hasumense*', and we tentatively assign it to this species, even though some evolution took place between Hadar and MLP times. The variation in the development of the ectostylid, and its complete absence in some teeth, raises again the issue of the validity of the genus *Eurygnathohippus* van Hoepen, 1930. It was said to be characterized by the development of this stylid, and restricted to Africa (Bernor *et al.*, 2010). However, as noted by Eisenmann & Geraads (2007), not all African hipparions have well-developed ectostylids, and this stylid may be present in non-African forms, as recently confirmed by Jukar *et al.* (2019) who assigned a few isolated teeth from India to *Eurygnathohippus*. In any case, the hypothesized existence of a clade defined by a single apomorphy is not falsifiable, and it might well be that the ectostylid developed in parallel as an adaptive feature linked to diet (Eisenmann & Geraads, 2007).

Artiodactyla

Camelidae

Camelus grattardi Geraads, 2014

The relative abundance of camels is one of the most interesting features of the MLP mammal assemblage. While this family is extremely rare in all African sites, with the single

exception of Tighennif in Algeria (Martini & Geraads, 2018), ten MLP specimens, including a partial cranium, have been recovered from the Seraitu Unit. They have been described in detail (Geraads *et al.*, 2019), and their implications for the phylogeny of *Camelus*, of which they are among the earliest representatives, have recently been discussed (Geraads *et al.*, 2020), and they will not be re-described here.

Hippopotamidae

Hippo remains are common throughout the MLP sequence; they include a relatively complete cranium, some mandibles and many fragmentary specimens. Neither the size distribution of the many collected astragali, nor other remains, suggest that more than one species is present.

'Trilobophorus' afarensis Gèze, 1985

The cranium MLP-1886[S] has not been fully cleaned yet, and only its ventral aspect can be observed. It belongs to a juvenile individual, with DP4 still in place and M2 erupting. This young age certainly explains why the P1 is still close to the canine. The length from occipital condyle to the level of the front side of the canines is 455 mm. The distance between the lateral sides of the canines is 210 mm. These measurements match those of the mandibles, of which there are four relatively complete, but largely edentulous specimens (Figs. 2J-K). They are homogeneous in their size (Suppl. Table 4) and morphology. There are three incisors, of rather small size, on each side; the central one (i2) is inserted slightly higher than i1 and i3, and is smaller than i1, and smaller or equal in size to i3. In accordance with the small size of the incisors, the symphysis is long and relatively thin in the sagittal plane, definitely thinner than in specimens from Hadar and Kanapoi (Boisserie, 2020, fig. 5). Anteriorly, the mandible is not expanded transversely, and the canine is inserted at the front end of the premolar arch, instead of being distinctly farther laterally and forward as in many hippos. The diastemas between the canine and p1, and between p1 and p2 are quite short.

Probably because hippos do not display many diagnostic characters at a low taxonomic level, their systematics in the African Pliocene and Pleistocene is still unsettled (e.g., Weston & Boisserie, 2010; Boisserie, 2020). In many instances neither species nor even genus identification could be proposed, and the few taxa that are well characterized are those that were described from specific, time-constrained localities.

It is clear that despite its similar age, geographic proximity, and similar anatomy of the rostral part of the mandible, the MLP hippo can be readily distinguished from *Hexaprotodon bruneti* from the Hata Mb of the Bouri Fm, which has a much larger i3 (Boisserie & White, 2004).

Much confusion surrounds the Hadar hippos. They were first studied by Gèze (1980, 1985) who named three taxa, *Trilobophorus*, based upon the new species *T. afarensis* whose holotype is cranium AL-74-20 from Geraru, and *Hexaprotodon coryndoni*, whose holotype is AL-170-1 from the Denen Dora Mb. The latter is about as large as the MLP hippo, but the rostral portion of the mandible is much longer and much more splayed out (Gèze, 1980, pl. 13), and this species is clearly different.

Locality AL-74 in the Lee Adoyta area is dated to slightly less than 2.78 Ma (K. Reed, pers. com. to DG, Nov. 21, 2020); it is thus younger than the Hadar Fm, but similar in age to the Seraitu unit. Boisserie (2020) suggested that the Geraru (Lee Adoyta) and Hadar hippos are different, and indeed, the few measurements of AL-74-20 provided by Gèze (1980) indicate an animal slightly smaller than the Hadar form (measurements from Boisserie, 2020): length M1-M3 = 104, vs. 116-137 at Hadar, width over canine processes = 248 vs. 270-348 for the width over canine alveoli that is a smaller dimension, at Hadar. Thus, the name *T. afarensis* should be

restricted to the Geraru (Lee Adoyta) form, and not applied to the Hadar Fm hippo(s). No mandible from Geraru has ever been described, but the type cranium matches in size the MLP cranium and mandibles and we tentatively refer the MLP form to this species. The name *Trilobophorus* might be useless but, pending a revision of these Plio-Pleistocene African forms, it is safer not to regard it as a synonym of either *Hippopotamus* or *Hexaprotodon*.

Suidae

There are three suid taxa at Mille-Logya. A large one can readily be identified as *Notochoerus*, but the identification of the smaller ones is more difficult, because the time-period covered by the MLP corresponds to the transition between *Kolpochoerus afarensis* and its descendants, as well as to the emergence of *Metridiochoerus*. There is no definite evidence for the presence of *Nyanzachoerus*.

Metridiochoerus sp.

This genus is best known from the Pleistocene, but early forms appear as early as the Usno Formation (White et al., 2006). At that time, they are still hard to tell apart from *Kolpochoerus* teeth, but it seems that some MLP teeth that are more hypsodont, more complex, and have more flattened walls with incipient grooves, are likely to belong to *Metridiochoerus* (Fig. 2N–P). The only specimen that we definitely refer to this genus is a piece of mandible with p2–p4 MLP-2681[S]. The p2 is poorly preserved, but was certainly quite small; p3 is not much shorter than p4, but much narrower (Suppl. Table 5). The teeth are smaller than those of *Kolpochoerus* (including *K. afarensis* from Hadar: Cooke, 1978) or *Notochoerus*, but fall within the range of *Metridiochoerus* (Harris & White, 1979, Appendix V). They resemble the partial premolars of a *Metridiochoerus* from Omo Shungura B12 (Harris & White, 1979, fig.101).

Other specimens are more difficult to identify with certainty. MLP-1877[out] is a maxilla with complete, but imperfectly preserved cheek-tooth row (Fig. 2P). On M3, the anterior pair of cusps have rounded walls, but the premolars are small (Suppl. Table 5), even smaller than those of *K. afarensis* (Cooke, 1978, fig. 8).

MLP-2133[S] (Fig. 2O) is a mandible with m1–m3 whose m3 resembles *Kolpochoerus* in occlusal view (e.g., Harris & White, 1979, fig. 71) but the cuspids are more contiguous; it also resembles LD-445-1 assigned to *Metridiochoerus* by Lazagabaster *et al.*, (2018, fig. 4A) but is lower-crowned.

The right M3 MLP-2655[S] (Fig. 2N) resembles early *Metridiochoerus* teeth from Omo (White *et al.*, 2006, fig.1), and is identified as *Metridiochoerus* by A. Souron (pers. com., 2/2021). However, compared to W730 from the Usno Fm, the lingual wall of the paracone is less grooved and less flat, the metacone is less complex, and the crown is less hypsodont. All these differences are unexpected if the two teeth belong to the same lineage, given the earlier age of the Omo tooth (c. 3.4 Ma). MLP-2655 is also less tall and less *Metridiochoerus*-like than LD 115307 from Ledi-Geraru (Lazagabaster *et al.*, 2018, fig. 4C); thus, its identification remains uncertain.

Kolpochoerus sp.

Premolars that we assign to *Kolpochoerus* are larger than those of *Metridiochoerus*; the molars are low-crowned, their morphology is simpler, and the main pillars more rounded (Fig. 2Q–R). However, because molars of early forms of *Metridiochoerus* were doubtless similar to those of *Kolpochoerus*, identifications of many specimens remain uncertain. MLP-1415[S] (Fig. 2Q) is an almost unworn M3, with a talon consisting of a main distal pillar, plus about 5

accessory ones. The tooth resembles W730 from Usno, but the protocone is less lingually flattened, the metacone is simpler, and the tooth is lower-crowned. MLP-1013[S] is a mandible fragment with worn molars (Fig. 2R); m3 has quite a simple morphology, rounded pillars, and is shorter than all teeth assigned to *Metridiochoerus* by White et al. (2006). The same is true of the m3 MLP-1489[U], which is quite small, although it comes from the younger stratigraphic unit; it is associated with a large p4. MLP-1966[S] is also a large p4.

There is no complete third molar from the Gafura unit, but the few third molars from the Seraitu and Uraitele unit are only slightly larger than those of *K. afarensis* from Hadar, and as small as teeth of *K. limnetes* from Omo Shungura Mb B (Suppl. Figs. 3, 4). They are also about as large as those of *K. phillipi* from Lee Adoyta (Lazagabaster et al., 2018), and Matabaietu at c. 2.5 Ma. (Souron et al., 2013). On a geographic basis, assignment to this latter species is the most likely but it is not certain that isolated teeth of *K. phillipi* could easily be distinguished from those of *K. limnetes*, and we prefer to leave the species identification open.

Notochoerus euilus (Hopwood, 1926)

This species is known throughout the MLP sequence. The most complete specimen is MLP-152[G], consisting of cranial fragments with complete tooth-row, but due to the strong wear gradient, only M3 is well-preserved. The premolars were quite small, as usual in this genus. MLP-1101[S] is a fragment of symphysis showing two small central incisors, with a thick coat of cement. MLP-2359[G] consists of associated p4 and m2. The size of p4 (14.6 x 12.3) is close to the lower end of the range of *N. euilus* from Hadar (Fessaha, 1999, and our own measurements), which confirms the trend towards smaller premolars in the *Nyanzachoerus jaegeri* – *Notochoerus* lineage.

Size ranges of third molar length and width are large at any time period, but the trend towards increasing size through time is clear at Omo (Cooke, 2007). Those from Shungura Mb B are slightly longer and slightly narrower than those from Hadar (Fessaha, 1999, and our own measurements: Suppl. Fig. 5). The MLP ones (Fig. 2L–M), mostly from the Gafura unit, compares well with either of these samples, or the small Middle Lomekwi sample, but the wide range of the measurements prevents more precise conclusions. In any case, the MLP teeth are distinctly broader than those assigned to *N. clarki* by White & Suwa (2004).

Giraffidae

Giraffa pygmaea Harris, 1976

The mandible MLP-2406 (Fig. 3I) is among the smallest *Giraffa* specimens of eastern Africa (Suppl. Table 6, and Geraads et al., 2013, fig.3). It is slightly smaller than *G. stillei*, defined at Laetoli but best known from Omo and Hadar (Harris, 1976; Geraads et al., 2013), and best fits *G. pygmaea*, a species that is probably quite rare, although present in several sites (Harris et al., 2010). Its teeth resemble those of other *Giraffa*, the most useful tooth for discrimination being the third premolar. As in *G. stillei*, but in contrast to the larger *G. jumae* and *G. camelopardalis*, the elements that make up the cristids remain isolated until advanced wear, but a lingual wall blocks the mesosinusid in MLP-2406, as in most *G. jumae*, whereas this wall is less complete, and usually absent, in *G. stillei*. It thus seems (sample size is small) that *G. pygmaea* shows a mix of characters of the two larger species, but transitional forms are known, such as AL 716-2 from the Kada Hadar Mb of the Hadar Fm (Geraads et al., 2013), so that neither size nor morphology allow a clear species distinction. The distal metacarpals MLP-1378[U] and MLP-1443[S] are small enough (distal W = c. 66 for both) to be of the same species.

Giraffa cf. gracilis Arambourg, 1947

Most of the giraffe remains from MLP are too large to belong to *G. pygmaea*. Their size range is similar to that of the modern giraffe, in which it is rather large, largely owing to the strong sexual dimorphism. They could either be referred to two distinct species, the smaller one being more common, or to a single one (the same issue arose at Hadar; Geraads *et al.*, 2013). Because cranial remains are absent, and sample size is small, and because assignment of the specimens to either a large or a small species is not always unambiguous, the most parsimonious option is to regard them all as con-specific. They are too incomplete to display distinctive morphological features and, on a size basis, we assign them to *G. cf. gracilis*, a species slightly larger than *G. stillei* (discussion in Geraads *et al.*, 2013).

The MLP specimens include an upper premolar MLP-2435[G] (22.5 x 28.5), an upper molar half MLP-2266[S], two lower molars MLP-1919[out] and MLP-1967[S], and some postcranials: a set of associated cervical vertebrae MLP-2540[S] the size of a living female giraffe, associated proximal metacarpal (prox. TD = 85.5) and radius MLP-431[S] (prox. art. W = 105), a proximal metacarpal MLP-2547[U] (prox. TD 78.5), a tibia MLP-2349[U] (length = 555; dist. W = 81), a metatarsal fragment MLP-1384[U], a proximal metatarsal MLP-1336[U], and astragali MLP-1711[S], MLP-1809[S], MLP-1887[S], and MLP-2356[S] (resp. medial H = 84, 78, 81, 79; distal W = 59, 59, 65, 58.5). We also refer to *G. gracilis* a distal tibia and partial tarsus MLP-850[U] that clearly shows that the cuneiforms are fused, and that the cubonavicular accordingly lacks a lateral groove for the tendon of the *m. peroneus longus*, so that there is only one metatarsal facet, as in the living giraffe.

Sivatherium maurusium (Pomel, 1892)

The teeth of this large, short-limbed giraffid can easily be identified by their large size and higher tooth crown, while long bones are shorter and broader. These features are also observable in *S. maurusium* of other sites, such as Hadar (Geraads *et al.*, 2013). The species is not common at MLP, but present in all three units. The lower molars MLP-797[G], MLP-1734[U], and MLP-2470[G], and upper molars MLP-390[G], MLP-2415[G] and MLP-2816[S] are mostly identified as *S. maurusium* by their large size, but postcranials have a distinctive morphology. A capitatotrapezoid MLP-2194[S] is too broad for *Giraffa* (APD 61, TD = 64). The distal metacarpals MLP-799[S] and MLP-2572[S] are broader relative to their anteroposterior depth (dist. TD = 86.5, 91; dist. APD = 49.3, 50) than those of *Giraffa*, and this also true of a distal humerus MLP-50[out] (dist. artic. W = 120; min. APD = 44). A distal radio-ulna MLP-2038[S] is also broad, with the ulna more laterally positioned than in *Giraffa*.

Bovidae

This is by far the most common family at MLP, as usual in Africa during the Plio-Pleistocene. Almost half of the identifiable specimens, mostly represented by teeth, belong to Alcelaphini. They are followed in decreasing order of abundance by the Reduncini, Bovini, Aepycerotini, Antilopini, and Tragelaphini. There is no definite evidence of hippotragins. Identification to tribe level is usually easy for cranial or dental material, even fragmentary, but the scarcity of cranial material other than horncores and the frequent distortion of the latter often make identification at lower taxonomic level difficult. Still, 17 taxa can be recognized. See Suppl. Table 7 for horncore basal diameters.

Tribe Tragelaphini

Tragelaphins are rather common in the Uraitele unit, much rarer in the Seraitu unit, and not definitely known in the Gafura unit. We assign them to three different species, but two of them certainly belong to a single lineage.

Tragelaphus cf. nakuae Arambourg, 1941

Bibi (2011) revised the evolution of the lineage leading to *T. nakuae* Arambourg, 1941, a species best known from the Turkana Basin, of which a closely related form was described from Hadar (Reed and Bibi, 2010). He distinguished a late form, *T. nakuae*, with horncores that are more twisted, relatively shorter, and more anteroposteriorly compressed (Suppl. Fig. 6), and an early form that he called *T. rastafari*. In addition, the top of the occipital of *T. nakuae* is raised in a thick transverse torus, obviously in connection with horncore changes. Although this was not mentioned by them, it is also clear that horncore basal divergence is on average stronger in *T. nakuae*, at least 90°. According to Bibi (2011), the transition must have occurred between 2.95 and 2.74, a time interval that had yielded no diagnostic specimen at that time.

Several horncore pieces from the Uraitele unit belong to a large *Tragelaphus* that cannot be separated from either *T. rastafari* or *T. nakuae*, but MLP-1454[U] preserves the top of the braincase, which shows that there is an incipient transverse parietal thickening, although less conspicuous than in typical *T. nakuae*. Given that this is an apomorphic trait, we favour an attribution of other Uraitele horncores to this species, which is also in accordance with the age of this unit, at certainly less than 2.74 Ma.

Tragelaphus rastafari Bibi, 2011

A partial frontal with almost complete right horncore MLP-1872[S], cannot be assigned to *T. nakuae*. The degree of compression is low (although within the range of *T. nakuae*: Bibi, 2011, fig. 3) but the horncores are much less divergent, much longer, and much more slender, as the ratio horncore length / bipedicle width is about 4.5, much greater than in *T. nakuae*; all these features are similar to those of *T. rastafari*. A difference with the latter, however, is that the degree of spiraling is weaker.

MLP-1872 is remarkably similar to the frontlet LD 196-1 from Gurumaha (c. 2.8 Ma) that Bibi *et al.* (2017) felt unable to assign to either *T. rastafari* or *T. nakuae*, presumably because, as in MLP-1872, torsion is weaker than in typical *T. rastafari*. The existence of these two specimens, very close geographically and chronologically, suggests that these are not just aberrant forms, but they may testify instead to a transitional morphology, in which torsion is already weaker than in *T. rastafari*, while other characters remain unchanged. On balance, both MLP-1872 and LD 196-1 share more features with *T. rastafari* than with *T. nakuae*, and we believe that they can be assigned to the former species.

Tragelaphus cf. *gaudryi* Thomas, 1884

Two specimens, MLP-1428[S] and MLP-2337[U] are reminiscent of the modern kudu, *T. imberbis* and *T. strepsiceros*, and of a close relative of the latter, *T. gaudryi*, first described from Algeria, but best known from Omo (Gentry, 1985), and also reported from Ledi-Geraru (Bibi *et al.*, 2017). MLP-1428 is the basal part of a horncore showing little compression, and differing from those of *T. rastafari* / *T. nakuae* in the absence of keels, replaced by a mere posterolateral change of curvature, and a still fainter anterior one. There is a shallow postcornual fossa, but no other cranial character is visible. MLP-2337 (Fig. 3H) is a frontlet with almost complete left horncore. The horncores diverge by about 90°, and the divergence distinctly increases upwards. The imperfectly preserved left horncore forms a loose spiral, describing a complete whorl, being overall similar to that of *T. strepsiceros*, the greater kudu. It is anterolaterally to posteromedially compressed, and bears no keels, at least basally.

Because of the close geographic and chronological proximity of the sites, we are inclined to assign the MLP kudu to the same species as at Ledi-Geraru, *T. gaudryi*, but the phylogeny of kudu during the late Pliocene / early Pleistocene remains unclear. Bibi *et al.* (2017) assumed that *T. lockwoodi* from the lower Hadar members is ancestral to *T. strepsiceros* which appears only much later, while the common form during this time gap, *T. gaudryi*, is not closely related. They acknowledged, however, that distinguishing a large *T. gaudryi* from a small and primitive *T. strepsiceros* is not straightforward. The absence of keels in MLP-2337 is

seemingly the main difference with *T. gaudryi*, but what is called a ‘keel’ is sometimes no more than a change in curvature, and the specimens from Ledi-Geraru do not appear in fact very different in this regard.

Tragelaphin dental remains are mostly known from the Uraitele unit, and much less common in the Seraitu unit. On a size basis, two species are present, presumably the larger *T. rastafari* / *T. nakuae*, and the smaller *T. cf. gaudryi*. The best specimen is a mandible of the latter, MLP-2636[U] (L p3-p4 = 29.7; L m1-m3 = 58.2; L m3 = 26); as in most *Omo T. gaudryi*, the premetacristid and paracristid of p4 are closely adjacent, but not fully fused (Gentry, 1985).

Tribe Bovini

Pelorovis ? cf. *kaisensis* Geraads & Thomas, 1994

MLP-52[S] are horncore pieces, of which five were used to tentatively reconstruct a large, long, and almost straight horncore. However, while the basal three pieces definitely fit together, the last two pieces might in fact belong to its counterpart (of which a basal fragment is also preserved) so that the precise course of the horn remains somewhat uncertain. The reconstructed horncore is longer (about 630 mm) than in most contemporaneous bovins. The absence of frontal pieces prevents precise orientation, but its size and relatively straight course indicate that it would have emerged almost transversely from the skull. It is likely that its slight curvature was backwards, and that the tip was slightly directed either downwards or upwards. The cross-section is egg-shaped, with a hint of a keel along the convex (anterior ?) border, and it is, remarkably, little compressed dorsoventrally. Few bovin species show similar characters. Late Pliocene to early Pleistocene eastern African *Pelorovis turkanensis* Harris, 1991 and *P. oldowayensis* Reck, 1928, as well as the North African *P. praeafricanus* Arambourg, 1979 have strongly curved horncores with an oval cross-section. *Pelorovis* (or *Syncerus*) *antiquus* Duvernoy, 1851 is a pan African species with rather straight horncores (Gentry, 2010), but they are larger, much more dorsoventrally compressed (Geraads & Thomas, 1994), they usually bear distinct keels, and the species is not definitely known before the late early Pleistocene.

MLP-52 best matches the type (and only definitely known specimen) of *P. Kaisensis* Geraads & Thomas, 1994, from Kaiso village in Uganda, c. 2.5 Ma, which is larger than MLP-52, but is otherwise similar in its rather straight course with a slightly recurved tip, its moderate dorsoventral compression (120 x 92) and absence of keels. Positive identification would be risky based on a single specimen, however. Gentry (2010) suggested that the type of *P. Kaisensis* might belong to a male *Simatherium shungurensense* Geraads, 1995, the type of which is indeed probably female, but this synonymy is doubtful because the latter has horncores that are directed much more backwards, and have a triangular cross-section (Geraads, 1995), an unlikely character for a female whose male fully lacks keels.

Bibi *et al.* (2017) described as cf. *Syncerus* two horncores from Lee Adoyta, of which one resembles MLP-52. The geographic and chronological proximity prompt us to believe that we are dealing with the same form as at MLP but the Lee Adoyta horncore is smaller, and bears clear keels. We keep them as separate until further material comes to light. According to J. Rowan (pers. com.), a horncore piece from the somewhat younger Busidima Fm at Maka'amitalu, referred to *Syncerus* by him, could be related as well, but is less compressed. Thus, it seems that straight-horned buffaloes are not rare in the eastern African Plio-Pleistocene, but they cannot unambiguously be assigned to either *Pelorovis* or *Syncerus*.

Ugandax coryndonae Gentry, 2006

MLP-1791[S] is the basal part of a horncore that was not very long, and shows basal sinuses, a cross-section that is triangular but much rounded, with no keels, and is not

compressed. The absence of keels and presence of sinuses show that it is not a tragelaphin, and it must be bovin, showing resemblance with *Ugandax coryndonae* from Hadar (Gentry, 2006; Geraads *et al.*, 2012) and Ledi-Geraru (Bibi *et al.*, 2017). This species usually has at least a well-marked keel, but Geraads *et al.* (2012) observed that the horncore of AL 359-4 from the Kada Hadar Member is more rounded than those from earlier in the sequence.

There are a few incomplete bovin tooth series and a number of isolated teeth. Among these teeth, an m3 MLP-1770[out] (L=40mm) stands out, as its very derived morphology looks anachronic, and its facies differs from most MLP fossils, suggesting that it might derive from much younger sediments (together with a few other reduncin and *Phacochoerus* teeth). The lengths at mid-height of the remaining 10 m3s range from 36.3 to 46 mm. The largest m3 is from the Uraitele unit, and those from the Gafura unit are among the smallest ones, suggesting that overall size increase might have occurred, but sample size is too small to confirm this. However, the lengths of 40 m3s from the Hadar Fm at Hadar, mostly attributable to *U. coryndonae*, range from 33.4 to 42.8, so that some size increase in this lineage is likely. The largest tooth, MLP-2285[U], reaches the size of *Pelorovis* from Omo Mb G (Gentry, 1985, fig.7), suggesting that it belongs to *P. cf. kaisensis*; despite its large size, its morphology is quite simple for a bovin, but not different from that of the smallest m3s that are probably of *Ugandax*. The only premolar that is definitely a p4 is in a mandibular piece MLP-1371[S]. Contrary to most modern African buffaloes, the lingual valley is wide open and the metaconid slanting backwards, as in most *Ugandax* from Hadar.

Tribe Reduncini

Kobus sigmoidalis Arambourg, 1941

MLP-1375[S] (Fig. 3A) is a complete left horncore that definitively establishes the occurrence of this species at MLP, permitting the confident identification of a few other partial specimens. It is large and slender, not very compressed at the base but the compression increases upwards; the basal divergence is about 50° but this also increases upwards. In lateral view, there is first a strong backwards curvature, but it decreases upwards, and the tip is slightly curved forwards.

MLP-1232[out] is a very imperfect braincase showing temporal lines close to each other, open craniofacial angle, broad occipital, and anterior basioccipital tuberosities not very broad for a reduncin. Most other specimens are from the Seraitu unit.

Kobus sigmoidalis is best known from the Turkana Basin, but has also been reported from Olduvai (Gentry & Gentry, 1978), and from Ledi-Geraru (Bibi *et al.*, 2017). It is unknown at Hadar (Geraads *et al.*, 2012), and not definitely known from the Gafura unit, suggesting immigration c. 2.9 Ma. The MLP form is comparable in size to the Ledi-Geraru one (Bibi *et al.*, 2017), and averages smaller than in Omo Shungura Member G (Gentry & Gentry, 1978; Gentry, 1985) but variation is large in all sites.

Kobus n. sp. Rowan et al.

Several horncores from the Gafura and Seraitu units differ from those of the previous species in their poor transverse compression, or even slight anteroposterior compression (Suppl. Fig. 7), greater basal divergence, and lack of backward curvature basally (Fig. 3B). They are almost straight basally in lateral view, with even a slight forward curvature that increases upwards, and their divergence also increases upwards, so that an incipient homonymous torsion may be visible. There is little doubt that they are closely related to the Hadar form that Geraads *et al.* (2012) called *K. oricornus*, although they acknowledged that it differs in a number of features from the Omo population, upon which this species is based (Gentry, 1985). This Hadar and Ledi-Geraru form will be given a new species name by Rowan

et al. (J. Rowan, pers. comm.) and we agree with them that distinction from the Omo form is warranted. We therefore assign the common MLP *Kobus* to this species.

Tribe Aepycerotini

Aepyceros cf. *melampus* (Lichstenstein, 1812)

Aepyceros is less common than at Hadar, and is certainly of a species different from the Hadar *A. datoadeni*, as shown by basal horncore measurements (Suppl. Fig. 8). The smallest specimen is certainly juvenile, but all others, from the Seraitu and Uraitele units, are larger than *A. datoadeni* that is common throughout most of the Hadar but is replaced in the Kada Hadar 2 submember by a larger form (Geraads *et al.*, 2012), probably the one that is present here. This form is also distinctly larger than *A. shungurae* from Omo, and it must belong to a distinct lineage. It is similar in size to *A. melampus*, and no significant feature separates it from the living impala, but the MLP form is represented by small pieces only (Fig. 3G), preventing definite identification. The replacement of *A. datoadeni* by a form close to *A. melampus* seems to have occurred rather abruptly at c. 3 Ma, suggesting immigration rather than evolutionary change.

Tribe Alcelaphini

Damaliscus sp.

MLP-1366[U] (Fig. 3C) is an almost complete horncore, moderately inclined in side view, little divergent from its counterpart, regularly curved backwards, somewhat flattened laterally, with transverse ridges, and with an incipient but distinct liration. Although the presence of a basal sinus cannot be ascertained, there is little doubt that it is alcelaphin. It was regarded by Alemseged *et al.* (2020) as close to *Damaliscus ademassui* from Gamedah in the Middle Awash dated to c. 2.5 Ma, but is in fact less compressed transversally, its basal diameters being intermediate between *D. pygargus* and *D. lunatus* (see e.g., Vrba, 1971, fig. 1). MLP-622[U] is a less complete horncore that is certainly of the same species.

No specimen showing positive resemblance to these horncores is known in the much richer Seraitu unit and underlying Gafura unit, so we can tentatively assume that this form is restricted to the Uraitele unit.

Damaliborea grayi Geraads, Bobe, and Reed, 2012

Like other bovids, the most common alcelaphin at MLP, is mainly represented by horncores, all from the Seraitu unit (Fig. 3D–E). This alcelaphin is closely similar to the species that is present in the Denen Dora Mb of the Hadar Fm, and likely descends from *D. elisabethae* of the Sidi Hakoma Mb. Geraads *et al.* (2012) observed that in the Kada Hadar Mb, there is a disjunction of the lengths of alcelaphin m3s, suggesting that this lineage split at that time into a larger and a smaller species. This disjunction is still clearer at MLP (Suppl. Fig. 9), and the range of basal horncore measurements, similar to that of *D. grayi* from Hadar, looks large for a single species (Suppl. Table 7), although there is no clear disjunction in their distribution. We keep this name for the larger form, and separate the smaller one as a distinct species below, although it is difficult to positively assign horncores in the middle of the size range to either species.

Most of the horncores cannot be properly oriented, as they lack sufficient parts of the frontal bone, but this can be done on a frontlet MLP-2532[S] (Fig. 3E), and on the horncore MLP-2267[S] (Fig. 3D). The horncores are uprightly inserted (in side view, the angle between the posterior border and the parietal plane is about 80°), close to each other (this proximity is exaggerated by crushing on MLP-2532). They are almost parallel in their lower part (crushing makes them convergent on MLP-2532) but the divergence increases upwards which, together with a forward curvature, gives them a distinct spiral shape. Their course is thus similar to that

of *Kobus* n.sp. Rowan *et al.* horncores, but they are more uprightly inserted, and less divergent; they also resemble horncores of *Menelikia*, but most specimens clearly show that the pedicle is hollowed by a single large sinus, so their tribal attribution is not doubtful. They are inserted on short pedicles, they are robust at the base, but their diameter decreases first quickly, then more slowly upwards, so that they were probably less short than their basal part suggests. MLP-2532 shows that there is no postcornual fossa. In their general course, the horncores are also similar to those of *Beatragus vrbae* Bibi *et al.*, 2017, but they are distinctly shorter, and the basal cross section is almost circular, in contrast to the antero-posterior compression typical of *Beatragus*.

Damalborea sp.1

In the Seraitu unit, some horncores of rather small size have the same course and incipient torsion as those described above as *D. grayi*, but are more slender, and less thickened in their basal portion. They resemble horncores of *Numidocapra* (including *Rabaticeras*; see Gentry, 2010) but are too incomplete for in-depth comparisons. It is likely that most of the smaller teeth belong to this form.

Alcelaphini gen. et sp. indet. 1

The base of a small horncore with a circular cross-section MLP-712[S] resembles *Aepyceros* in its distinct spiraling and transverse ridges, but the single large basal sinus rules out this identification (*Aepyceros* may have sinuses, but they are smaller).

Alcelaphini gen. et sp. indet. 2

A single basal alcelaphin horncore fragment with part of the frontal, MLP-1357[S] is small, little compressed, and differs from MLP-712 in the lack of increasing divergence upwards or spiraling. It is certainly distinct from *Damalborea* but we do not attempt identification of this single piece; some of the smaller alcelaphin teeth might belong here.

Connochaetes cf. *gentryi* Harris, 1991

MLP-668[U] is the basal part of a horncore, but the frontal bone is wholly absent, and it cannot be oriented. However, its resemblance to horncores of *Connochaetes* (including *Oreonagor* Pomel, 1895), especially in the anterolateral to posteromedial basal expansion, allows a positive identification. It is less dorsoventrally flattened, and smaller than in modern male *C. taurinus*, and we tentatively assign it to the best-known species of this period, which is probably identical with *Connochaetes africanus* (Hopwood, 1934) from Olduvai, as suggested by Bibi *et al.* (2017). It might also be identical with *Oreonagor tournoueri* (Thomas, 1884), a species based upon a partial frontlet from Aïn Jourdel in Algeria, which is primitive in the posterolateral orientation of its horncores.

Tribe Antilopini

Gazella harmonae Geraads, Bobe, and Reed, 2012

This is by far the most common *Gazella* species at MLP (because the several genera formerly lumped under *Gazella* are distinguished on molecular characters, we use this genus name in its old acceptance); it is especially common in the Seraitu unit, but absent from the Gafura unit. Their horncore characters (Fig. 2F) are unlike those of other gazelles, but similar to those of a few specimens from Omo, Olduvai, and the Upper Ndolanya beds of Laetoli (Gentry & Gentry, 1978; Gentry, 1985, 1987), which were united under '*Gazella* sp. (3)' by Gentry (2010). They are of rather small size, long and slender, uprightly inserted, moderately compressed (Suppl. Fig. 10) and not clearly flattened laterally, with maximum transverse diameter variable in position, and diameters decreasing slowly upwards. They are poorly curved backwards and never curving inwards in their basal part, but often show increasing divergence upwards, giving them some incipient spiraling. Geraads *et al.* (2012) named *G. harmonae* on the basis of a single partial skull from the Kada Hadar Mb of the Hadar Fm,

and tentatively included Gentry's species under this name. Because of its distinctive horncore characters, the MLP form can be confidently included here as well, even though the horncores of the holotype are less transversely compressed. If the Olduvai specimens are also of this species, they are somewhat larger, likely because of their younger age.

Gazella sp.1

The only specimen of *Gazella* that is definitely not of *G. harmonae* is the horncore base MLP-0509[G]. It is more strongly curved backwards than those of *G. harmonae*, and is thus more like the Omo *Gazella*. An additional difference is the presence of a small sinus in the pedicle. Species identification cannot be reached on the basis of this single incomplete specimen.

Thus, there is a clear distinction between the Gafura unit, where only *Gazella* sp.1 is documented, and the overlying Seraitu and Uraitele units, with *G. harmonae* only, but it remains to be confirmed by further discoveries, because the presence of *G. harmonae* at Hadar suggests that its absence in the Gafura unit may be due to incomplete sampling.

Tribe 'Neotragini'

Raphicerus ? sp.

MLP-793[G] is a small, almost straight horncore (11.5 x 9.5), uprightly inserted directly above the orbit, and moderately compressed transversely; there is large, shallow postcornual fossa. These characters best fit *Raphicerus*, a genus reported in several eastern African sites, but small bovids do not display many diagnostic criteria.

Carnivora

Felidae

Panthera aff. *leo* L.

MLP-522[S] is a P3 (24.1 x 14.4) whose length is close to the average of *P. leo*, but it has a distinct talon bearing a wear facet in the distal part of the lingual side, which makes it broader than in this species. Such a talon is usually better marked in *P. onca*, the jaguar, but it is interesting that KNM-ER-44535 from Koobi Fora, assigned to *P. leo* (Werdelin & Lewis 2013), also has a broad distal part. MLP-1520[U] is an imperfect low crowned p3 (16.6 x 8.8+). The accessory cuspids are stronger than in living forms, but no *Dinofelis* from eastern Africa has such a large p3, and we assign it to a large *Panthera*. MLP-1249[S] is a partial left Mc III that probably belongs to the same species.

Dinofelis sp.

The only specimen that almost certainly belongs to this genus is the Mc V MLP-2581[out] (probably Seraitu unit) that lacks the central part of the diaphysis, preventing estimates of its length. The proximal epiphysis virtually lacks a medial process, so that it is not much broader than the diaphysis, in sharp contrast to *Panthera*. The MLP proximal epiphysis is similar to *Dinofelis* in that "the articulation with metacarpal IV is extremely flat, with minimal superomedial projection" (Werdelin & Lewis, 2001:178, their fig.19A).

Hyaenidae

Crocota sp.

A few isolated teeth and postcranials are similar to those of the living spotted hyena, but differ in details that prevent formal identification. MLP-2317[U] is an incomplete hyaenid p4

(L = c. 20.5; W = c. 12.5), certainly too small for *Crocota eturono*, but within the size range of several other species. We tentatively identify it as *Crocota* sp. MLP-388[S] is a Mt II (L = 87; max.dist.W = 15.2; W of shaft = 12.8); MLP-423[S] and MLP-471[S] are third metatarsals whose outline of the proximal articulation is more like living *Hyaena* than like *Crocota*, but the palmar process at the proximal end is weaker than in *Hyaena*. MLP-1519[U] is an associated set including proximal and distal tibia, astragalus, and metatarsal fragments. The astragalus has a lateroplantar expansion that is stronger than in *C. ultra* ER-3765 (Werdelin & Lewis, 2013, fig. 7.19), but is more similar to this specimen than to other Koobi Fora hyaenids.

Pachycrocota sp. ?

MLP-2562[U] is a partial maxilla and premaxilla with I3, canine root (20.3 x 14.9), P1 (7.6 x 7.3), and P2 (19.6 x 14.3). There is a long I3-C diastema, testifying to a large lower canine; P2 is large, rectangular, and low-crowned. These features might fit a large *Crocota* such as *C. eturono*, but all teeth are inserted almost vertically in bone, whereas I3 and the canine are more obliquely set in *Crocota*. This suggests a deeper snout than in this genus, more like *Pachycrocota*, a genus that has been described from East and South Africa (Werdelin, 1999; Turner & Antón, 1996), but whose presence at Hadar is uncertain (Geraads *et al.*, 2015). Because this identification is not contradicted by the tooth morphology, we tentatively assign it to this genus.

Mustelidae ?

Enhydriodon sp. ?

A second metatarsal MLP-2756[S] is definitely neither felid nor hyenid; it might belong to *Enhydriodon*, a gigantic otter known from several sites in eastern Africa but, to our knowledge, this bone has never been described in this genus, making definite identification impossible.

Rodentia

Spalacidae

Tachyoryctes cf. *splendens* (Rüppell, 1835)

From Mille-Logya there is a single specimen (MLP-1693) attributed to *Tachyoryctes* cf. *splendens*. The specimen is a left mandible fragment with m1 and m2 preserved though the lingual margin of m1 is broken. The m1 measures approximately 4.2 mm in length (width is unattainable due to breakage) and the m2 measures approximately 3.4 mm, which is larger and outside the range described for Pliocene *T. pliocaenicus* from Hadar (Sabatier, 1978, 1979). The specimen is securely identified to *Tachyoryctes* and tentatively assigned to *T. cf. splendens* pending further comparisons with original fossil material.

Eastern African mole rats (or root rats) of the genus *Tachyoryctes* are poorly known from the fossil record. There are two extant species in Africa, *T. splendens* and *T. macrocephalus*. The former is distributed in eastern Africa from Ethiopia south to Tanzania and west of Lake Victoria in Uganda, Rwanda and Burundi. The larger *T. macrocephalus* is restricted to the Bale Mountains of Ethiopia (Wilson & Reader, 2005). In addition to the extant species three fossil species are known. The oldest, *T. makooka*, was described from the Upper Miocene of the Middle Awash area of Ethiopia (López-Antoñanzas & Wesselman, 2013). *Tachyoryctes pliocaenicus* is known from Pliocene deposits at Hadar (Sabatier, 1978, 1979) and *T. konjiti* is known from Pleistocene deposits at Melka-Kunturé (López-Antoñanzas & Wesselman, 2013). The clade has its origins in Asia and ancestral representatives such as *Pronakalimys andrewsi* from Fort Ternan and *Prokanisamys* from Jebel Zelten appear in Africa during the Miocene.

Hystriidae

Hystrix sp.

Specimen MLP-1676[U] is an isolated left p4 or m2 (based on morphology and size). The length is approximately 9.6 mm, width unknown. MLP-1834[U] is a right maxillary fragment preserving the distal portion of ?P4-M2. The disto-buccal portion of M2 is broken. The tooth is heavily worn. MLP-2259[U] are two isolated teeth. One is a left molar (likely m1 or m3 based on size); it measures approximately 9.3 mm in length and 8.4 mm across. The second tooth is an isolated right molar, likely a p4 or m2 (based on size and morphology); this tooth measures approximately 10.3 mm in length and 8.5 mm in width. These teeth are too large to be *H. leakeyi*, known from Laetoli, but do fit within the range of *H. cristata*. Beyond that, most fossil specimens of *Hystrix* are not identified to species because the cusp and dentine wear patterns vary significantly with wear as do measurements.

Other vertebrates

These have not been studied in detail yet. In addition to *Homo*, Primates are not rare, and include *Theropithecus* and other Cercopithecidae. Among birds, A. Louchart (pers. com.) identified a member of the Anatidae, perhaps *Sarkidiornis melanotos*, the knob-billed duck or *Plectropterus gambensis*, the spur-winged goose. Several *Struthio* bone fragments have been found at Uraitele. Large ostriches have been mentioned from a number of Pleistocene Old-World sites; they are likely attributable to *Struthio asiaticus* (see review in Mourer-Chauviré and Geraads, 2008). Crocodile teeth are widespread. A vertebra has been identified as of a large *Python* sp. by S. Bailón (pers. com.), and K. Stewart (pers. com.) identified bagrid and clariid fishes.

Taxonomic diversity in the Lower Awash valley

There are some taxonomic differences between the MLP fauna and the nearby sites of Ledi-Geraru, about 30 km away, which are in the 2.84–2.58 Ma time range (DiMaggio *et al.*, 2015). Several bovid taxa from Ledi-Geraru have been identified on the basis of one or two individuals only but have no match at MLP. These are cf. *Menelikia lyrocera*, *Beatragus vrbae*, *Parmularius* aff. *pachyceras*, cf. *Parantidorcas latifrons*, and cf. *Antilope* sp. (Bibi *et al.*, 2017). It may be that one or two of these have not yet been sampled or recognized at MLP, or were misidentified at Ledi-Geraru, but this is certainly not true of all of them. Lazagabaster *et al.* (2018) identified *Notochoerus* cf. *capensis* at Ledi-Geraru, but this is disputable, as the teeth are much smaller than in this species, and very similar to the MLP ones. The *Kolpochoerus* is probably the same in both areas, as well as the *Metridiochoerus*, even though species identifications are difficult. Among hipparions, both *Eurygnathohippus hasumense* and *E. afarensis* are listed at Ledi-Geraru (DiMaggio *et al.*, 2015), whereas there is no evidence of more than one species at MLP. The only relatively common species at MLP that are missing at Ledi-Geraru are *Gazella harmonae*, a cercopithecoid smaller than *Theropithecus*, and *Camelus*, represented by 10 specimens at MLP.

Except the latter, none of the taxa present in either area but absent in the other is represented by more than very few specimens; it is unlikely that all of these differences can be explained by the vagaries of sampling, but this cannot be formally demonstrated, as abundance data from Ledi-Geraru have not been published. The slightly greater diversity observed at Ledi-Geraru might result from the more fluvial character of the deposits, but this remains to be demonstrated by taphonomic analyses.

Farther away, at Bouri Hata, c. 2.5 Ma, the differences greatly increase, with a hippo that is definitely distinct (*Hexaprotodon bruneti*), and many different bovids (*Beatragus whitei*, cf. *Numidocapra crassicornis*, cf. *Rabaticeras arambourgi*, *Megalotragus kattwinkeli*,

Parmularius rugosus, *Antidorcas* sp., *Gazella janenschi*, *Hippotragus gigas*, cf. *Oryx* sp., *Kobus kob*, *Tragelaphus strepsiceros*, *T. pricei*: Heinzelin *et al.*, 1999). However, some of these differences might be more apparent than real, as the Bouri bovid fauna has not been studied in detail.

Late Pliocene to early Pleistocene faunal changes in the Lower Awash Valley

Changes in taxonomic composition at MLP

In terms of taxonomic composition, the MLP mammal fauna resembles the Hadar one, about 50 km away, where the youngest sediments are dated to c. 2.9 Ma. (Wynn *et al.*, 2008). These are basically similar assemblages, with no major immigration wave or extinction event, except perhaps that of *Metridiochoerus*, so that most observed changes can be interpreted in terms of biological evolution and/or of local ecological changes with time. Table 1 (slightly modified from Alemseged *et al.*, 2020) provides the distribution of taxa across the main sedimentary units.

Of the three MLP faunal units, the Seraitu unit is by far the richest, so that it is mainly in this unit that faunal changes relative to the Hadar Fm are apparent. There is no change that could be definitely dated to the transition between the Kada Hadar Mb and the Gafura unit, which is not totally unexpected, as these may slightly overlap in time. The extinction of *Nyanzachoerus*, and the replacement of *Aepyceros datoadeni* by *A. cf. melampus* probably occurred within the timespan of the Kada Hadar Mb.

Sample size in the Gafura unit is too small to assert that differences in species composition with the overlying Seraitu units are not due to chance or taphonomy. For instance, no identified alcelaphin is present in the Gafura unit, but this is probably because there is no well-preserved horncore. However, *Metridiochoerus* has not been definitely identified in this unit. We also note that *Raphicerus* and *Gazella* sp. 1 are absent after the Gafura unit, but these are rare taxa.

There are instead a number of important differences between the Seraitu unit and the Hadar Fm. '*Eurygnathohippus*' is probably of the same species, but it underwent a size reduction; the hippo could be of the same lineage, but it is also significantly smaller. If the identification is correct, *Metridiochoerus* is a newcomer, as it has not been positively identified in the Hadar Fm. The very small *Giraffa pygmaea* is definitely documented. Among bovids, *Pelorovis* is of a different species; some size increase probably occurred in the *Ugandax coryndonae* lineage; there are no more hippotragins, and no evidence of *Parmularius*, but *Kobus sigmoidalis* is a newcomer. In connection with the size reduction in some lineages, it is interesting to plot the distribution of non-bovin bovid astragali (Suppl. Fig. 11). It shows that a gap that was apparent in the Hadar distribution is now filled, or at least shifted towards smaller sizes. Perhaps not too much weight should be placed on this because, while all MLP astragali were systematically collected, this was certainly not true at Hadar, but this observation confirms that some change occurred in the ecological structure of the mammal community.

The transition from the Seraitu to the Uraitele unit occurred at c. 2.5 Ma, but it may be that the faunal changes that are recorded happened somewhat earlier, within the Seraitu unit times. These are the replacement of *T. rastafari* by typical *T. nakuae*, the appearance of *Damaliscus* and *Connochaetes*, and the extinction of *Kobus* n. sp. Rowan *et al.* and *Damalborea*, but perhaps also of some rare taxa. This gives a decidedly more modern aspect to the Uraitele fauna.

Changes in faunal relative abundance

In addition to these taxonomic and evolutionary changes, there are important alterations in the abundances of several groups, which are of major ecological significance, as briefly discussed by Alemseged *et al.* (2020). While the Gafura assemblage still resembles the Hadar ones, the Seraitu one has a lower number of suids, but many more grazing antelopes (Fig. 4), unambiguously pointing to open habitats.

We updated the correspondence analysis performed by Alemseged *et al.* (2020), based upon abundances (number of specimens) of the main taxa in the three successive units of the MLP, and in the three main members of the Hadar Fm at Hadar. We deleted the Hippotragini that are very uncommon, but added some other taxa (Suppl. Table 8). It confirms that the Gafura assemblage is still close to the Hadar one, but that later assemblages stand apart, especially because of the abundance of alcelaphins and antilopins, suggesting open and dry environments (Fig. 5). As this change was contemporaneous with the replacement of *Australopithecus* by *Homo* in the area, it is reasonable to suspect that this open environment was suitable for early *Homo* to emerge or immigrate.

DiMaggio *et al.* (2015) performed a similar CA on the roughly contemporaneous assemblages of Gurumaha and Lee Adoyta, based upon dietary preferences and locomotory adaptations. It also showed that grazers are much more abundant than at Hadar, suggesting similar conditions as at MLP. We disagree, however, with their conclusion that "The Ledi-Geraru communities appear to sample habitats unlike any modern African habitat" because, as first shown by Bonis *et al.* (1992), all fossil faunas are systematically shifted in CFAs relative to modern ones, presumably mostly for taphonomic reasons, and raw comparisons between fossil and modern faunas are misleading. Still, in the correspondence analysis published by Robinson *et al.* (2017, fig. 2), all Hadar and Ledi-Geraru sites plot outside all modern localities, suggesting low precipitations and strong seasonality similar to the modern Serengeti, even though it is likely that these fossil communities have no modern analog (Faith *et al.*, 2019). Unfortunately, details of the faunal composition were not provided by DiMaggio *et al.* (2015) or Robinson *et al.* (2017), so that direct comparisons of the paleoecology and timing of the faunal change with MLP are currently not possible, but it is likely that we are dealing with changes at regional scale at least.

Interestingly, the Uraitele unit seems to witness a partial return to more woody conditions, with less of all open country antelopes, but more tragelaphins, giraffes, and primates. This can be parallelized with the observation that the Hadar habitat at 2.35 Ma, as represented by the Maka'amitalu (MAK) early *Homo* locality, is not as open as the habitats at 2.82–2.58 Ma in Lee Adoyta (DiMaggio *et al.*, 2015).

Conclusion

The evolution of the MLP faunal assemblages from almost 3 Ma to about 2.4 Ma testifies to environmental changes towards more open conditions, contemporaneous with the local replacement of *Australopithecus afarensis*, still present in the KH Member at Hadar, by *Homo*, present in the Uraitele unit and at Ledi Geraru. Our analyses thus confirm the conclusions reached by Di Maggio *et al.* (2015) and Robinson *et al.* (2017) in the nearby sites of Ledi-Geraru, but they also refine them, as they suggest that the main changes occurred between the Gafura and Seraitu units, at c. 2.8–2.9 Ma. In addition to providing new fossils pertaining to poorly documented lineages, such as camels, kudus, or early *Metridiochoerus*, further research at Mille-Logya will hopefully refine the timing and details of these changes.

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Supplementary Information includes Suppl. Tables 1 to 8 and Suppl. Figures 1 to 11.

Figure captions

- Fig. 1. A: location of the MLP area and of some other research projects in the Afar depression; B: extent of the main collecting units, with plot of individual fossil discoveries; those outside the main polygons cannot be definitely assigned to a collecting unit, but are within the 2.9 – 2.4 time-range.
- Fig. 2. A-D: '*Eurygnathohippus*' cf. *hasumense*; A: MLP-1592, left upper tooth row, occlusal view. B: MLP-785, left lower tooth row m1-m3, occlusal view. C: MLP-512, metatarsal. D: MLP-2135, metatarsal. E: *Elephas recki*, MLP-556, lower m3. F: *Ceratotherium mauritanicum*, MLP-950, right DP4. G: *Diceros* sp., MLP-382, right p2. H-K: *Deinotherium bozasi* P3s (all shown as if from the left side); H: MLP-2797. I-K specimens from the Shungura Fm, Omo. I: Omo L596-620. J: Omo 75-3153. K: Omo 133. L-M: *Notochoerus euilus*; L: MLP-476, left M3 (L1: occlusal view; L2: lingual view). M: MLP-663, left m3 (M1: occlusal view; M2: buccal view. N-P: *Metridiochoerus* sp.; N: MLP-2655, right M3 (N1: occlusal view; N2: lingual view). O: MLP-2133, left m1-m3. P: MLP-1877, right P2-M3. Q-R: *Kolpochoerus* sp.; Q: MLP-2655, right M3. Q: MLP-1415, right M3 (Q1: occlusal view; Q2: lingual view; Q3: buccal view); R: MLP-1013, right lower molars. Scale bar = 5 cm for Figs. A, B, N-R, 10 cm for Figs. C-G, L-M, 20 cm for Figs. H-K.
- Fig. 3. A: *Kobus sigmoidalis*, MLP-1375, left horncore in A1, lateral, A2, anterior, and A3, medial views. B: *Kobus* n.sp. Rowan et al., MLP-774, right horncore in B1, anterior, B2, posterior views. C: *Damaliscus* sp., MLP-1366, right horncore in C1, anterior, C2, lateral views. D: *Damaliborea grayi*, MLP-2267, right horncore in D1, medial, D2, anterior views. E: *Damaliborea grayi*, MLP-2532, frontlet in anterior view. F: *Gazella harmonae*, MLP-1653, left basal horncore in F1, lateral, F2, anterior views. G: *Aepyceros* cf. *melampus*, MLP-2329, right basal horncore in G1, lateral, G2, anterior views. H: *Tragelaphus* cf. *gaudryi*, MLP-2337, frontlet in anterior view. I: *Giraffa pygmaea*, MLP-2406, right lower tooth-row. J-K: '*Trilobophorus*' *afarensis*; J, MLP-2041, lower jaw, front view. K, MLP-1370bis, left lower jaw, K1, medial view showing the shape of the symphysis, K2, front view showing the relative sizes of the incisors. Scale bar = 5 cm for Fig. I, 10 cm for Figs. F, J-K, 20 cm for all others.
- Fig. 4. Pie diagrams comparing the proportions of some of the main groups in the Gafura (NISP = 158) and Seraitu (NISP = 789) assemblages.
- Fig. 5. Correspondence analysis on the faunal assemblages from the Hadar Fm members and MLP units.