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The Late Pliocene to Early Pleistocene Lomekwi faunas, West Turkana, Kenya: systematics, paleoecology, and biochronology

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ABSTRACT

We describe here the vertebrate fauna collected by the West Turkana Paleo Project at Lomekwi, a site best known for yielding the holotype of *Kenyanthropus platyops* and Lomekwian stone tools, and consisting of several collecting areas providing fossil samples ranging in age from about 3.6 to 2.2 Ma. Analysis of the newly recovered material, alongside a thorough revision of earlier collections, has led to the identification of 85 vertebrate taxa, which provide biochronological indications that help refine the site's chronology and shed light on the paleoenvironmental conditions prevailing during a critical period of early hominin diversification. The newly described fauna illustrates that during the time of *Kenyanthropus,* hominins shared their landscapes with a rich assemblage of vertebrates, including abundant megaherbivores, some 28 species of artiodactyls, diverse large and medium-size carnivores, and giant crocodiles as apex predators in the lakes and rivers of the Turkana region in the Pliocene. Among primates, the recurring association of *Theropithecus* with hominins is found at Lomekwi as it is elsewhere. Paleoenvironmental proxies from the Turkana region emphasize the complex and dynamic nature of the habitats that supported this rich biodiversity.

1. Introduction

1.1. History

The paleontological site of Lomekwi in West Turkana, Kenya, has produced a large collection of vertebrates dating from the early Late Pliocene to the earliest Pleistocene. Among these specimens, there is the holotype of the hominin species *Kenyanthropus platyops* (from locality LO6) dating to c. 3.5 Ma, and the paratype from LO5, dating to c. 3.3 Ma. Lomekwi is also renowned as the site of the earliest known stone tools, discovered at the LOM 3 locality and dated to 3.3 Ma (Harmand et al., 2015). Although the associated fauna from LOM 3 is not analyzed in this study, the archaeological site lies within the broader LO5 collecting area described here. Despite its importance, the paleontological context of the hominins and archaeological sites remains to be fully documented. A thorough study of the Lomekwi fauna can help answer questions about the paleoecology of these early hominins and the environments of the earliest archaeological sites. Here we present the first comprehensive description of fossil vertebrates from the paleontological sites at Lomekwi, dating from 3.6 to 2.2 Ma.

The time interval from 3.6 to 2.2 Ma is of considerable interest for African paleoanthropologists, archaeologists, and paleontologists because it represents the first known diversification of hominin species at about 3.6 to 3.3 Ma (Brunet et al., 1996; Haile-Selassie et al., 2012, 2015, 2016; Leakey and Harris, 1987; McNutt et al., 2021; Spoor et al., 2010, 2016), the first occurrences of archaeological materials in eastern Africa - and globally (de la Torre, 2019; Harmand et al., 2015; McPherron et al., 2010), and a transition from environments dominated

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by woodlands and wooded grasslands in the Pliocene to the more open conditions of the Pleistocene (Bobe, 2006; Bobe et al., 2022; deMenocal, 2011; Villaseñor et al., 2023; Vrba, 1988). The hominin clade further diversified with the emergence of *Homo* and *Paranthropus* around 3 Ma or shortly thereafter (Bobe and Wood, 2022; Plummer et al., 2023; Villmoare et al., 2015).

Research at Lomekwi began in 1980, when a team from the National Museums of Kenya initiated paleontological and geological surveys of sedimentary sequences between the Lomekwi and Topernawi river drainages west of Lake Turkana. Fieldwork in West Turkana in the 1980s under the umbrella of the West Turkana Paleo Project (WTPP) resulted in the recovery of several key hominin specimens (Brown et al., 1985; Walker et al., 1986) and a collection of fossil vertebrates dating from the Late Pliocene and Early Pleistocene described in a monograph by John Harris and colleagues (Harris et al., 1988). However, Harris and colleagues lamented “the relatively small samples retrieved from the West Turkana localities”, and especially “the sparse mammalian faunas from horizons predating the Tulu Bor Tuff” (a tuff dated to 3.4 Ma: Brown and McDougall, 2011). Since 1996, archaeological fieldwork has been led by the West Turkana Archaeology Project (WTAP), which has resulted in the documentation of about 40 archaeological sites in the Nachukui Formation (Brugal and Roche, 2022; Brugal et al., 2003). Meave Leakey led renewed fieldwork at Lomekwi in 1998–1999, resulting in the discovery and description of *Kenyanthropus platyops* from locality LO6, with other hominin specimens from localities LO4, LO5, LO9 (Leakey et al., 2001). In 2009, a crew led by Kyalo Manthi (National Museums of Kenya) surveyed the Lomekwi sites, and this resulted in the recovery of additional remains attributed to *K. platyops*, as well other faunal taxa. In 2012, Kyalo Manthi, Michael Plavcan (University of Arkansas), and Carol Ward (University of Missouri) launched the West Turkana Paleo Project (WTPP) with a focus on Pliocene localities. Field efforts by the WTPP between 2016 and 2021 significantly increased the number of fossil vertebrates from the time window 3.9–2.2 Ma, most of which are described here for the first time.

1.2. Context

The Lomekwi sites occur in the Nachukui Formation, a sedimentary sequence that spans from about 4.3 Ma to 0.7 Ma. After several decades of fieldwork, the sedimentology and geochronology of the sequence are relatively well established (Feibel, 2011; Feibel and Brown, 1993; Lepre et al., 2011; Roche et al., 2003; Sier et al., 2017). The Nachukui Formation is best understood as part of the Omo Group deposits that also include the Koobi Fora, Shungura, and Usno Formations straddling the border of Kenya and Ethiopia (Brown, 1994, 1995; Brown and McDougall, 2011; Feibel, 1999, 2011; Feibel et al., 1989). The specimens described here derive from the lower members of the Nachukui Formation: the Kataboi, Lomekwi, Lokalalei, and lower Kalochoro Members.

During the earlier part of the Lomekwi sequence, i.e., in the upper Kataboi Member (c.3.6 to 3.44 Ma), the Omo-Turkana region was dominated by a large and shallow lake that fluctuated in size. This is called the Lokochot lake (Feibel, 2011). The holotype of *Kenyanthropus platyops* from locality LO6 was preserved along the western margins of this lake (Leakey et al., 2001). By 3.4 Ma, the lake no longer existed and was replaced by a large river that crossed the Omo-Turkana Basin and exited toward the Indian Ocean. Thus, many of the fossil sites from 3.4 to c.2.4 Ma derive from fluvial floodplain deposits (the Tulu Bor floodplain) (Feibel, 2011). Most of the other hominin fossils derive from LO5 and LO4 which represent the lower portions of the Lomekwi Member, close to 3.3 Ma (Leakey et al., 2001), and also have been attributed to *Kenyanthropus platyops* (Cerling et al., 2013; Leakey et al., 2001; Spoor et al., 2016). Hominins and associated fauna also have been recovered from LO9 and LO10 which represents middle and upper portions of the Lomekwi Member (Leakey et al., 2001). However, in this study, we do not evaluate the hominin fossils themselves beyond their relevance to the associated faunal assemblages and paleoenvironmental context.

The fossils from Lomekwi are broadly contemporaneous with the Tulu Bor Member of the Koobi Fora Formation and Members B and C of the Shungura Formation.

2. Material and methods

We examined a total of 1885 fossil specimens housed at the National Museums of Kenya in Nairobi, the majority of which were collected by the West Turkana Paleo Project (WTPP), supplemented by several notable specimens from earlier fieldwork (Suppl. data2). The most fossil-rich localities (Table 1) are LO5 and LO4 (including LO4E and, tentatively, LO4E east), dated to 3.5–3.2 Ma (Harris et al., 1988), each yielding over 600 specimens (Leakey et al., 2001). These are followed by LO9 and LO10, dated to approximately 2.9 Ma, with more than 200 specimens each (Leakey et al., 2001). In contrast, the earliest locality, LO6, as well as the early Pleistocene localities LO1, LO3, and LO8 (Harris et al., 1988), are considerably less productive. The fossiliferous localities form well-defined spatial clusters, and only a small number of specimens have reported GPS coordinates outside these core areas (Fig. 1). Specimens were collected with standard surface collection protocols. All fossils collected were mapped using GPS and checked against geological maps to confirm geochronological setting. Upper teeth are in uppercase, lower teeth in lowercase. Abbreviations: L = length; W = width; max. = maximum.

The Lomekwi fossils were directly compared with those from several relevant Kenyan sites in the National Museums of Kenya, Nairobi, and indirectly with those from Ethiopian sites in the National Museums of Ethiopia, Addis Ababa, from Moroccan sites in the Institut National des Sciences de l’Archéologie et du Patrimoine, Rabat, Morocco, and from Laetoli in the Museum für Naturkunde, Berlin, Germany. Modern comparative collections are housed in the Muséum National d’Histoire Naturelle, Paris.

3. Systematic paleontology

3.1. Cercopithecidae

3.1.1. Colobinae

3.1.1.1. Rhinocolobus sp. and/or Paracolobus sp.. Except for the partial skeleton KNM-WT 16827 of *Paracolobus mutiwa* from LO1 (Harris et al., 1988; Anderson, 2021), colobines are mostly represented by isolated teeth (Fig. 2S) and a few postcranials. Based upon their size, these teeth could belong to either *Rhinocolobus turkanaensis* or *P. mutiwa*, although they can be slightly larger or smaller than in these taxa. Both species are present at Omo (Leakey, 1987) and Koobi Fora (Jablonski et al., 2008), but formal identification is impossible, although they are definitely larger than modern colobines or fossil *Colobus*. Some of the postcranials can be identified as colobine based on their morphological characters, and it might be that an in-depth study would allow identification of some more specimens. A proximal ulna KNM-WT 71864 from LO5 has a straight caudal border and a rectangular, not retroflexed olecranon, and is perhaps also colobine. KNM-WT 48231 from LO5 is a tibial diaphysis that is quite deep anteroposteriorly at mid-length, unlike the similar sized *Theropithecus*, but resembling the smaller *Colobus freedmani* KNM-ER 5896. KNM-WT 69465 from LO4E is a talus the size of that of

Table 1
Number of specimens identified by us in the main localities.

Site	LO6	LO4s. l.	LO5	LO9	LO10	LO1	LO3	LO8
Approx. age (Ma)	3.6	3.4	3.3	3	2.9	2.52	2.4	2.2
Number	88	521	593	232	208	94	67	63

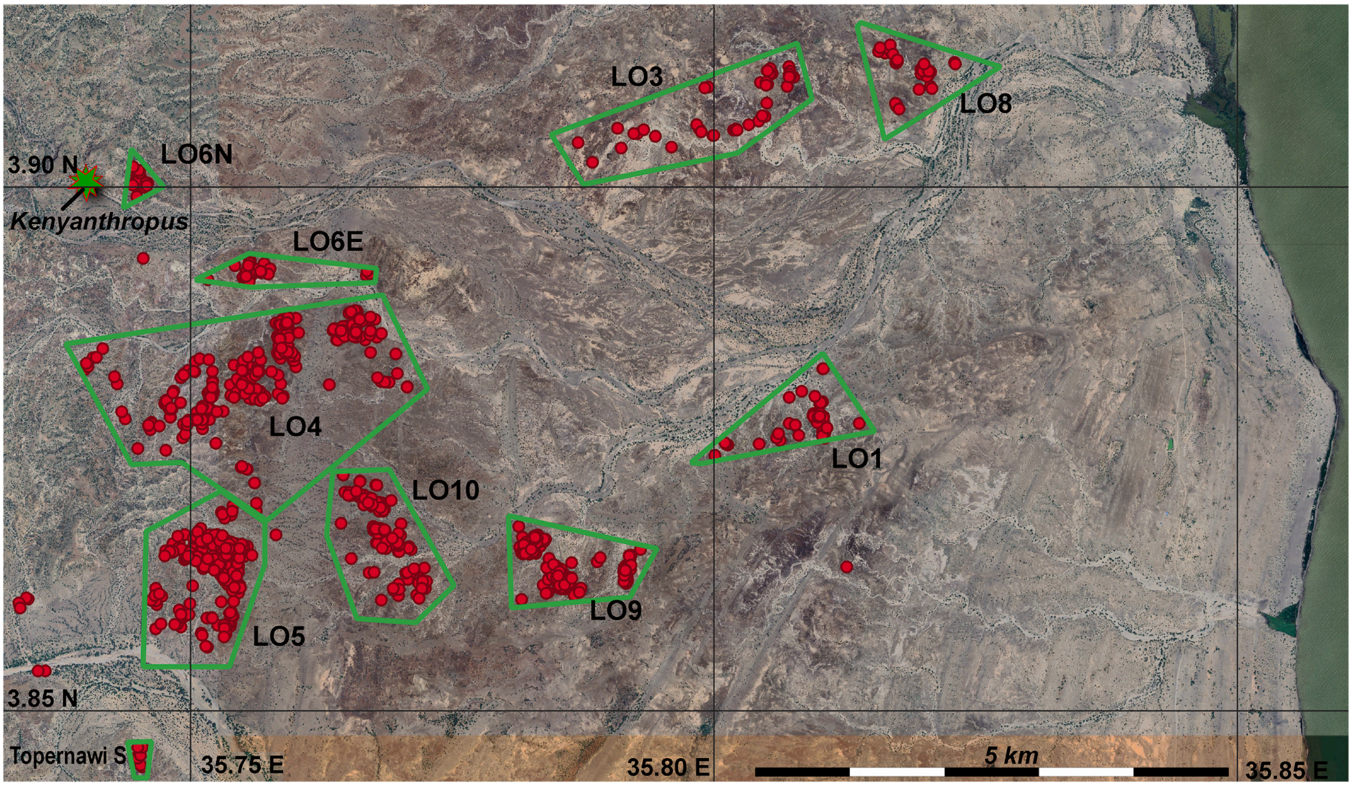

Fig. 1. Map of the Lomekwi area (Google Earth) with the occurrences of fossil mammals identified by us, the approximate extent of the main collecting areas, and the location of the type specimen of *Kenyanthropus platyops* (Leakey et al., 2001).

Theropithecus, but the lips of the trochlea are strongly divergent distally, unlike in this genus, but more like that seen in colobines (Strasser, 1988). This specimen could represent *P. mutiwa*, although there are some differences with this species (Anderson, 2021, Fig. 21).

3.1.1.2. Cercopithecoides sp.?. The upper molar KNM-WT 75507 from LO4E is the only colobine tooth that is definitely too small (L = 7.3 mm; W = 6.8 mm) to belong to either of the previous species.

3.1.2. Cercopithecinae

3.1.2.1. Parapapio sp.. Harris et al. (1988) assigned to this genus the mandibles KNM-WT 16751 and KNM-WT 16752, both from LO4. We keep these identifications, although distinction of the former specimen from *Theropithecus* might be due to weathering. In addition, KNM-WT 77121 from LO8 (Fig. 2R) is a large m3 comparable in size to the species that Jablonski et al. (2008) called '*Parapapio* sp. indet. A′ from Koobi Fora; it can be confidently assigned to this genus. KNM-WT 77160 from LO5 (Fig. 2P) is similar but smaller. Identification of other specimens is less secure. Among them, KNM-WT 71836 from LO9 is an almost unworn upper molar that resembles *Theropithecus* but is quite brachyodont. KNM-WT 75500 from LO9 (Fig. 2Q) is an upper molar that lacks the strong crests of *Theropithecus*. *Parapapio* (or a closely related genus) is not common at that time at Koobi Fora (Jablonski et al., 2008), and has not been reported from Omo.

3.1.2.2. Theropithecus brumpti Arambourg, 1947. The most complete specimen is the skeleton KNM-WT 39368 from LO5 (Jablonski et al., 2002). An almost complete female mandible KNM-WT 48327 from the same site (Fig. 2O) can be assigned to *T. brumpti* on the basis of the presence of a mandibular fossa, probably shallower than it was in life because of crushing. KNM-WT 69009, also from LO5, is a male partial mandible with worn teeth; the very incompletely preserved corpus is slightly depressed below the premolars; the canine is very large, and p3 has a very long, oblique anterior flange; both teeth are much larger than in specimens that we assign to *T.* cf. *oswaldi* (Fig. 3, Suppl. data2). Many other teeth and partial jaws belong to *Theropithecus*, but species identification is impossible, because of the similarity of the two species and intra-specific variation. However, it is likely that most of them belong to *T. brumpti*, because it is by far the most common species in the Turkana Basin at that time (Eck, 1987; Eck and Jablonski, 1987; Jablonski et al., 2008; Frost et al., 2022), and because their teeth are larger for their age than those of *T. oswaldi*. For instance, teeth from LO4, LO5, and LO6 are distinctly larger than those of *T. oswaldi darti* from the roughly contemporaneous Sidi Hakoma Mb of the Hadar Fm (Fig. 3, Suppl. data2). Those from LO9 and LO10 are comparable in size to those of *T. oswaldi* from the much younger Upper Burgi Mb of the Koobi Fora Fm. The Lomekwi teeth match better the measurements of the *T. brumpti* teeth from Koobi Fora; still, those from LO4, LO5, and LO6 are somewhat larger than those from the Lokochot Mb, while those from LO9 and LO10 correspond in size to those of *T. brumpti* from Shungura Mb C and average somewhat larger than those from the Tulu Bor Mb. Other teeth from these two localities are also quite large, especially a p4 KNM-WT 75932, a m1 or m2 KNM-WT 73074, and canines KNM-WT 71761 and KNM-WT 75506 that are 15 and 17.1 mm wide, respectively; these dimensions are not reached before the Upper Burgi Mb at Koobi Fora. Thus, overall, the Lomekwi teeth look somewhat larger than those from Omo or Koobi Fora; whether this is a merely a sample bias, a regional variation, or an indication that the ages of the Lomekwi localities lie in the younger part of their ranges rather than in the earlier, remains to be determined.

The humerus KNM-WT 69168 from LO1 is assigned to *Theropithecus* because of its size (max. length = 220 mm; max. distal W = 40 mm; max. distal depth = 26.5 mm) and laterally shifted distal end, as in several specimens from Koobi Fora. Identification of other humeri is more tentative. The ulnae KNM-WT 48232 and KNM-WT 69213 from LO5 have at least some olecranon retroflexion.

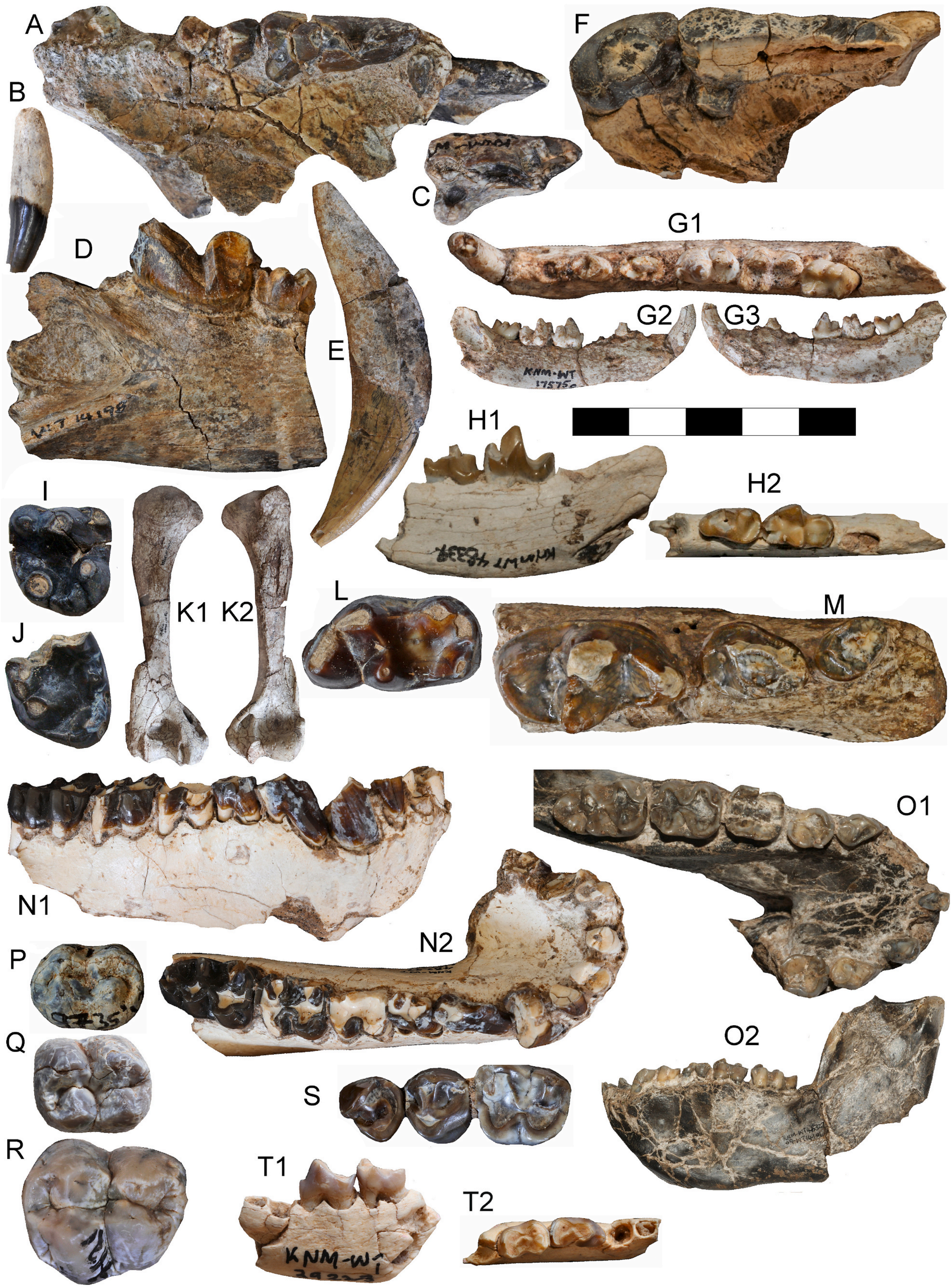

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Fig. 2. Carnivora and Primates. A) KNM-WT 71794 (LO4E), *Panthera* sp.nov.?, left maxilla, occlusal view; B) KNM-WT 73014 (LO5), *Felis* cf. *silvestris*, right upper canine, labial view; C) KNM-WT 39932 (LO4E), Cf. *Lynx* sp., incomplete left upper P4, occlusal view; D) KNM-WT 48216 (LO9?), *Dinofelis* cf. *aronoki*, right mandible with incomplete p4, and m1, lateral view; E) KNM-WT 71898 (LO5) *Homotherium* sp., left upper canine, lingual view; F) KNM-WT 39214 (LO5), *Crocuta eturono*, left upper P3–P4, occlusal view; G) KNM-WT 17575 (LO1), *Mungos dietrichi*, right mandible: G1, occlusal view, G2, lingual view, G3, buccal view; H) KNM-WT 48339 (LO5), *Herpestes* cf. *palaeoserengetensis*, right mandible with p4–m1: H1, lingual view, H2, occlusal view; I) KNM-WT 39625 (LO4), *Enhydriodon* sp., left upper P4, occlusal view; J) KNM-WT 39625 (LO4), *Enhydriodon* sp., right upper incomplete M1(reversed), occlusal view; K) KNM-WT 39331 (LO4), *Enhydriodon* sp., left humerus: K1, front view, K2, posterior view; L) KNM-WT 38764 (LO1), *'Viverra' leakeyi*, right m1, occlusal view; M) KNM-WT 40180 (LO4E), *Lutra* nov. sp.?, left mandible with p3–m1, occlusal view; N) KNM-WT 48247 (LO5), *Theropithecus oswaldi* ?, partial mandible: N1, right lateral view, N2, occlusal view; O) KNM-WT 48327 (LO5), *Theropithecus brumpti*, partial mandible: O1, occlusal view, O2, left lateral view; P) KNM-WT 77160 (LO5), *Parapapio* sp., right upper molar, occlusal view; Q) KNM-WT 75500 (LO9), *Parapapio* sp.?, right upper molar, occlusal view; R) KNM-WT 77121 (LO8), *Parapapio* sp., left M3, occlusal view; S) KNM-WT 48225 (LO5), Colobinae indet., left P3–M1, occlusal view; T) KNM-WT 39223 (LO5?), Hyracoidea gen. et sp. indet.?, mandible fragment with ?p3–p4: T1, left lateral view, T2, occlusal view. Scale equals 50 mm for Figs. A, D, F, G2, G3, I, J, N, O1, 100 mm for Fig. E, O2, 200 mm for Fig. K, 25 mm for all others.

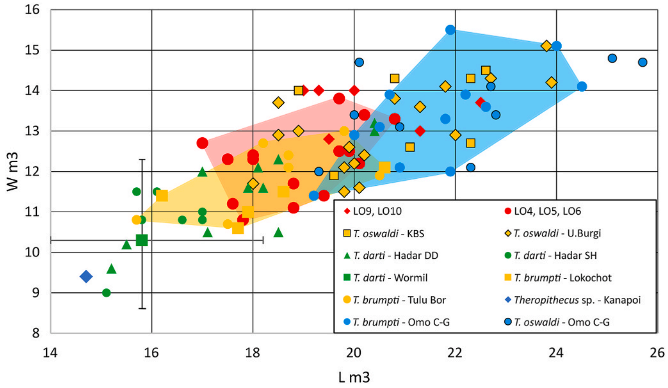

Fig. 3. Plot of length x width measurements of lower third molars of *Theropithecus*. Data from Eck (1987); Eck and Jablonski (1987); Jablonski et al. (2008), Frost (2001); Frost et al. (2014); Frost et al. (2020), 2023; Primo Database). Ranges of values are shown for *T. darti* (or *T. oswaldi darti*) from Wormil, and convex hulls for the LO4, LO5, and LO6 sample, for *T. brumpti* from the Lokochot and Tulu Bor Mb at Koobi Fora, and for *T. brumpti* from Mb C-G of the Shungura Fm.

KNM-WT 48221 from LO5 is an astragalus that has a narrow trochlea (much narrower than in Colobinae or Papionini) that broadens only slightly anteriorly, and a very wide medial malleolar facet. It does not fully conform with other *Theropithecus* but matches this genus (especially KNM-KNM-ER 3842 assigned to cf. *Theropithecus* by Jablonski et al., 2008) better than others. KNM-WT 69233 from LO10 also has a rather narrow, parallel-sided tibial trochlea, and is probably also of *Theropithecus*. KNM-WT 69465 from LO4E also fits better *Theropithecus* than other Turkana cercopithecids in its rather narrow trochlea, which has a deep central groove, as in KNM-ER 3842.

3.1.2.3. Theropithecus cf. oswaldi (Andrews, 1916). KNM-WT 48247 (Fig. 2N) from LO5 is a partial mandible with well-preserved right toothrow; the p3 is relatively short, and the preserved upper part of the corpus shows no indication of a mandibular fossa. We tentatively refer it to *T. oswaldi*, a species that is much less common in the Turkana Basin than *T. brumpti*. There is no definite evidence of a small cercopithecine, or of another genus than those mentioned above, but their presence cannot be excluded, as there are several fragmentary specimens. In any case, there is no doubt that *Theropithecus* was by far the dominant taxon among Cercopithecidae, even though this may be due in part to a taphonomic or collecting bias.

3.2. Carnivora

3.2.1. Canidae

3.2.1.1. Nyctereutes cf. barryi Werdelin and Dehghani, 2011. KNM-WT 39938 from LO4W is a much-weathered partial mandible with worn and poorly preserved m1 whose large talonid is indicative of *Nyctereutes*, but with at most an incipient subangular lobe, in contrast to most representatives of this genus. KNM-WT 71916 from LO5 is a partial maxilla with incomplete M1, whose enlarged lingual part, together with the large size of M2 alveolus, also suggest *Nyctereutes*. The size and dental proportions of these specimens are close to those of *N. lockwoodi* from the Hadar Fm (Geraads et al., 2010) and ?*N. barryi* from Laetoli (Werdelin and Dehghani, 2011). These two species differ in some cranial characters, not observable here, but also in the lack of subangular lobe in the Laetoli species. Accordingly, we tentatively assign the Lomekwi form to this species.

Nyctereutes is very rare in the East African fossil record and has not been reported from Omo (Howell and Petter, 1976) or Koobi Fora (Werdelin and Lewis, 2013).

3.2.1.2. Lupulella sp.. KNM-WT 40178 from LO4W is a mandible lacking molars; the premolars are slenderer than those of *Nyctereutes*. KNM-WT 48340 from LO5 is also a partial mandible lacking the molars. Together with a few isolated teeth, these specimens certainly represent a jackal, but the lack of molars prevents detailed comparisons. On the whole, canids are quite rare at Lomekwi, as they are at Koobi Fora (Werdelin and Lewis, 2013). Canids are fully absent from Omo.

3.2.2. Mustelidae

3.2.2.1. Enhydriodon sp.. A few incomplete teeth represent a giant bunodont otter. The P4 KNM-WT 39625 from LO4 (Fig. 2I) differs from that of *E. dikikae* Geraads et al. (2011) from the Basal Mb of the Hadar Fm (c. 3.5 Ma) in its slightly larger parastyle, and in the absence of crista connecting the paracone to the protocone, which is smaller and less lingually located, resulting in a less triangular tooth outline. In this latter feature, it resembles *E. omoensis* from Omo (Grohé et al., 2022). There is no clear difference with *E. ekecaman* from Kanapoi (Werdelin, 2003; Werdelin and Manthi, 2012), except the distinctly larger size (Table 2). KNM-WT 75529 could be part of another P4.

On the M1 KNM-WT 39625 (Fig. 2J), the hypocone is distinctly smaller than in both *E. dikikae* and *E. omoensis*. Compared to *E. ekecaman*, the cingulum and hypocone of the incomplete Lomekwi M1 are weaker, and the buccal part is longer (Werdelin, 2003; Werdelin and Manthi, 2012). *Enhydriodon afman* from Koobi Fora (Werdelin and Lewis, 2013) and *E. kamuhangerei* from Uganda (Morales and Pickford, 2005) are known only by m1s, preventing comparison with the Lomekwi upper teeth.

A complete femur KNM-WT 37400 from LO4, a distal femur KNM-WT 48346 from LO1, and a humerus KNM-WT 39331 from LO4 (Fig. 2K), are also of *Enhydriodon* (and were identified as such on the accompanying tags by M. Lewis). The humerus is about a quarter smaller than that of *E. dikikae*. The femur was studied by Lewis (2008); it is somewhat smaller than those from Hadar and Dikika, and much smaller than the Omo one, which has a much more proximally directed head and a more medial lesser trochanter (Grohé et al., 2022).

Distinction between all these species is not clear-cut; it is rather unlikely that several lineages coexisted in the Turkana Basin, and we may surmise that some of the differences in size and morphology result

Table 2
Comparative measurements of East African giant otters.

	L P4	W P4	L M1	W M1	L m1	W m1	L m2	W m2
Lomekwi								
WT-39926							9.3	8.2
WT-39625	18.5	20	17.2	c.21.5				
E. dikikae								
Dikika 56-9	21	22.6	20.8	25.8				
Dikika 24-1					26	16.2		
E. ekecaman								
KP-10034	16.5		12.1	19.8	21.2	13.5		
E. afman								
ER-3110					26.4	16.5		
ER-3108							11.8	13.9
E. kamuhangerei					26	15.9		
E. omoensis								
Omo L56-1					32.1	18.3		
Omo L2-148							10.1	12.4
Omo P791-18	25.8	26.7	20.6	27				

from evolutionary changes or regional variations.

3.2.2.2. *Lutra s.l. nov. sp.?.*

KNM-WT 40180 from LO4E (Fig. 2M) is a partial mandible with incomplete p4, lacking the tip of the main cuspid, and slightly eroded m1 (p4 = 10.0 × 7.0 mm; m1 17.2 × 8.9 mm). The relatively small size of the talonid shows that it belongs to a fish-eating otter (*Lutra* s. l.). It is the size of Koobi Fora specimens assigned to *Torolutra* Petter et al., 1991, by Werdelin and Lewis (2013) but the p4 is broader, the trigonid of m1 is more widely open, with the metaconid more distally located, and the talonid is distinctly shorter, with a less distinct hypoconid. At least the characters of m1 are more reminiscent of *Lutra* s. str., but a revision of African fish-eating otters remains to be undertaken, as already discussed by Geraads et al. (2015). Indeed, of the diagnostic characters listed by Petter to define her new genus *Torolutra* (translated in Grohé et al., 2022: "Mandible with a relatively deep masseteric fossa separated from the ventral margin of the ramus and with the anterior border located behind the alveolus for m2; p4 robust, with an oval outline, surrounded by a thick and continuous cingulid; m1 with tall and sharp trigonid cuspids, the protoconid being the tallest trigonid cuspid, a narrow talonid, with a flat and obliquely oriented lingual face of the hypoconid.") only the first one is not found in *Lutra*, and is quite subtle. In fact, the conspicuous, rather lingually located hypoconid of the specimens assigned to "*Torolutra*" (KNM-ER 4568, KNM-ER 5895 [and KNM-ER 44462, not studied by Werdelin & Lewis]) make the talonid distinctly less flat than in *Lutra*, and this is perhaps the best diagnostic feature of this taxon. The talonid of KNM-WT 40180 is more *Lutra*-like, but shorter than that KNM-ER 1486, the much-worn holotype of *Hydrictis gudho* Werdelin & Lewis,2011.

KNM-WT 16858 from LO4 is a mandible fragment with badly broken p4 and m1; it could be of a smaller individual of the same species.

3.2.3. *Herpestidae*

3.2.3.1. *Mungos dietrichi Petter, 1963.*

KNM-WT 17575 from LO1 is an associated mandible and maxilla (Fig. 2G). The characters of its lower teeth allow confident assignment (following Harris et al., 1988) to *M. dietrichi*, a species of mongoose only known from Laetoli and Olduvai (Petter, 1963, 1973, 1987; Werdelin and Dehghani, 2011). The upper P4, however, is somewhat longer relative to its breadth than LAET 3741 (Petter, 1987, Fig. 7.2.11); we do not know whether this has taxonomic significance. A mandible with broken m1-m2, KNM-WT 71918 from LO4E, is probably of the same species.

3.2.3.2. *Herpestes cf. palaeoserengetensis Dietrich, 1942.*

Pending a revision of the fossil forms, we include *Galerella* in *Herpestes* s.l. KNM-WT 39333 from LO5 is a partial cranium with a well-preserved palate but lacking most teeth except right P3 and M1. It resembles modern *Herpestes* and thus probably belongs to the Laetoli species, the only one known in the Pliocene of East Africa (Petter, 1987; Werdelin and Dehghani, 2011), even though the P3 is somewhat larger (P3 = 6.05 × 3.9 mm; max. width of M1 = 6.5 mm). KNM-WT 48339 from LO5 (Fig. 2H) is a partial mandible with p4-m1, certainly of the same species. Sample size is small for the fossil forms, but the lower teeth appear to be slightly broader than those of extant *Herpestes* species and *H. abdelalii* from Ahl al Oughlam, in connection with the less open trigonid of m1 (paraconid less forwardly directed). Figure 8.11 in Werdelin and Dehghani (2011) shows this for the Laetoli m1 L5315, but this is still more true of KNM-WT 48339, especially for p4 (Table 3). KNM-WT 71927 from LO5 is a mandibular fragment with m1 and the m2 alveolus.

Herpestids are very poorly known at Omo (Wesselman, 1984), and unknown at Koobi Fora, presumably because of taphonomic or collecting biases.

3.2.4. *Viverridae*

3.2.4.1. *Civettictis leakeyi (Petter, 1963).*

KNM-WT 38764 from LO1 (Fig. 2L) is an m1 that much resembles the m1 of the living *Civettictis civetta*, but looks less derived in having the trigonid cuspids less closely appressed against each other and perhaps less high; it is also larger (16.3 × 8.5 mm) than the m1s of *C. civetta* (12.2–15 x 7.4–8.6 mm in a modern sample). This tooth also resembles '*Viverra*' *leakeyi* Petter, 1963, first described from Laetoli on upper teeth, and later recognized at Omo (Petter and Howell, 1977) and Ahl al Oughlam, Morocco (Geraads, 1997); the m1 from this latter site has a trigonid that is slightly more widely open lingually and is still larger (17.7 × 9.5 mm), but an m1 from Shungura Fm Mb E (Omo 151-745) is virtually identical with the Lomekwi tooth. *Civettictis vulpidens* from Langebaanweg is of similar size, but has a much longer m1 trigonid (Churcher et al., 2025). KNM-WT 39923 from LO4E is a weathered, smaller m1 (14.3 × 7.3 mm) that is probably of the same species. A maxilla preserving only the I3, canine, and P1, but lacking other cheek-teeth, KNM-WT 16852 from LO10 was assigned to *Civettictis* by Harris et al. (1988). It probably belongs to *C. leakeyi* as well.

Table 3
Comparative measurements of *Herpestes*. Laetoli and modern data from Petter (1987).

	p4 L	p4 W	m1 L	m1 W
WT-48339	5.7	3.3	6.5	4
WT-71927			7	4.1
H.pulverulentus, modern, mean	5.45	2.6	6.1	3.45
H.abdelalii AaO (mean)	6.4	3.2	7.1	3.9
H.palaeoserengetensis Laetoli	5.7	2.7	7	4
	6	2.3	7.6	4.1

KNM-WT 39934 from LO4W is an incomplete M1 that resembles that of *Pseudocivetta ingens*, present at Koobi Fora (Werdelin and Lewis, 2013), Omo (Petter and Howell, 1977) and Olduvai (Petter, 1966) but is smaller; we do not attempt generic identification.

3.2.5. Hyaenidae

3.2.5.1. Crocuta eturono Werdelin and Lewis, 2013. The type of this large relative of the spotted hyena is KNM-WT 40181 from LO6S, and several other specimens from LO4, LO5, and LO6 can be assigned to the same species, on the basis of their large size and broad premolars (Suppl. data1, fig. A–C; Suppl. data2); even the more recent *C. ultra* and *C. crocuta* average smaller. The main specimens not mentioned by Lewis and Werdelin (2022) are KNM-WT 39214 from LO5 (Fig. 2F), a maxilla with P3 and a very long P4, and KNM-WT 48344 from LO4E, an m1 fully lacking a metaconid. Those from LO9 and LO10 are also large, but could belong to *C. ultra,* a common form in late Pliocene/early Pleistocene deposits. *Crocuta eturono* is a rare species but is also present at Koobi Fora (Werdelin and Lewis, 2013), at Dikika (Geraads et al., 2015), and at Hadar and East Gona (Lewis and Werdelin, 2022).

KNM-WT 16831 from LO4 is a poorly preserved ulna identified as *Homotherium* by Harris et al., 1988 (as KNM-WT 16881) but the caudal border is too concave, the anconeal process not distally inclined, and the shaft diameters sharply decrease distally; these authors were probably misled by its large size, and the bone is in fact clearly hyenid; we tentatively assign it to *C. eturono*.

Several West Turkana and Koobi Fora specimens were assigned to *Pachycrocuta* by Werdelin (1999). Later, recognition of *Crocuta eturono* by Werdelin and Lewis (2013) led them to re-assign KNM-ER 3748 to this new species, and to remove *Pachycrocuta* from the Koobi Fora fauna list. It remains to be ascertained whether it should also be removed from the Lomekwi fauna list. Of the specimens studied by Werdelin (1999), KNM-WT 16849 from LO5, with its very large premolars (the largest p3 in Suppl. data1 fig. C), and KNM-WT 16851 from LO10 would be the best supports for retaining this genus but the sample of *C. eturono* is still too small to fully assess its variation, and it is more parsimonious to include these specimens in this species. We tentatively remove *Pachycrocuta* from the Lomekwi list.

3.2.5.2. Crocuta venustula Ewer, 1955. A smaller species of *Crocuta* is represented at LO4W by a p3, KNM-WT 39928, at LO4E by a mandible fragment KNM-WT 69008, at LO5 by a p3 KNM-WT 16853, and possibly at LO9 by a partial m1 KNM-WT 77197 that has a metaconid, but whose talonid is short enough for *Crocuta*. KNM-WT 39928 is not much smaller than the smallest p3s of *C. ultra*, but is significantly earlier, and most likely represents a form close to *C. 'dietrichi'* from Laetoli (Petter and Howell, 1989; Werdelin and Dehghani, 2011), regarded (along with *C. dbaa* Geraads, 1997) as a synonym of *C. venustula* Ewer, 1955, by Lewis and Werdelin (2022), to which they assigned this specimen. It must be stressed that species delimitation in Pliocene and Pleistocene African hyenas is not easy, as they form a size continuum, but the large size difference between this specimen and the larger, contemporaneous, *C. eturono* implies species distinction.

3.2.5.3. Crocuta ultra Ewer, 1954. In addition to the LO9 and LO10 specimens mentioned above, KNM-WT 39209 from LO8 is also smaller than *C. eturono*, and should probably be referred to *C. ultra*, as done by Lewis and Werdelin (2022).

3.2.5.4. Hyaena sp. and/or Ikelohyaena cf. abronia (Hendey, 1974). A few isolated teeth attest the presence of a small hyenid with narrow teeth that could be close to either the *H. makapani* described at Koobi Fora (Werdelin and Lewis, 2013), *I.* cf. *abronia* from Laetoli (Werdelin and Dehghani, 2011), or *Parahyaena* from Kanapoi (Werdelin and Manthi, 2012). These are a p4 KNM-WT 72987 from LO3, and a p2 KNM-WT 71805 from LO9.

3.2.6. Felidae

3.2.6.1. Felis cf. silvestris Schreber, 1777. KNM-WT 73014 from LO5 (Fig. 2B) is a felid upper canine that fits *F. silvestris* or a similar small cat in size.

3.2.6.2. Cf. Lynx sp.. A few teeth and postcranials indicate the presence of a felid the size of a serval or caracal, but the protocone of an incomplete P4 KNM-WT 39932 from LO4E (Fig. 2C) is stronger than in these species, and more like that of a lynx, but generic identification is very tentative. A similar-sized felid is present at Koobi Fora (Werdelin and Lewis, 2013). KNM-WT 69540 from LO5 is a felid unprepared metacarpal that could be of the same taxon, but is straighter and more slender than in lynxes.

3.2.6.3. Panthera sp. nov.?. KNM-WT 71794 from LO4E (Fig. 2A) is a maxilla with the base of the canine, and P3-M1 is poor condition. It is close to the average size for modern *Panthera pardus*, but differs in the rather large size of M1 (obviously a primitive character), and in the greater length of P4 relative to P3, to the canine, or to the distance between the canine and P4, compared to other African leopard-size *Panthera* (Suppl. data1, Fig. D; Suppl. data2). In this regard, it is probably still more different from the Laetoli leopard (Werdelin and Dehghani, 2011), which has a long lower p3. Such a long P4 is also found in *Dinofelis*, but the canine is much smaller and distinctly less transversely compressed than in this genus. Interestingly, these P3/P4 proportions are close to those found in the jaguar, *P. onca* (the P3/P4 length proportions of the Lomekwi maxilla would fit within the larger sample available to Hemmer, 2022, Fig. 2), but the canine is distinctly larger in the jaguar. If KNM-WT 71794 is not just a *P. pardus* outlier, more detailed analysis might say whether this resemblance with *P. onca* only reflects the primitive tooth proportions, is a mere convergence, or supports Hemmer's hypothesis of an African origin for jaguars.

A few other Lomekwi specimens might also be of a relative of *Panthera*. KNM-WT 77313 is an astragalus the size of that of *D. aronoki*, but the bone is less massive, the trochlea more asymmetrical, and the head smaller, and it definitely better matches *Panthera* (modern specimens and KNM-ER, 2013); we tentatively assign it to *Panthera*. KNM-WT 71797 from LO4W is a P3, the size of a small *P. pardus*.

KNM-WT 39224 from LO5 is a damaged p4 (mesiodistal length = 19.5 mm, buccolingual width = 9.5 mm) whose anterior accessory cuspid is better separated from the main cuspid than in *Panthera*, but the crown and especially the anterior cuspid are too low for *Dinofelis*. It might belong to *Panthera* sp.nov.?

3.2.6.4. Dinofelis sp.. An isolated lower carnassial, KNM-WT 48214 from LO6 and a mandible fragment bearing the poorly preserved carnassial, KNM-WT 48216 (Fig. 2D) from LO9 (but its coordinates indicate instead LO10), are intermediate in size (respectively 23.6 x 11.3 and 23.1 x ? mm) between *P. pardus* and *P. leo*. In KNM-WT 48214, the mesial edge of the paraconid is more vertical and straighter than in most *Panthera*, but resemble instead the *Dinofelis* from Ahl al Oughlam (Geraads, 2004) and *D. aronoki* KNM-ER 1549. They might belong to the *Panthera* sp. nov.? described above, but we prefer to assign them to *Dinofelis*. Both teeth are somewhat smaller than those of *D. aronoki* from Koobi Fora, however. In KNM-WT 48216, the m1 is less slender than those of the Koobi Fora *Dinofelis* (Werdelin & Lewis, 213), but not than the one from Ahl al Oughlam (Geraads, 2004). On the partial p4, the distal cingulum is not very elevated, but the tooth is decidedly narrower than in *Panthera*. The upper canine KNM-WT 16846 from LO4 was identified as *Dinofelis petteri* by Werdelin and Lewis (2001); its measurements are almost identical to those of KNM-ER 3880 (*D. aronoki* according to Werdelin and Lewis, 2013). KNM-WT 69487 from LO5 is the anterior part of an upper carnassial, whose parastyle is taller than long, in contrast to that of *Panthera*. The proximal ulna KNM-WT 39643 from LO4 was identified as “probably *D. aronoki*” by M. Lewis on its accompanying tag. The edentulous mandible KNM-WT 16832 from LO10 was assigned to *D. petteri* by Werdelin and Lewis (2001); the long m1 (from the alveolus) relative to p4 and the posterior location of the mental foramen support the identification as *Dinofelis*, but the long p3 (certainly longer than half that of m1), the very robust canine, and the long diastema compared to the best mandible of *D. petteri*, KNM-KP 30397 from Kanapoi, are differences that, in our opinion, preclude this identification. KNM-WT 75613 from LO9 is a calcaneus whose articular part is more expanded laterally than in *Panthera*, but as in KNM-ER 4419 (*D. aronoki* according to Werdelin and Lewis, 2001), KNM-ER 722 and KNM-ER 40482 (*D. piveteaui*). It seems safer not to attempt species identification for the Lomekwi *Dinofelis*.

3.2.6.5. Homotherium sp.. KNM-WT 71898 from LO5 (Fig. 2E) is an unmistakable nice upper canine. It shows no crenulation, but the cutting edges are slightly worn. It is slightly longer and more slender than an upper canine from Laetoli (Werdelin and Dehghani, 2011) and many other *Homotherium*, but its size and compression are close to the average for this genus (Suppl. data1, Fig. E; Suppl. data2). KNM-WT 69344 is a p4 fragment, also from LO5, again with crenulations worn out.

KNM-WT 16833 from LO4 is a distal metapodial, identified as *Homotherium* by M. Lewis on its tag. KNM-WT 39229 from LO5 is a weathered partial humerus; the distal medial epicondyle is weaker than in *Panthera* or *Dinofelis*. KNM-WT 39654 from LO4W include tarsal elements that suffered matrix expansion, but are possibly of *Homotherium*.

3.3. Proboscidea

3.3.1. Deinotheriidae

3.3.1.1. Deinotherium bozasi Arambourg, 1934. Harris et al. (1988) reported mostly fragments from Lomekwi, but they include a poorly preserved M1 from LO2. Recent collections include a complete p3 from LO4W, KNM-WT 71967, and an M2 KNM-WT 69527 from LO4E. Measurements of all these teeth are similar to those of other East African sites (p3: mesiodistal length = 75 mm, buccolingual width = 56.5 mm; Fig. E; M2: mesiodistal length = c. 112 mm, buccolingual width = c. 112 mm; Suppl. data2). There is no doubt that it belongs to the common deinothere of the Pliocene and Pleistocene of Africa (Arambourg, 1947; Harris, 1983a; Sanders, 2011).

3.3.2. Elephantidae

3.3.2.1. Elephas recki Dietrich, 1915. Elephants are uncommon and complete molars are extremely rare (Table 4). *Elephas*, certainly the dominant genus, is represented by members of the lineage *E. ekorensis* – *E. recki*; the latter species has been subdivided by Beden (1979) into successive subspecies. However, although the general trends noticed by him (enamel thinning, increase in the number of plates, hypsodonty) are certainly correct, isolated teeth or even tooth fragments cannot reliably be identified to subspecies (Todd, 2005). Even identification at species level is difficult without knowledge of the geological age, and more than once, species identification had to be revised after reevaluation of the age of the specimen. KNM-WT 73002 from LO3 looks quite primitive and would probably be identified as *E. ekorensis* if found in older deposits; KNM-WT 71983 from LO4E is rather derived for its geologic age, being distinctly higher than broad. Rather than attempting identifications that might lead to circular reasoning, we prefer to assign all new material to *E. recki*.

Table 4
Dental measurements of the new specimens of *Elephas recki* from Lomekwi.

	site	tooth	L	W	H	N plates
WT-38957	LO8	m3	230+	98	–	−11
WT-71983	LO4	M3	230	–	c.100	−11
WT-73002	LO3	M>	–	103	–	−7
WT-75704	LO3	M3	240	83	98	12x
WT-77243	LO10	M2	180	73	–	x7
WT-77314	LO5	m3	230+	98	–	−8−

A few specimens were assigned to *Loxodonta adaurora* by Harris et al. (1988), who characterized this species by its “thick enamel and widely spaced plates”; unfortunately, this applies to any primitive elephant, and we tentatively include these specimens into *E. recki* as well.

3.3.2.2. Loxodonta cf. exoptata Dietrich, 1942. Harris et al. (1988) assigned the very brachydont molar KNM-WT 16458 from LO4 to *L. exoptata*, on the basis of its central sinus, leading to the formation of a loxodont pattern in worn plates; this is the only distinctly loxodont specimen, and no molar from the recent collections displays a similar pattern, but we keep this species in the fauna list. However, the coexistence of two species of *Loxodonta* at LO4 and the survival of the type-subspecies of *L. adaurora* until the early Pleistocene of LO8 (Saarinen and Lister, 2023) are unlikely.

3.4. Perissodactyla

3.4.1. Rhinocerotidae

3.4.1.1. Diceros bicornis L.. A skull with associated mandible KNM-WT 41576 from LO1 (Fig. 4D), briefly mentioned by Geraads (2005), is one of the best-preserved rhino skulls of the East African Plio-Pleistocene. Their morphology is that of the modern *D. bicornis*, and measurements are close to the mean values for modern specimens of this species (Guérin, 1980), so that it can confidently be identified as *D. bicornis*, showing that this species was definitely present at the Plio-Pleistocene boundary. KNM-WT 16731 from LO3 is an occipital, also of *Diceros*.

A partial tarsus with associated Mt-IV KNM-WT 38850 from LO4 is clearly of this genus because the Mt-IV is much slenderer than in *Ceratotherium*, the cuboid facet does not occupy the entire proximal surface, the cuboid is distinctly higher laterally than medially, and the astragalus trochlea is strongly asymmetrical. Other specimens are far less complete, but many of them can be identified to the genus level, showing that *Diceros* is not much less abundant than *Ceratotherium*.

3.4.1.2. Ceratotherium cf. simum (Burchell, 1817). The molars are more primitive than those of the modern *C. simum* and are reminiscent of early forms of the ‘white’ rhino, often called *C. praecox* or *C. efficax* but that Geraads (2005, 2010, 2020) assigned to *C. mauritanicum*. Intermediate forms are not always readily identifiable to species. Overall, upper molars from early Lomekwi sites look more derived than the contemporaneous or later teeth from Hadar in their more oblique lophs. Because we know that *C. mauritanicum* survived in North Africa well after the emergence of *C. simum* in East Africa, we tentatively suggest that the split took place around that time, the Lomekwi rhino possibly being the earliest representative of the branch leading to *C. simum*.

3.4.2. Equidae

3.4.2.1. ‘Hipparion’ cf. hasumense Eisenmann, 1983. Equids are represented by a number of isolated teeth, some postcranials, and a few partial tooth-rows (Fig. 4A–C). We assign them to a form close to the species defined at Koobi Fora in levels dated to c. 3 Ma, but that taxon might be present in earlier levels as well. There is no obvious evidence that more than one species is present at Lomekwi, but identification of isolated equid teeth is too uncertain to be sure about this. Harris et al. (1988) also assigned the Lomekwi material to ’*Eurygnathohippus*’ *hasumense*.

Fig. 4. Perissodactyla, Hippopotamidae, and crocodiles. A) KNM-WT 69857 (LO5), *Hipparion* cf. *hasumense*, right upper tooth series; B) KNM-WT 69563 (LO4E), *Hipparion* cf. *hasumense*, right lower tooth series; C) KNM-WT 69413 (LO4E), *Hipparion* cf. *hasumense*, left metacarpal: C1, proximal view, C2, anterior view; D) KNM-WT 41576 (LO1), *Diceros* cf. *bicornis*, cranium: D1, right lateral view, D2, ventral view; E) KNM-WT 75638 (LO4E), *'Hippopotamus' protamphibius*, mandibular symphysis, front view; F) KNM-WT 38973 (LO5), *'Hippopotamus' protamphibius*, mandibular symphysis, front view; G) KNM-WT 38974 (LO3), *'Hippopotamus' protamphibius*, mandibular symphysis, front view; H) KNM-WT 77311 (LO5), *Mecistops* sp., snout fragment, dorsal view (front towards the top of the page, the arrow points to the premaxilla/maxilla suture); I) KNM-WT 38981 (LO5), *Crocodylus thorbjarnarsoni*, snout: I1, ventral view, I2, dorsal view. Scale equals 150 mm for Fig. D, 120 mm for Figs. C and E–I, 40 mm for Figs. A–B.

In the upper teeth, the protocone is long and moderately compressed. In the lower teeth, the premolars are not much larger than the molars. The ectostylid is absent or quite small on p2, but increases in size towards the center of the tooth-row, although it is almost certainly absent in a few teeth (KNM-WT 75882 from LO4E; KNM-WT 77165 from LO6S; KNM-WT 69489 from LO5), and decreases again towards m3, in which it is usually absent. The double knot is of the 'caballine' type. The complete lower series KNM-WT 69563 from LO4E clearly shows these features, as well as the small difference in size between molars and premolars.

KNM-WT 69413 from LO4E (Fig. 4C) is a complete Mc III whose dimensions (Suppl. data1, Fig. F; Suppl. data2) are comparable to specimens from Hadar probably belonging to '*E.*' *hasumense*, but do not much differ either from '*H.*' *pomeli* from the latest Pliocene of Morocco (Eisenmann and Geraads, 2007), or from metacarpals from the Middle Awash that might belong to '*H.*' *feibeli*; the best match is perhaps with AL361-1 from the Kada Hadar Mb, which Eisenmann (1976) called '*H.*' *afarense*. Obviously, the material at hand prevents definite identifications.

3.4.2.2. Equus sp.. The lower molar (probably m2) KNM-WT 77182 from LO8 has a labially (rather than mesially) directed anterior 'horn' of the prefossetid and is thus almost certainly of *Equus*; two P2s from the same locality (KNM-WT 38777 and KNM-WT 38785), whose protocone is connected to the protoloph might also be of this genus.

3.5. Artiodactyla

3.5.1. Camelidae

3.5.1.1. Camelus grattardi Geraads, 2014. KNM-WT 71974 from LO5 is a lower molar, and KNM-WT 75544 from LO3 is an incomplete upper molar of members of the Camelidae. This family, so abundant today, is exceedingly rare in the African fossil record, especially in eastern Africa (Harris et al., 2010; Geraads et al., 2019). The tooth from LO3 probably belongs to *Camelus grattardi* Geraads, 2014, the only species known at that time in East Africa, but that from LO5 is roughly contemporaneous with the transition between *Paracamelus* and *Camelus*, and we prefer not to suggest identification at genus level. Present-day camels are adapted to barren lands, but it may be that these are only refuges where other ungulates are unable to thrive, and there is no evidence that Pliocene forms favored desert areas.

3.5.2. Hippopotamidae

3.5.2.1. 'Hippopotamus' protamphibius Arambourg, 1944. Hippos are not as common at Lomekwi as they usually are in East African sites of this age, and we may surmise that they were not systematically collected. Most hippo remains are isolated teeth and postcranials, and the best specimen of significance for taxonomic identification is a partial skull with associated partial mandible, KNM-WT 75638 from LO4E. The cranium preserves no teeth besides a P4 (erroneously glued to the lower jaw) and the M3s, but the front part of the mandible is well-preserved (Fig. 4E). The symphysis is short, but the mandible is much expanded across the canines, which are small. Remarkably, there are only four incisor alveoli, the central ones being by far the largest. It cannot entirely be ruled out that, the animal being rather old (although not senile), the third pair of incisors was shed with age, but there is no evidence for this. KNM-WT 38973 from LO5 (Fig. 4F) is similar: i1 much larger than i2, i3 doubtfully present, and in any case quite small. The difference in size between i1 and i2 is still greater in KNM-WT 38974 from LO3 (Fig. 4G), suggesting that the Lomekwi hippo became more and more clearly tetraprotodont, and Harris et al. (1988) mention that all West Turkana hippos are tetraprotodont. By contrast, all other hippos of this age are hexaprotodont. However, skull KNM-WT 16588 from LO1 bears three incisors in its left premaxilla (but only one in the left one), and this skull is longer relative to its breadth than the LO4E one; this might reflect an evolutionary change. Postcranials indicate a more lightly built animal than the modern *H. amphibius*.

In addition, Harris et al. (1988) assigned to *Hip*. cf. *kaisensis* a partial juvenile mandible KNM-WT 16386 from LO6, on the basis of its slightly larger size and greater hypsodonty of m1, but we do not believe that they justify species distinction.

Systematics of Pliocene hippos are still confused. In addition to pygmy species, several larger species have been named in the Turkana Basin alone. *Hippopotamus protamphibius* Arambourg, 1944 became tetraprotodont during the course of deposition of the Omo series (Gèze, 1980, 1985), the earliest tetraprotodont specimen being from locality L1, around 3 Ma. Its symphysis resembles KNM-WT 75638 in being short and broad. The Lomekwi specimen would be earlier but, given the overall similarity, it might be identified as *'Hippopotamus' protamphibius*, a species to which Harris et al. (1988) assigned most of the Lomekwi material. Assuming some variability in the number of incisors, we tentatively assign the LO1 skull to the same species, following Harris et al. (1988).

Boisserie (2020) identified the Kanapoi hippo as 'aff. *Hippopotamus* cf. sp. Hadar' (but this form can be called '*Hexaprotodon*' cf. *coryndoni*, since this is the name that was given to the Hadar form by Gèze, 1985). Compared to KNM-WT 75638, the Kanapoi hippo has a longer mandibular symphysis that is less expanded across the canines, and its six incisors are much less unequal in size. Thus, there seem to be no close connection between the Kanapoi and Lomekwi forms.

3.5.2.2. Hippopotamus sp.. KNM-WT 69474 from LO5 is a much-worn m3 whose size (L = 81.5 mm; W = 43.5 mm) definitely indicates a larger species, similar to that of the modern *H. amphibius* (m3 length in the previous species ranges from 58 to 62 mm, n = 4). Species identification is obviously impossible for an isolated tooth, but its large size is noticeable at this early age.

3.5.3. Suidae

3.5.3.1. Nyanzachoerus kanamensis Leakey, 1958. Few specimens from the recent collections can unambiguously be assigned to *N. kanamensis*, but Harris et al. (1988) identified a handful of specimens from LO4, LO5 and LO6. Of these, at least a complete M3 from LO6 KNM-WT 16266, and an m3 KNM-WT 16270 from LO4 (Fig. 5G) were certainly correctly identified.

3.5.3.2. Notochoerus jaegeri Coppens, 1971. We assign to this species KNM-WT 71900 from LO4W (Fig. 5I), a right mandible with complete m3 but lacking the premolars, and a beautiful mandible KNM-WT 77312 from LO5 (Fig. 5H), with all teeth except the incisors. On both specimens, the m3 has three fully formed pairs of pillars, plus a smaller fourth pair and a terminal central pillar. Thus, this tooth is slightly more derived than the average condition in *N. jaegeri* from Kanapoi (Geraads & Bobe, 2017), in which the fourth pair is usually distinctly smaller than the others but is similar to the type of this species from the Pliocene of Hamada Damous in Tunisia (Coppens, 1971), and its morphology fits within the Kanapoi variation. Metrically, it plots among the Kanapoi teeth (Suppl. data1, Fig. G; Suppl. data2). It differs from most m3s of *Notochoerus euilus* by being broader and more brachydont, whereas the latter species has distinctly hypsodont teeth. The mandible KNM-WT 71900 is noticeable because of its reduced symphyseal area, an impression accentuated by the absence of the incisor alveolar area, but it was certainly narrow (74 mm) across the diastema, like the mandible KNM-KP 30184, supposed to be a female of *N. jaegeri* by Geraads and Bobe (2020a), and the canines of KNM-WT 71900, although long, are indeed definitely more slender than in the males from Kanapoi.

Notochoerus jaegeri is a rather rare species, best known from Kanapoi, but some remains from the Denen Dora and Sidi Hakoma Hadar Formation Members are possibly also of this species, although they were included in *N. euilus* by Fessaha (1999). The range of their mediodistal x buccolingual dimensions includes that of KNM-WT 71900.

3.5.3.3. Notochoerus euilus (Hopwood, 1926). Notochoerus euilus is the most common suid at Lomekwi. The evolution of the genus is marked by a lengthening but also narrowing of the third molars (Cooke, 1976; Harris and White, 1979; White and Suwa, 2004). Lower m3s from the lower part of the Lomekwi succession are at about the same evolutionary stage as those from Hadar, and can be called *N. euilus*, while a tooth from LO3 is distinctly longer, and better matches the more derived species *N. scotti* (Fig. 6B, Suppl. data2). Upper M3s from LO4 and LO5, however, look distinctly more derived, and one of them (KNM-WT 16363 from LO5) even plots with Omo teeth of significantly younger age (Fig. 6A; Suppl. data2). This specimen was accordingly included in *N. scotti* by Harris et al. (1988). This discrepancy between the size of the upper and lower teeth, and the derived proportions of some teeth remain

Fig. 5. Suidae. A) KNM-WT 69065 (LO6S), *Kolpochoerus* cf. *afarensis*, left lower m3, occlusal view; B) KNM-WT 16264 (LO4), *Kolpochoerus* cf. *afarensis*, right lower m3, occlusal view; C) KNM-WT 16152 (LO10), *Kolpochoerus* cf. *afarensis*, left upper M3, occlusal view; D) KNM-WT 77302 (LO4E), *Metridiochoerus* cf. *shawi*, right lower m3: D1, occlusal view, D2, buccal view; E) KNM-WT 73142 (LO10), *Metridiochoerus* cf. *shawi*, right lower m3: E1, occlusal view, E2, buccal view; F) KNM-WT 73172 (LO9), *Metridiochoerus* cf. *shawi*, right upper M3: F1, occlusal view, F2, buccal view; G) KNM-WT 16270 (LO4), *Nyanzachoerus kanamensis*, left lower m3: G1, buccal view, G2, occlusal view; H) KNM-WT 77312 (LO5), *Notochoerus jaegeri*, mandible: H1, dorsal view, H2, occlusal view of left m3; I) KNM-WT 71900 (LO4W), *Notochoerus jaegeri*, right m3, occlusal view; J) KNM-WT 48352 (LO5), *Notochoerus euilus*, left m3, occlusal view. Scale equals 200 mm for Fig. H1, 50 mm for all others.

unexplained. A larger sample might solve the issue. For now, we regard the co-occurrence of both the ancestral and daughter species as unlikely and, although the metric range of variation of the teeth is large, we prefer not to draw an arbitrary limit within them; thus, we recognize only *N. euilus* at LO4 and LO5.

3.5.3.4. Kolpochoerus afarensis Cooke, 1978 and K. limnetes (Hopwood, 1926). The genus is not rare and represented in the new collections by about 20 teeth including some well-preserved third molars (Fig. 5A–C). Sample size is small, but upper M3s from LO8 (whose size matches the teeth from Omo D-E-F) are distinctly larger than that from LO10 (whose size matches those from Hadar and Omo B) (Fig. 6C; Suppl. data2). Some of the lower ones from the earliest localities (Fig. 5A and B; Fig. 6D; Suppl. data2) are smaller, and could even be called *K. millensis*, a species defined at Woranso-Mille in Ethiopia, from sites dated to c. 3.8–3.6 Ma (Haile-Selassie and Simpson, 2013). The Turkana Basin *Kolpochoerus* has traditionally been identified as *K. limnetes* but, in size, the early Lomekwi forms clearly fit better *K. afarensis* from the Lower Awash Valley.

3.5.3.5. Metridiochoerus cf. shawi (Dale, 1948). A few specimens, including several M3s/m3s document the earliest known representatives of the genus *Metridiochoerus* (Fig. 5D–F). They resemble the teeth that White et al. (2006) tentatively called *M. shawi*, from Usno and the lower part of the Shungura sequence. They are also similar in size but, surprisingly, the teeth from LO4 and LO5 are larger than those from LO3 and LO9; the difference is slight and sample size is small, however

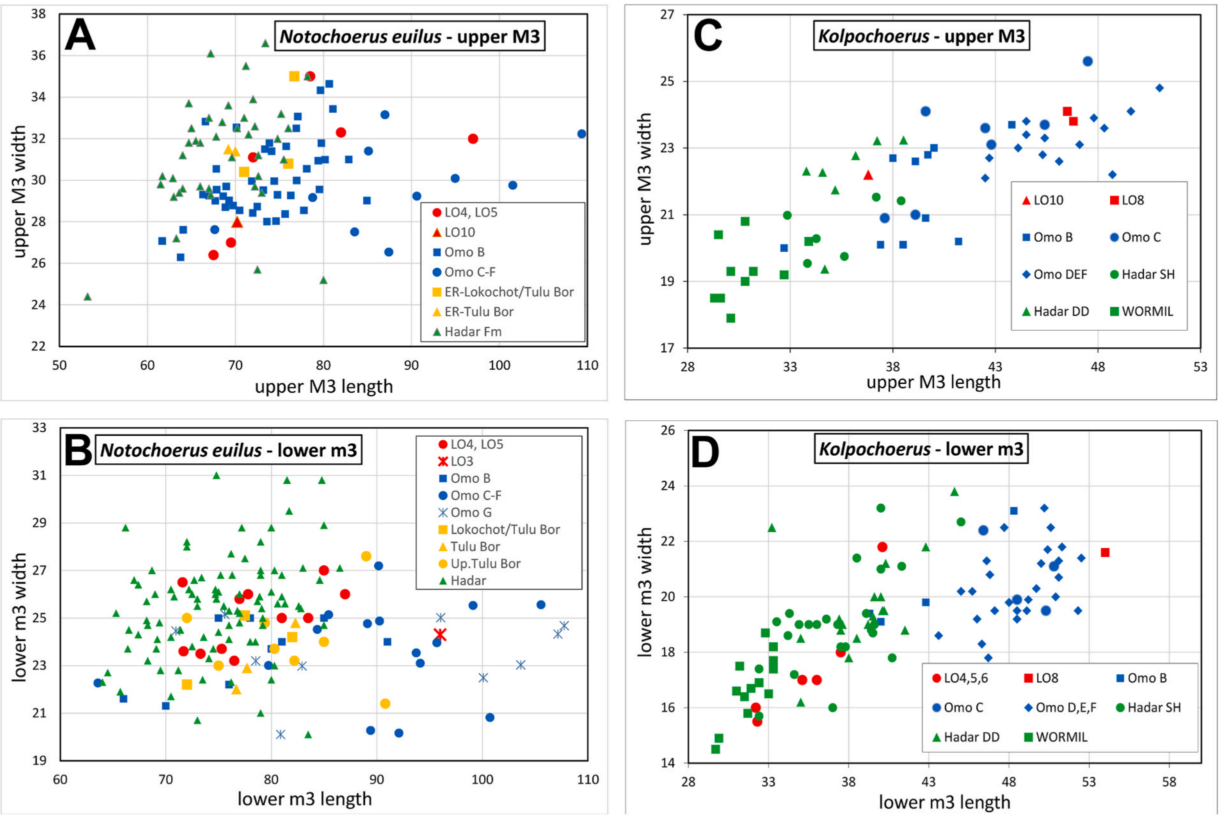

Fig. 6. Length x width biplots of suid third molars. A: *Notochoerus* upper M3s. B: *Notochoerus euilus* lower m3s. C: *Kolpochoerus* upper M3s. D: *Kolpochoerus* lower m3s. Data from Harris, 1983b, Cooke (1976, digitized), Haile-Selassie and Simpson (2013), Geraads et al. (2021), and personal data.

(Suppl. data 1, Fig. M; Suppl. data2).

3.5.3.6. Metridiochoerus cf. andrewsi Hopwood, 1926. If *M. shawi* is regarded as a valid species, the only specimen that could be referred to the type-species of the genus is KNM-WT 16279 from LO8, an incomplete m3 or M3 talon(id), which is far more hypsodont than those of *M. shawi*. Species distinction is not doubtful, but alternative identifications, like *M. hopwoodi*, could be possible as well.

3.5.3.7. Suidae gen. et sp. indet. KNM-WT 48357 is a suid molar from LO4E. It is rather worn, and details are hardly visible, but it looks anachronic, as it resembles Miocene suids. The catalogue says that it was found “In a channel below the Omo (paleo) system.” We suspect it is not from the main Lomekwi deposits, and we do not include it in the list.

We have not attempted identification of suid post-cranials at genus level.

3.5.4. Giraffidae

3.5.4.1. Sivatherium maurusium (Pomel, 1892). Harris et al. (1988) reported only an m3 from LO3. From the same site, KNM-WT 75687 is a large part of horn (often called ossicone, but this name should be restricted to *Giraffa* and close relatives); the species is also present at LO9 (p4 KNM-WT 73054) and at LO5 (upper premolar KNM-WT 69520 and m3 KNM-WT 75694). The third lower molars are similar in size, and also very similar to other m3s from Koobi Fora (Harris et al., 1988; Harris, 1991b, and personal data) and Laetoli (Robinson, 2011, and personal data). The p4s are of the same size as the Hadar specimens (Geraads et al., 2013b), and no evolution in size is apparent during that limited time period, although a general trend towards smaller size and shorter metapodials can be evidenced during the whole Pliocene (Geraads, 1996).

3.5.4.2. Giraffa pygmaea Harris, 1976, Giraffa jumae Leakey, 1965, and/or Giraffa stillei Harris, 1976. Giraffes are represented by two incomplete ossicones, dental remains and a few tarsal bones. Of the few morphological features that allow the distinction between the various species potentially present at that time (Geraads et al., 2013a,b), the only observable one is the presence of two articular facets for the metatarsal on the cubonavicular KNM-WT 69180 from LO1, in contrast to *G. camelopardalis*. Other identifications (Suppl. data 2) rest upon measurements only.

At LO5, the full size-range is present; the rare *G. pygmaea* is documented by an upper tooth-series KNM-WT 73062, while larger teeth attest to at least another species (*G. stillei* and/or *G. jumae*; Fig. 7F). Association of at least two taxa is the rule in other sites, but the largest taxon is absent from LO6, and the smallest from the youngest sites. Study of the Omo giraffes and revision of the Koobi Fora ones might allow more precise taxonomic assignments, but distinction between species is far from clear-cut, as can be seen by the astragalus measurements (Suppl. data1, Fig. I; Suppl. data2).

3.5.5. Bovidae

3.5.5.1. Tragelaphini

3.5.5.1.1. Tragelaphus cf. kyaloi Harris, 1991a. Most dental measurements (mesiodistal length of m3 = 31.1–34.7 mm; n = 7) are homogeneous in the lower and middle parts of the Lomekwi sequence; the section of most horncore pieces is more rectangular than in the *T. saraitu – T. rastafari – T. nakuae* lineage (Reed and Bibi, 2010), and more like in the rare *T. kyaloi*, defined at Kosia and also present at Kanapoi (Geraads & Bobe, 2020), and we tentatively assign them to this species.

3.5.5.1.2. Tragelaphus cf. rastafari Bibi, 2011 and/or T. nakuae Arambourg, 1941. The most complete tragelaphin remain from Lomekwi is KNM-WT 39208 from LO5, a braincase with part of the left

Fig. 7. Ruminantia. A) KNM-WT 73243 (LO5), *Damaliscus* aff. *lunatus*, partial cranium: A1, right lateral view, A2, front view; B) KNM-WT 69175 (LO4W), *Aepyceros shungurae*, frontlet: B1, left lateral view, B2, front view; A1; C) KNM-WT 39208 (LO5), *Tragelaphus* cf. *nakuae*, braincase: C1, occipital view, C2, dorsal view; D) KNM-WT 40246 (LO5), *Damaliscus* cf. *lunatus* frontlet: D1, left lateral view, D2, front view; E) KNM-WT 69252 (LO3), 'Ovibovini' gen. et sp. indet., right upper tooth-row, occlusal view; F) KNM-WT 48319 (LO4W), *Giraffa* cf. *stillei*, left lower tooth-row, occlusal view. Scale equals 50 mm for Fig. E, 100 mm for Fig. F, 200 mm for all others.

horncore (Fig. 7C), which clearly belongs to the *T. rastafari* – *T. nakuae* lineage. It lacks the strong transverse supraoccipital torus of the latter species, which emerges from the former at c. 2.8 Ma (Bibi, 2011). KNM-WT 39208 is of large size (occipital width = 142 mm; occipital height from top of foramen magnum = 75 mm), but some horncores of *T. rastafari* from the Sidi Hakoma and Denen Dora Mbs of the Hadar Fm approach this size, however. Horncore pieces from younger Lomekwi sites might belong to *T. nakuae*, to which Harris et al. (1988) assigned all Lomekwi tragelaphins (Suppl. data1, Fig. J; Suppl. data2).

3.5.5.1.3. Tragelaphus medium and small size. KNM-WT 16473, a maxilla fragment from LO5, is distinctly smaller than in the previous species. Harris et al. (1988) also mentioned a small mandibular fragment from LO3. These specimens certainly belong to at least one additional species, not retrieved by the recent field seasons.

3.5.5.2. Bovini

3.5.5.2.1. Bovini gen. et sp. indet. A. KNM-WT 73245 from LO9 consists of a mandible fragment that is undoubtedly bovin, a pair of horncores that resemble a very small *Pelorovis turkanaensis*, a species known from the Upper Burgi onwards at Koobi Fora, and of a reduncin m3. The latter specimen shows that the catalogue # KNM-WT 73245 includes two taxa, so that the bovin nature of the horncores is not fully established. Still, we believe this is the most likely identification, but absence of information regarding their insertion on the skull forbids genus attribution.

3.5.5.2.2. Bovini gen. et sp. indet. B. KNM-WT 16508 from LO8 is a skull part, from the orbits to the occipital condyles, unfortunately strongly distorted. The horncores, of which only the base is preserved, are strongly compressed anteroposteriorly, diverge by about 50°, and are inserted above the orbits and moderately inclined backwards. Harris et al. (1988) assigned it to *Ugandax* n.sp., but the skull is too crushed for reliable identification. It is unlikely to be of the same taxon as sp. A, because horncores similar to those of *P. turkanaensis* were certainly inserted farther back on the skull and farther apart. Size range of dental remains also suggests that two species might be present among the Bovini.

3.5.5.3. Reduncini. There are many horn-cores but most of them lack their cranial insertions, making identifications difficult. There are at least two, and more probably three species.

3.5.5.3.1. Kobus sigmoidalis Arambourg, 1941. At Omo, the species is known from Shungura Member C onwards (Gentry, 1985), but it appears as early as the Moiti Mb at Koobi Fora (Harris, 1991a), and Harris et al. (1988) reported it from LO4. The new collections include some additional specimens from the early sites (LO4 and LO9), confirming that *K. sigmoidalis* definitely appears earlier in Kenya than at Omo. The species is known up to LO8.

3.5.5.3.2. Kobus oricornus Gentry, 1985 and Menelikia leakeyi Harris, 1991a. We include in this group the taxa called *K. oricornus*, *Kobus* sp. A, *Kobus* sp B, *Kobus* sp. C, *Kobus* sp. D, *Menelikia lyrocera*, and *Menelikia* sp. by Harris et al. (1988); the first four of them were lumped into *K. oricornus* by Harris, 1991a. Its horncores, which make up the bulk of reduncin horncores from Lomekwi, share the characters of being rather straight, with incipient to slight homonymous torsion, weak transverse or anteroposterior compression, moderate divergence in anterior view increasing upwards, and distinct inclination backwards. All these characters show some variability, and they might reflect the presence of two species, but the material at hand, which consists almost only of horncores lacking frontal insertions, does not allow for a clear distinction. It may be that we are dealing with a rather polymorphous species, gradually evolving from a more *K. oricornus*-like morphology (no torsion, strong inclination, anteroposterior compression) to a more *Menelikia*-like morphology (homonymous torsion, more upright insertion, slight transverse compression). However, some horncores from LO3 do have a *K. oricornus*-like morphology, supporting the suggestion by Harris, 1991a that this species survived later in the southern part of the Turkana Basin than at Omo, where it is restricted to Member B of the Shungura Fm. *Menelikia leakeyi* is known throughout the Tulu Bor Mb of the Koobi Fora Fm, and in Member C of the Shungura Fm; thus, if correctly identified here, it would also survive later in West Turkana.

3.5.5.3.3. Menelikia cf. lyrocera Arambourg, 1941. Harris et al. (1988) assigned the frontlet KNM-WT 16241 from LO7 (a locality not represented in the new collections) to the Caprini but acknowledged that it might belong instead to a small *Menelikia*. This is indeed the more likely identification, as *M. lyrocera* is abundant in contemporaneous Omo deposits, and this frontlet is only slightly smaller.

3.5.5.4. Hippotragini

3.5.5.4.1. Oryx sp.. Harris et al. (1988) had reported a single *Oryx* horncore from LO1, but KNM-WT 69003 from LO4E, a left horncore with part of the frontal, showing a large sinus in the horncore pedicel, seems to be another specimen. The horn-cores were almost parallel at their base, strongly inclined backwards (more so than in alcelaphins), and had a roughly circular cross-section (diameters about 30 x 30). The genus *Oryx* appears only later elsewhere in the Turkana Basin (Shungura Mb C at Omo: Gentry, 1985; Upper Burgi Mb at Koobi Fora: Harris, 1991a), but this might only be artefact of its rarity, as it is present in the Sidi Hakoma and Denen Dora Members of the Hadar Formation (Geraads et al., 2012).

The lower m3 KNM-WT 75930 from LO9 resembles Bovini, but the strong goat fold speaks against this. A few other teeth are perhaps of this tribe as well.

3.5.5.5. Alcelaphini. Alcelaphins are by far the most common bovids, especially in the older sites. The histogram of m3 length (one of the most common teeth, and the only one whose rank can be ascertained; Suppl. data2) clearly does not reflect a normal distribution, but suggests instead the presence of at least three taxa, of small, medium, and large size. Horncores, as usual in alcelaphins, are much less abundant than teeth, and most of them are only fragments lacking frontal insertions; they show that there are in fact more than three species, but identifications of horncore fragments are tentative.

3.5.5.5.1. Parmularius cf. parvicornis Gentry, 2011. KNM-WT 69202 from LO4W is a partial horncore with frontal; the horncore is small, has a moderate transverse compression, slight backward inclination, slight divergence from its counterpart, and absence of backward curvature. Some other horncores from LO5 and LO9 show the same small size, straight course, and moderate transverse compression, and probably belong to the same species. This horncore resembles that of *P. parvicornis* from Laetoli (Gentry, 1987, 2011) but is somewhat larger; the lengths of the m3s, mostly from LO5 and LO9, are similar to those of a small *Parmularius* from Hadar (Geraads et al., 2012).

3.5.5.5.2. Parmularius sp.. KNM-WT 16423 (LO1) and KNM-WT 16426 (LO5) are horncore bases showing posterobasal expansion, suggesting *Parmularius* rather than *Damaliscus*, but they are too incomplete for identification at species level.

3.5.5.5.3. Damaliscus cf. lunatus (Burchell, 1824). KNM-WT 40246 from LO5 (Fig. 7D) is a frontlet with almost complete horncores that are inserted rather uprightly, transversely compressed, little divergent at the base but with a slight heteronymous torsion. The horncores resemble those of *P. altidens* from Olduvai Bed I and the Ndolanya beds (Gentry and Gentry, 1978; Gentry, 2011), but the horncore pedicel is shorter (the base of the horncore is closer to the orbit), more like in *Damaliscus*. Size is smaller and torsion more distinct than in the widespread, later *D. niro*; horncores are inserted closer, and their curvature more regular than in *D. eppsi* Harris, 1991a, from the upper part of the Koobi Fora sequence. The modern features of this frontlet are unexpected at this age, but too little is known for formal identification.

A pair of horncores KNM-WT 16623 from LO5 attributed by Harris et al. (1988) to *Parmularius* is probably of the same species. KNM-WT 69251 from LO3 is a horncore without its basal insertion. It is little compressed but distinctly spiraled, thus resembling the early Pleistocene forms *D. agelaius* Gentry and Gentry, 1978 from Olduvai and *D. strepsiceras* Geraads et al., 2004a from Melka Kunture; it can provisionally be called *D.* cf. *lunatus*.

3.5.5.5.4. Damaliscus aff. lunatus (Burchell, 1824). KNM-WT 73243 from LO5 (Fig. 7A) is a partial cranium consisting of a braincase with both relatively complete horncores, and the left maxilla. It is of medium size (M1-M3 length = 65.5 mm), the anterior premolars not much reduced, and P2 was present. The horncores are inserted close together, rather far from the orbit, and are without transverse compression (anteroposterior diameter at base = 55 mm; transverse diameter = 56 mm). They are strongly curved backwards, moderately divergent at the base, but the divergence strongly increases upwards before lessening distally, resulting in a strong heteronymous torsion. The parietal plane is long (length of parietal bone from frontal suture to top of occipital = 78 mm), devoid of boss, and is strongly angled on the frontal plane (c. 105°).

Other measurements are: length from M3 to orbit = c.90 mm (estimate); diameters of orbit = 48 × 59 mm; distance from horncore to orbit = c. 55 mm; biorbital width = 154 mm; width across pedicles = 115 mm; max. occipital width = 120 mm; basioccipital width over posterior tuberosities = 52 mm; width over anterior tuberosities = 28.7 mm; length of parietal from frontal suture to top of occipital = 78 mm; width over center of supraorbital pits = 63 mm.

This species is assigned to *Damaliscus* rather than to *Parmularius* because of the absence of parietal boss, of a long, common pedicle of the horncores, and of basal swelling. The most noticeable characters of KNM-WT 73243 are the large size, absence of transverse compression of the horncores, their strong divergence beginning a short distance above the base, and the clear heteronymous torsion. These characters are close to those of the modern tsessebe, *D. lunatus lunatus*, but this subspecies is somewhat smaller (see, e.g., Vrba, 1971; Fig. 1). Modern East African

Damaliscus have instead less spiraled and more compressed horncores. KNM-WT 73243 probably belongs to a species distinct from *D. lunatus* but, because of the strong regional variation of horn shape in several antelope species, we prefer not to erect a new species name. In any case, KNM-WT 73243 is noticeable for its modern aspect contrasting, for instance, with *Damalborea* from contemporaneous localities in the Hadar Fm, Ethiopia (Geraads et al., 2012). This latter genus is rare in the Turkana Basin, where it was described as *P.* cf. *angusticornis* by Harris (1991; see Vrba, 1997; Gentry, 2010). In the Awash Valley, the fossil most similar to the LO5 cranium is the unpublished frontlet A.L. 542-1 from the Busidima Formation, postdating 2.9 Ma.

3.5.5.5.5. Damaliscus sp. A. KNM-WT 16421 from LO1 is the base of a horncore that curves distinctly backwards and is very uprightly inserted, as in *D. eppsi* from Upper Burgi and KBS Mbs at Koobi Fora (Harris, 1991a, figs. 5.51 and 5.52), but formal identification would be reckless. KNM-WT 16422, also from LO1, shows that the horncores were rather long.

3.5.5.5.6. Damaliscus cf. niro (Hopwood, 1936). KNM-WT 75570 from LO10 is a piece of horncore lacking the base, but probably of a distinctly larger species, perhaps related to the Pleistocene *D. niro*.

Other horncores do not preserve their frontal insertions, making orientation, hence identification, virtually impossible, but some probably also represent *Damaliscus*. The horncore piece KNM-WT 16239 from LO5 was assigned to the Caprini by Harris et al. (1988) but it is very incomplete and weathered and could well be an alcelaphin. The Caprini, a tribe very rare in eastern Africa, can probably be removed from the Lomekwi fauna lists.

3.5.5.5.7. Damalborea sp.?. KNM-WT 75635 from LO3 is a left horncore with part of the frontal. It looks alcelaphin, as also suggested by its large frontal sinus, but its tribal status cannot be definitely established. It was certainly short (the diameters decrease quickly upwards), is inserted above the orbit on quite a short pedicle, is distinctly compressed transversely, and curves towards the lateral side (or slightly towards the posterolateral side) with incipient homonymous torsion. In this rare direction of curvature, it resembles some Olduvai specimens of *Parmularius* (see Gentry and Gentry, 1978) but the horncore is farther away from the orbit in this genus. It also resembles *Damalborea* and *Rabaticeras*. The former is known throughout the Hadar Fm; its terminal members (Geraads et al., 2012) have short horncores whose divergence increases upwards and may show homonymous torsion. The latter is a pan-African genus of Pleistocene age, with clear homonymous torsion.

3.5.5.6. 'Ovibovini'

3.5.5.6.1. Gen. et sp. indet. We assign to this tribe, extremely rare in the African fossil record, the upper tooth series KNM-WT 69252 from LO3 (Fig. 7E). Their hypsodonty, short premolars, and molars that are long relative to their breadth resemble alcelaphins, but the angular lingual walls of the teeth completely differ from the rounded ones of this tribe. They much resemble instead the teeth of the paratype of *Makapania broomi* from Makapan (Wells and Cooke, 1956, Fig. 15), and we are confident about the tribal assignment. *Makapania* was first regarded as an alcelaphin, but Gentry (1970) moved it the Ovibovini (a tribe whose content is disputed). The only other African 'ovibovins' are *Budorcas* from Hadar (Gentry, 1996; Geraads et al., 2012), an incomplete horncore from Omo (Gentry, 1985), a mandible piece from Kanapoi (Geraads et al., 2013a,b), and perhaps *Nitidarcus asfawi* Vrba, 1997 from the Pleistocene of Ethiopia; these elements are too few to attempt detailed comparisons, and generic assignment of KNM-WT 69252 is impossible.

3.5.5.7. Antilopini

3.5.5.7.1. Gazella cf. harmonae Geraads et al., 2012. Gazelles are represented by teeth and incomplete horncores only, but in size (Suppl. data1, Fig. K; Suppl. data2), moderate compression, and upright insertion, most of them match the species that Gentry (1985) had recognized at Omo and Olduvai, and which is also present at Hadar (Geraads et al., 2012) and probably Mille-Logya (Geraads et al., 2021). If correctly identified, the species would be present through most of the Lomekwi succession (LO5, LO6, LO10, LO8).

3.5.5.7.2. Gazella sp.. KNM-WT 77116 from LO8 is the basal part of a horncore showing stronger transverse compression, and certainly of another species, perhaps the same as the one reported by Harris et al. (1988) as *G. janenschi*, a species best known from Laetoli. Following Gentry (2011), we doubt the presence of the large living species *G. granti*, and we assume that horncores of this species are recent intrusives.

3.5.5.7.3. Antidorcas sp.?. KNM-WT 71690 from LO9 is a horncore lacking the base, with a rapidly decreasing anteroposterior diameter and a sharp curve backwards. Identification as *Antidorcas* is tentative, but Harris et al. (1988) also reported a springbok horncore from the same site.

3.5.5.8. Aepycerotini

3.5.5.8.1. Aepyceros shungurae Gentry, 1985. The impala might be the most common antelope at Lomekwi, but only two frontlets and a female (hornless) cranium have been recovered; horncores pieces are common but hard to identify to species. The frontlet KNM-WT 69175 from LO4W (Fig. 7B) resembles *A. shungurae* from Omo (Gentry, 1985; the holotype is from Shungura Fm Member B11) and the lower part of the Koobi Fora sequence (Harris, 1991a) in its unexpanded frontal between the horncores, which are but slightly divergent. The Lomekwi *Aepyceros* much differs from *A. afarensis* from Woranso-Mille (Geraads et al., 2009) and from *A. dietrichi* Gentry, 2011 from Laetoli in its smaller size (Suppl. data1, Fig. L; Suppl. data2) and much smaller horncore divergence at the base. On the average, the anterior valley of p4 is less closed than at Omo, and more like the condition in *A. datoadeni* from Hadar (Geraads et al., 2012). Available characters do not allow a clear distinction from the latter, but identification with the Turkana species is more likely on the basis of geographic proximity.

The range of m3 mesiodistal length at mid-height is large (full range 19.5–24.2 mm; mean = 22.6 mm; Suppl. data1, Fig. M; Suppl. data2), and there is no trend towards size increase. By contrast, while horncores size range is large in any locality, those from LO9 and LO10 are among the largest ones, and may document the transition towards the next species, if they are of the same lineage.

3.5.5.8.2. Aepyceros cf. melampus (Lichstenstein, 1812). A frontlet KNM-WT 77248 from LO10 clearly differs from KNM-WT 69175 in the greater inflation of the frontal between horncores, and in its horncores that are larger, more divergent from the very base, and more distinctly spiraled. A horncore KNM-WT 69160 from LO3 was also more divergent from its counterpart than in the previous species. These features resemble those of the living impala, present at Koobi Fora from the Upper Burgi Member upwards (Harris, 1991a), in the Seraitu and Uraitele assemblages at Mille-Logya (Geraads et al., 2021), and perhaps in the Kada Hadar Member of Hadar (Geraads et al., 2012). All this is consistent with the replacement of primitive *Aepyceros* by *A. melampus* at c. 3 Ma.

3.5.5.9. Neotragini

3.5.5.9.1. Cf. Raphicerus sp.. Members of this tribe are rare in the fossil record, except at Laetoli, but this is probably because of their small size. Two horncores fit better *Raphicerus* than *Madoqua*, the common genus at Laetoli, in their relatively upright insertion, and a partial lower tooth row has an m3 with a large third lobe, again in contrast with *Madoqua*.

3.5.5.10. Cephalophini ?

3.5.5.10.1. Gen. et sp. indet. KNM-WT 68979 from LO5 is an upper molar with strong labial pillars but weak styles, completely lacking the mesostyle; the entostyle is fused with the protocone at this wear stage.

These characters are unlike all other tribes present at Lomekwi but match *Cephalophus sylvicultor*, the modern forest duiker. Formal identification and paleoecological conclusions would be risky based on this single tooth, however.

We have not attempted identification of bovid postcranials at genus level.

3.6. Lagomorpha

3.6.1. Serengetilagus praecapensis Dietrich, 1941

A few mandibles belong to hares, and preserve the p3, which is the most characteristic tooth but displays wide intra-specific variation. KNM-WT 48334 from LO5 (Fig. 8A), and KNM-WT 71914 from LO4W (Fig. 8B) can be assigned to *Serengetilagus praecapensis*, best known from Laetoli (Erbajeva and Angermann, 1983; Winkler and Tomida, 2011), but also reported from the Apak Mb at Lothagam (Winkler, 2003) and the Middle Awash (Wesselman et al., 2009).

3.6.2. Cf. Trischizolagus sp.

Mandible KNM-WT 72956 from LO5 (Fig. 8C) seems to differ from the previous ones. Unlike them, it has a deep paraflexid and a large mesofossetid. Either of these features may occasionally be present in *Serengetilagus* (Winkler and Tomida, 2011; Erbajeva and Angermann, 1983) but their association is unreported in this genus. It may be present, instead, in the Palaearctic *Trischizolagus* (Averianov and Tesakov, 1997; Čermak et al., 2019) especially in *T. meridionalis* from the latest Pliocene of Ahl al Oughlam, Morocco (Sen and Geraads, 2023), and in *T. raynali* (Geraads, 1994) from the Pleistocene of North Africa (Sen et al., 2024). However, the genus has never been reported from Eastern Africa, and formal identification would be risky on the basis of a single specimen. More material would be welcome.

3.7. Rodentia

3.7.1. Hystricidae

3.7.1.1. Hystrix cf. makapanensis Greenwood, 1958. A few teeth from LO4E, LO5, LO9, and LO10 belong to porcupines. Most of them are much worn, but KNM-WT 69189 from LO10 is a well-preserved and little worn upper molar, of moderate size (8.8 × 7.2 mm). Its noticeable features are an anterior mesoflexus opening labially and connecting the hypoflexus, and a posterior mesoflexus connecting the lingual mesofossette. These characters are shared by *Hystrix makapanensis* known in several eastern and southern African sites (Azzarà et al., 2022), but this species is somewhat larger, and identification would be premature.

3.7.2. Gerbillidae

3.7.2.1. Cf. Gerbilliscus sp.. KNM-WT 59708 from LO4W is a mandible with m2 (width c. 1.45 mm) and m3; the cuspids of m2 are completely fused into transverse crests, and there is no longitudinal connection. These features conform with *Gerbilliscus*, but the lack of m1 prevents definite identification.

3.7.3. Muridae

3.7.3.1. Golunda cf. gurai Sabatier, 1982. KNM-WT 59707 from LO5 (Fig. 8D) is a mandible with well-preserved, moderately worn molars.

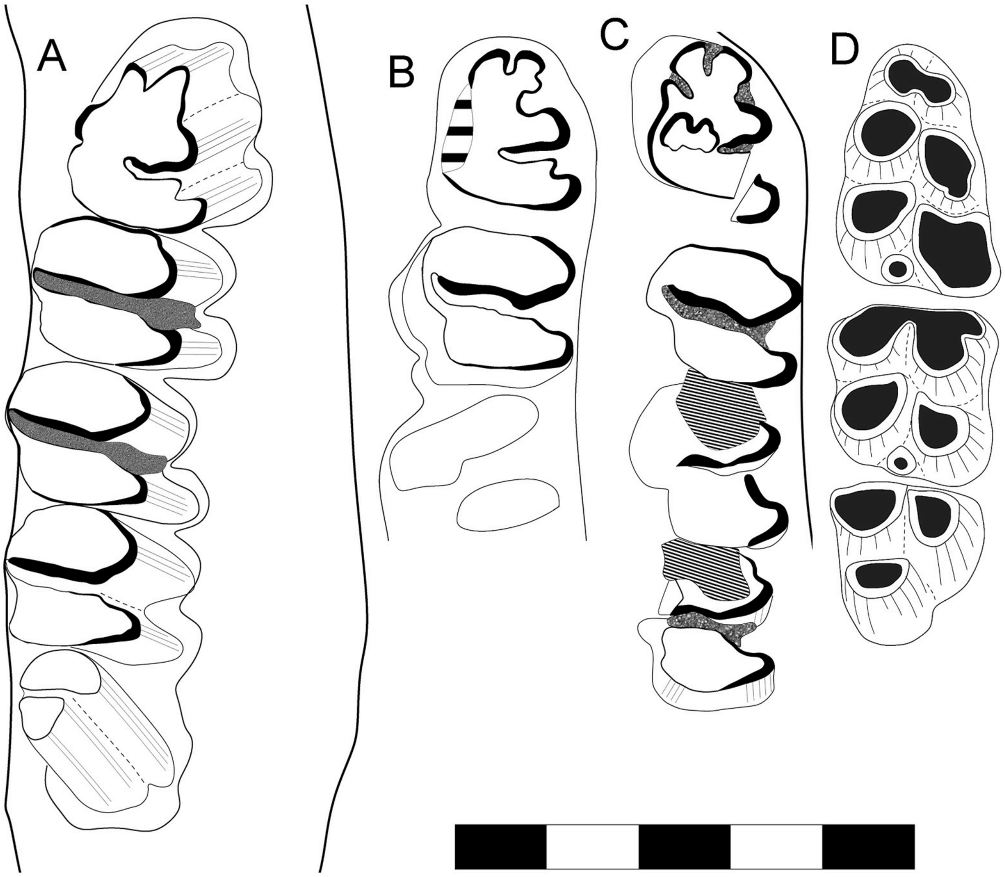

Fig. 8. Rodentia and Lagomorpha. A) KNM-WT 48334 (LO5), *Serengetilagus praecapensis*, right lower p3–m3; B) KNM-WT 71914 (LO4), *Serengetilagus praecapensis,* right lower p3–p4; C) KNM-WT 72956 (LO5), *Trischizolagus* sp.?, right lower p3–m2; D) KNM-WT 59707 (LO5), *Golunda* cf. *gurai*, right lower m1–m3. Scale equals 10 mm for Figs. A–C, 5 mm for Fig. D.

We tentatively assign it to *Golunda gurai*, a species defined at Hadar (Sabatier, 1982), and also recognized in Omo Mb B and C (Wesselman, 1984). The isolation of the tubercles and strong mesial displacement of the lingual tubercles relative to the labial ones are their main distinctive features. The anterior tubercles of m1 are connected (a rare feature at Hadar, but present on the single Omo m1) but have no accessory cuspid (tma) between them. There is a posterior accessory cuspid (cp) on m1 and m2, a strong anterolabial accessory cuspid (tE) and a weak medial one (c1) on m2, but none on m3. The teeth are slightly larger than the few teeth from Omo Mb B but very similar in size to those from Hadar (Table 5).

3.7.4. *Muridae gen. et sp. indet. A*

KNM-WT 39636 from LO8 is a murid mandible with m2 and m3. On m2, the connection of the anterior cuspids (tC and tD) and the smaller size (buccolingual width of m2 = c. 1.5 mm) clearly differ from *Golunda*, but in the absence of m1 no identification at genus level can be proposed.

3.8. *Reptiles*

3.8.1. *Chelonia*

KNM-WT 72995 from LO4E is a Chelonian osteoderm.

3.8.2. *Squamata (identifications, based on photos, by S. Bailón)*

3.8.2.1. Python sp.. Vertebras from LO4, LO5, LO9, and LO10 belong to *Python* sp.

3.8.2.2. Varanus sp.. Vertebrae from LO4 and LO5, and a maxilla from LO5, are of *Varanus* sp.

3.8.3. *Crocodylidae*

3.8.3.1. Euthecodon sp.. KNM-WT 71984 from LO4W is an unmistakable long, very slender rostrum of *Euthecodon*, a fish-eating crocodile first described from Egypt as *E. nitriae* Fourtau, 1920, but best-known from the Turkana Basin, where it is described as *E. brumpti* (Joleaud, 1920). A few other diagnostic specimens are present at LO4 and LO5. Pending revision of the genus, species identification would be premature, as the two species names might be synonymous (Brochu, 2020).

3.8.3.2. Crocodylus thorbjarnarsoni Brochu and Storrs, 2012. A symphyseal part of mandible KNM-WT 71973 from W of LO4W and a very large tooth KNM-WT 71881 from LO6 belong to this genus. Brochu and Storrs (2012) referred the partial skull KNM-WT 38977 from LO5 to the giant form *C. thorbjarnarsoni*, and it is likely that these two additional specimens are of the same species. KNM-WT 38981 from LO5 (Fig. 4I) is a snout; no obvious feature distinguishes it from the modern *C. niloticus*, but Brochu and Storrs (2012) and Brochu (2020) observed that Plio-Pleistocene East African specimens referred to *C. niloticus* belong in fact to *C. thorbjarnarsoni*, and we prefer to include all specimens into this latter species.

3.8.3.3. Mecistops sp.. KNM-WT 77311 from LO5 are pieces of a cranium with parts of the attached mandible, indicating a rather narrow snout, more like *M. cataphractus* than like *Crocodylus*; the nasals tips remain far from the external nares. KNM-WT 77311 resemble the *Mecistops* skull KNM-ER 929, but is slightly larger (snout width at Pmx/Mx constriction 79 vs. 69.5 mm). Another difference is that, in contrast to other East African *Mecistops* (Koobi Fora, Kanapoi, Omo; photos kindly provided by C. Brochu; Brochu, 2020), the dorsal premaxillary/maxillary suture does not run obliquely, but its middle part has a straight, transverse course (Fig. 4H). We have not attempted detailed comparisons of this specimen, however.

3.9. *Aves (preliminary identifications, based on photos, by A. Louchart)*

3.9.1. *cf. Mycteria sp.*

Two tarsometatarsus, from LO3 and LO10, probably belong to *Mycteria*, size of *M. ibis*, the yellow-billed stork, which lives and feeds in shallow waters.

3.9.2. *Struthio cf. molybdophanes*

The ostrich is represented by eggshells only, from LO5 and LO4W.

3.9.3. *Numididae indet*

A distal humerus from LO5 belongs to a Guinea fowl, *Numida* sp. or *Guttera* sp.

3.9.4. *Anas sp.*

A distal femur from LO4W is slightly larger than that of the mallard duck.

3.9.5. *Anhinga melanogaster Pennant, 1769*

Three bones from LO1, LO9, and LO10, can be referred to a ‘darter’, or snake-bird.

3.9.6. *Leptoptilos falconeri Milne-Edwards, 1868*

A single phalanx from LO1 belongs to an extinct species of marabou stork, one of the largest flying birds that ever existed.

3.10. *Pisces*

3.10.1. *Lates niloticus L*

Fish remains from LO4, LO5, and probably LO8 were identified by K. Stewart (*in litt.*) as *Lates niloticus*, the Nile perch; skull length indicates specimens almost 2 m long. *Lates* has been reported from a number of eastern and northeastern African sites, from the late Miocene onwards (Stewart, 2001).

3.10.2. *Siluriform ? indet*

KNM-WT 39232 from LO8 is a cranial roof that does not seem to match any known species, but is probably of a catfish (K. Stewart, pers. comm., 2024).

In addition, the Lomekwi collection contains a puzzling fossil, a mandible with two rather worn and imperfectly preserved teeth, KNM-WT 39223 (Fig. 2T); it is supposed to come from LO5, but no coordinates are available. It somewhat resembles lorisoids, but we think a much more likely identification is with one of the new Hyracoidea recently described by Vitek et al. (2024) from the Oligocene of Topernawi. As

Table 5
Measurements of *Golunda* teeth.

	m1		m2		m3	
	L	W	L	W	L	W
WT-59707[a]	2.7	1.75	2.0	1.9	1.8	1.7
Hadar (Sabatier, 1982)	2.44–2.9	1.69–2.04	1.95–2.34	1.89–2.22	1.65–1.96	1.65–2.00
Omo (Wesselman, 1984)	2.41	1.67	2.01	1.77–1.84	–	1.7

[a] Measurements of WT-59707 are approximate.

noticed by Vitek (*comm. pers.*), the teeth (p3 and p4 if it is a hyracoid) have a weaker or absent paraconid, but we think the similarities outweigh the differences. The Topernawi hyracoids were collected very close to some of the LO5 fossils (westernmost specimens of Fig. 1, which are definitely not of Oligocene age) and it is likely that KNM-WT 39223 also comes from this area where Oligocene and Pliocene sediments must be in close contact. Therefore, we do not include it in the Lomekwi fauna list.

4. Discussion

4.1. Faunal diversity, taxonomic and evolutionary faunal changes

The total number of specimens identified by us in the eight main localities amounts to 1866, distributed as shown in Table 1. Localities dated to c. 3.5 to 3.3 Ma are the best sampled, and have, accordingly, the longest fauna lists (Table 6). While absence of evidence should be treated with caution, particularly in less well-sampled localities, some tentative shifts in faunal composition through time can nonetheless be identified.

Among Primates, *Theropithecus* is the most abundant taxon, with most specimens likely belonging to the species *T. brumpti*. This species is also common in the Lokochot and Tulu Bor members of the Koobi Fora Formation and Shungura Members B-D. The presence of *Theropithecus* in the Lomekwi hominin localities reinforces a long-standing faunal association between these monkeys and early hominins, beginning with the appearance of both *Theropithecus* and *Australopithecus* at Kanapoi more than 4 Ma (Bobe et al., 2020). The apparent disappearance of *Theropithecus* at LO8 is probably only due to the very low sample size of fossils from this collecting area.

Localities LO4 and LO5 each have 12 species of Carnivora, which can be regarded as a high number for assemblages consisting of between 500 and 600 specimens. As elsewhere in Africa, the carnivore fauna is dominated by hyenids, and as many as three species of *Crocuta* may have coexisted at LO5 and LO9, of which only the medium-size *C. ultra* (probable ancestor the modern spotted hyena) survived in the younger sites. The diversity of felids is also remarkable, with up to five species of various sizes at LO5. In addition to the large felids, *Dinofelis*, *Megantereon*, and *Panthera*, the Lomekwi localities have a noteworthy representation of mesocarnivores including cf. *Lynx*, *Felis*, the civet-like *'Viverra'*, *Herpestes*, *Mungos*, the giant otter *Enhydriodon*, the fish-eating *Lutra*, *Nyctereutes* (with no living representatives in Africa), and *Lupulella*. This diversity is not unusual in healthy African ecosystems but emphasizes that hominins lived in environments with a thriving fauna of medium-size and large carnivores.

There are few recognized lineages among East African bovids, but the Lomekwi specimens included in the *Kobus oricornus/Menelikia leakeyi* group could document such a local change, over a longer period than at Omo or Hadar. The material is unfortunately too incomplete to confirm this evolution. Another fairly certain transition is the replacement of *Aepyceros shungurae* by *A. melampus* at c. 3 Ma, but most other bovids also lack a sufficient number of diagnostic elements to define their chronological range and evolution.

Several species of mammalian megaherbivores occurred at Lomekwi: the two genera of rhinocerotids *Diceros* and *Ceratotherium*, the proboscideans *Deinotherium*, *Elephas*, and perhaps *Loxodonta*, the giraffids *Sivatherium* and *Giraffa*, two species of hippopotamids, and the rare camel *Camelus*. Thus, all genera of very large mammals that could potentially be present are documented, at least in the richest sites. At the small end of the mammalian spectrum in body mass, Lomekwi also has a representation of hares, i.e., *Serengetilagus*, and rodents, e.g., *Hystrix*, *Gerbilliscus*, and *Golunda*.

Vertebrates other than mammals are also represented in the Lomekwi sample, including the gigantic crocodile *Crocodylus thorbjarnarsoni*, the slender-snouted *Mecistops*, and the fish-eating crocodile *Euthecodon*. Turtles, squamates (*Varanus*, *Python*), birds, and fish enrich our view of biodiversity in the Pliocene Turkana region.

Paleoenvironmental reconstructions of the Omo-Turkana Basin during the late Pliocene and earliest Pleistocene emphasize the heterogeneous and dynamic nature of the vegetation, with extensive woodlands but also forests and wooded grasslands (Negash et al., 2024; Villaseñor et al., 2023). The Lomekwi hominin localities provide a view of rich biodiversity, first along the shores of a fluctuating freshwater late (the Lokochot lake c.3.5 Ma) and then the Tulu Bor floodplains that dominated the basin from 3.4 to 2.4 Ma. The vertebrate fauna included formidable predators like *Panthera*, *Dinofelis*, and *Megantereon* on land, with the gigantic crocodile *Crocodylus thorbjarnarsoni* dominating the lakes and rivers. A high diversity of megaherbivores, mesocarnivores, and bovids and suids would have established the complex ecological systems to which hominins seem to have been well adapted.

As in most East African localities of this age, bovids form the bulk of the large mammal assemblages, with proportions varying between about 47 and 64 % in the richest sites (Suppl. data1, Fig. N). The Pliocene sites are dominated by *Aepyceros* and alcelaphins, antilopins being also well-represented; these tribes are especially common at LO9, testifying to open country. Both tribes are decidedly more common than at Omo, where the Shungura Member B assemblage is dominated by *Aepyceros*, Tragelaphini, and Bovini (two tribes that are rare at Lomekwi). In the Pleistocene sites, the reduncins become dominant, suggesting an environment that becomes less dry, but not woodier, near the Plio-Pleistocene boundary. This does not imply a regional climate change, but may result merely from the proximity of these Pleistocene sites (LO1, LO3 and LO8) to the center of the floodplain or early Pleistocene lakes. The variations in relative abundance of the Suidae are remarkably slight, and they are always much less common than bovids, in contrast to the Omo Shungura Fm, where they outnumber them before 3 Ma, although their abundance sharply decreases in the Late Pliocene (Bobe and Behrensmeyer, 2004).

Except at LO6 and LO1 that seem to sample peculiar and poor assemblages, cercopithecids are not rare, but consist mostly of the terrestrial *Theropithecus*.

Thus, the main change in the large mammal assemblage is the increase in number of water-dependent reduncins but, as mentioned above, this does not imply a regional climate change. On the whole, the faunal composition is rather stable, and the area was perhaps less well-vegetated than assumed previously (Leakey et al., 2001; Harmand et al., 2015).

4.2. Biochronology

The biostratigraphic frame of the Lomekwi area is already well-known, and the vertebrate fauna obviously does not demand major changes in the dating of the sites, but it does suggest some possible adjustments (Fig. 9) and, perhaps more importantly, it cautions against the indiscriminate use of evolutionary changes in some commonly used taxa for high resolution biochronology.

The *Theropithecus* m3s from LO4 and LO5 are large. Because they probably belong to *T. brumpti* rather than to *T oswaldi*, it is not surprising that they are distinctly larger than those from the Woranso Mille sites, from the Sidi Hakoma Mb of the Hadar Formation, and even from the Denen Dora Mb, but they also average larger than those from the Lokochot and Tulu Bor Members at Koobi Fora, assigned to *T. brumpti* (Jablonski et al., 2008); this relatively large size would rather support an age closer to 3.2 Ma than to 3.4 Ma for LO4 and LO5.

Proboscidean remains are incomplete, but most of them fit in the *Elephas recki* complex, although KNM-WT 73002 and KNM-WT 71983, discussed above, seem to be out of place, supporting recent suggestions (e.g. Larramendi et al., 2020) that the evolution of this group was not as simple as previously thought.

In the Lomekwi area, *Equus* is first attested at LO8 (2.3–2.1 Ma), and the genus has not been identified at LO1 and LO3, suggesting that these sites may be older than 2.33 Ma, the date of the appearance of the genus

Table 6
Distribution of the various taxa in the Lomekwi sites. Taxa identified by Harris et al. (1988) but not seen by us are indicated between brackets (x).

	LO6	LO4	LO5	LO9	LO10	LO1	LO3	LO8
Approximate age (Ma)	3.6	3.4	3.3	3	2.9	2.52	2.4	2.2
Rhinocolobus sp./*Paracolobus* sp.	x	x	x			x		
Cercopithecoides sp.?		x						
Parapapio sp.		x	x	x				x
Theropithecus brumpti			x					
Theropithecus cf. *oswaldi*	x	x	x	x	x	x	x	
Nyctereutes cf. *barryi*		x	x					
Lupulella sp.		x	x					
Enhydriodon sp.		x	?			x		
Lutra s.l. nov. sp.?		x						
Mungos dietrichi		x		(x)		x		
Herpestes cf. *palaeoserengetensis*			x					
Civettictis leakeyi		?			?	x		
Crocuta eturono	x	x	x	x	?			
Crocuta venustula		x	x	?				
Crocuta ultra			?	x	x	x		?
Hyaena sp. ?				x		(x)	x	
Felis cf. *silvestris*			x					
Cf. *Lynx* sp.		?	?					
Panthera sp. nov.?		x	?		?			
Dinofelis sp.	?	?	x	x	x			
Homotherium sp.		x	x	?				
Deinotherium bozasi	x	x	x	x			(x)	
Elephas recki		x	x	x	x	x	x	x
Loxodonta cf. *exoptata*		x						
Diceros bicornis	sp.	sp.	sp.	sp.	(x)	x	sp.	
Ceratotherium cf. *simum*		x	x		(x)		x	
‘*Hipparion*’ cf. *hasumense*	x	x	x	x	x	x	x	x
Equus sp.								x
Camelus grattardi			?				x	
‘*Hippopotamus*’ *protamphibius*	x	x	x	x	x	x	x	x
Hippopotamus sp. (large)			x					
Nyanzachoerus kanamensis	x	x	?					
Notochoerus jaegeri		x	x					
Notochoerus euilus	x	x	x	x	x	x	x	
Kolpochoerus afarensis	x	x	x	sp.	sp.	sp.		
Kolpochoerus limnetes							x	x
Metridiochoerus cf. *shawi*		x	x	x	x		x	
Metridiochoerus cf. *andrewsi*								x
Sivatherium maurusium			x	x			x	
Giraffa pygmaea			x	x				
Giraffa jumae ?		x	x	x	x	x	x	x
Giraffa stillei/gracilis	x	x	x		x	x	x	x
Tragelaphus cf. *kyaloi*	?	?	?					
Tragelaphus nakuae/rastafari		x	x				x	(x)
Tragelaphus small			x					
Tragelaphini indet.				x	x	x		x
Bovini indet.	x	x	x	x	x	?	x	x
Kobus sigmoidalis		x		x	?	?		x
Kobus oricornus/Menelikia		x	x			x	x	x
Oryx sp.		x	?	?	?		(x)	
Parmularius cf. *parvicornis*		x	x	x				
Parmularius sp.			x			x		
Damaliscus cf. *lunatus*		x					x	
Damaliscus aff. *lunatus*			x					
Damaliscus sp. A						x		
Damaliscus cf. *niro*					x			
Damalborea sp.?	x	x			x			x
‘Ovibovini’ indet.							x	
Gazella cf. *harmonae*	x	x	x		x			x
Gazella sp.				x		x		x
Antidorcas sp.				cf.			(x)	
Aepyceros shungurae	sp.	x	x	sp.	(x)	(sp.)	(x)	
Aepyceros cf. *melampus*					x		x	(sp.)
Cf. *Raphicerus* sp.		x	x		x			
Cephalophini ? indet.			x					
Serengetilagus praecapensis		x	x	?				
Cf. *Trischizolagus* sp.			x					
Hystrix cf. *makapanensis*		x	x	x	x			
Cf. *Gerbilliscus* sp.		x						
Golunda cf. *gurai*			x					
Muridae indet.								x
Chelonia indet.		x						
Euthecodon sp.		x	x					

(*continued on next page*)

Table 6 (*continued*)

	LO6	LO4	LO5	LO9	LO10	LO1	LO3	LO8
Python sp.	x	x	x	x	x			
Varanus sp.		x	x					
Euthecodon sp.		x	x					
Crocodylus thorbjarnarsoni	x	x	x	?				
Mecistops sp.			x					
Mycteria sp.					x		x	
Struthio cf. *molybdophanes*		x	x					
Numididae indet.			x					
Anas sp.		x						
Anhinga sp.				x	x	x		
Leptoptilos falconeri						x		
Lates niloticus		x	x					x
Siluriform ?								x
Number of taxa	**19**	**54**	**60**	**33**	**30**	**25**	**25**	**21**

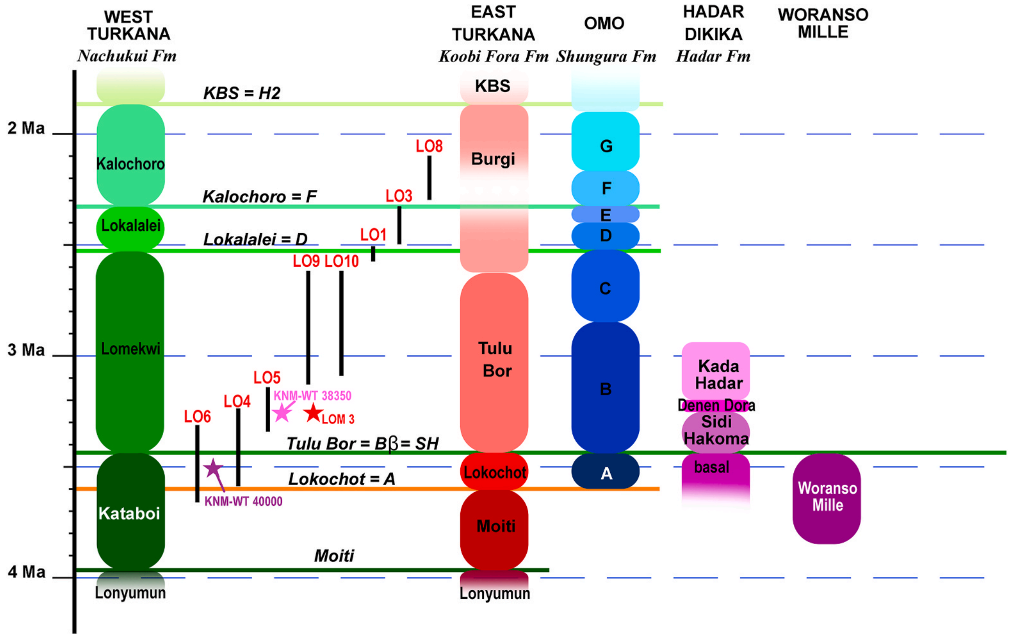

Fig. 9. Chronology of the Lomekwi sites compared to some other East African localities, with the main formations, their members, and the main tuffs; positions of the holotype and paratype of *Kenyanthropus platyops*, and of the archaeological site of Lomekwi 3 are also indicated.

in East Africa (Geraads et al., 2004b). The *Ceratotherium* from LO4 and LO5 seems to be a forerunner of the modern *C. simum*, and looks more derived than the Hadar form.

The most common hippo is already tetraprotodont at LO4 and LO5, as in Omo locality L1, dated to c. 3 Ma, and LO5 also has a hippo of large size; thus, both taxa suggest an age not much greater than 3 Ma.

Among Suidae, the most noticeable event is the disappearance of *Notochoerus jaegeri* and *Nyanzachoerus kanamensis* after LO5; these two taxa that are best known from Kanapoi (Geraads and Bobe, 2020a). *Nyanzachoerus kanamensis* is also known from Koobi Fora, up to the Tulu Bor Mb, and from Member A of the Shungura Fm, but *N. jaegeri* is unknown in these sites; its latest previously documented occurrence in the Turkana Basin is Ekora (Harris and White, 1979), supporting an early age for LO4 and LO5. The *Kolpochoerus* from the early Lomekwi sites are distinctly smaller than those from Omo B, and compare better with those of *K. afarensis* from the Hadar Fm, but most of them are even smaller, especially those from LO6, and should perhaps be called *K. millensis*, defined at Woranso-Mille in sites dating to between 3.8 and 3.6 Ma, thus pushing the early Lomekwi sites towards this age. By contrast, *Notochoerus* third molars from LO4 and LO5, especially upper ones, average slightly longer and narrower than those from Hadar, although not than those from the Tulu Bor Member.

The Bovidae also testify to diachronic changes. *Kobus sigmoidalis*, present at LO4, is not known before Member C at Omo, although it is already present in the Moiti Member of Koobi Fora. In the *K. oricornus*/*Menelikia* group, *K. oricornus* seems to survive until LO3, whereas it is restricted to Member B at Omo, and *M. leakeyi* also survives later than at Omo. Modern-looking representatives of *Damaliscus* are present at LO4 and LO5, and the *Tragelaphus* from LO5 is large for its age.

Thus, although the evolutionary stages of large mammals are generally in good agreement with the dating of the localities, there are also several instances of discrepancies between them. In a few cases, fossils may have been transported or re-deposited, but in most instances, especially among suids and bovids, there is strong evidence, either of diachronic changes along the Rift, or of differentiation of local populations, if not species, within narrow groups. The best candidates are perhaps the complexes of *Elephas recki*, early *Kolpochoerus* and *Notochoerus*, and *Kobus oricornus/Menelikia*. Closely related living species of mammals may be virtually indistinguishable on the basis of their skeleton and would likely be confused if found as fossils; this may well have happened in the past, and only finer analyses might be able to tell them apart.

CRediT authorship contribution statement

Denis Geraads: Writing – original draft, Methodology,

Investigation, Formal analysis, Data curation, Conceptualization. **René Bobe:** Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Thomas A. Püschel:** Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Carol V. Ward:** Writing – original draft, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **J. Michael Plavcan:** Writing – original draft, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Fredrick Kyalo Manthi:** Writing – original draft, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Denis GERAADS reports travel was provided by National Science Foundation. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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