



## The large carnivores from 'Ubeidiya (early Pleistocene, Israel): biochronological and biogeographical implications

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### ABSTRACT

The archaeological site of 'Ubeidiya provides a unique, rich faunal assemblage, as well as evidence for the presence of early hominins in the Levant. Paleontological analysis of the faunal community is pertinent to understanding the biochronology and the timing of hominin dispersal events from Africa to Eurasia. This study presents the large carnivores from the recent seasons of excavations (1989–1999) and previously published material. Based on biochronological correlations of the carnivore guild and paleomagnetism, the age of the site is 1.5–1.2 Ma. This date is 100–200,000 years earlier than previous estimates. Of specific importance is the presence of the African origin saber tooth *Megantereon* cf. *M. whitei* and the Eurasian origin canids *Canis moschbachensis* and *Lycaon lycaonoides*.

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### Introduction

During the early Pleistocene, hominins dispersed from Africa into Eurasia by various routes from different regions (Schick and Dong, 1993; Gabunia and Vekua, 1995; Larick and Ciochon, 1996; Bar-Yosef, 1998; Arribas and Palmqvist, 1999; Bar-Yosef and Belfer-Cohen, 2001; Antón and Swisher, 2004; Langbroek, 2004; Martínez-Navarro, 2004). The large biogeographic range, from the Iberian Peninsula to China, covered by hominins in less than 200,000 years after their initial dispersal ca. 1.8–1.9 Ma (Bar-Yosef and Belfer-Cohen, 2001) attests to their ecologically successful adaptations.

Paleoanthropological sites in Eurasia that predate 1.0 Ma are rare and include Dmanisi (Georgia), dated to ca. 1.7–1.9 Ma (Dzarpardize et al., 1992; Dean and Delson, 1995; Gabunia and Vekua, 1995; Lordkipanidze et al., 2005, 2007); Pirro Nord in Italy, dated to 1.3–1.6 Ma (Arzarello et al., 2006); Fuente Nueva-3 and Barranco León (Orce, Spain), dated to ca. 1.3 Ma (Martínez-Navarro et al., 1997; Oms et al., 2000; Toro et al., 2003; Palmqvist et al., 2005); Sima del Elefante, Atapuerca (Spain), dated to 1.2 Ma (Carbonell et al., 2008); Modjokerto and Sangiran (Java; Swisher et al., 1994; Huffman, 2001; Larick et al., 2001) dated as early as ca. 1.8–1.6 Ma; sites in the Nihewan and Yuanmou basins in China dated to ca. 1.71–1.66 Ma (Zhu et al., 2001, 2003, 2004); and 'Ubeidiya in Israel which has been dated ca. 1.4 Ma (Tchernov, 1987; Fig. 1).

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The site of 'Ubeidiya, situated in the central Jordan Valley is one of the earliest sites outside of Africa to attest to this early dispersal event. The site yielded a wealth of lithic (Bar-Yosef and Goren-Inbar, 1993) and faunal material (Haas, 1966; Tchernov, 1986) and a few human remains (Belmaker et al., 2002). The location of the site, in the Levantine Corridor, has made it a valuable site for understanding early hominin dispersal routes and the role of hominins within the carnivore guild (Bar-Yosef, 1994). Dating of the site has been based on long-range biochronological considerations and indicates an age of 1.4–1.0 Ma (Tchernov, 1987).

Since the detailed publication of the fauna (Haas, 1966; Tchernov, 1986), and specifically the carnivores (Balleisio, 1986), several recent seasons of excavations (1989–1994 and 1997–1999) have resulted in a wealth of new fossil material. The aim of this paper is to revise the fossil inventory and systematics of the 'Ubeidiya carnivore assemblage through the 1989–1999 excavation seasons, and to reevaluate the biochronology of the site and the structure of the carnivore guild in light of the dispersal of African taxa into Eurasia during the early Pleistocene.

### The site and previous chronological estimations

The site of 'Ubeidiya lies about 3 km south of the Sea of Galilee, on the flanks of the western escarpment of the Jordan Rift (Fig. 1). The exposure of the tilted layers at 'Ubeidiya was the subject of systematic excavations from 1960 through 1974 (Stekelis, 1966; Stekelis et al., 1969; Bar-Yosef and Goren-Inbar, 1993), and later in 1989–1994 and 1997–1999 (Shea and Bar-Yosef, 1998).

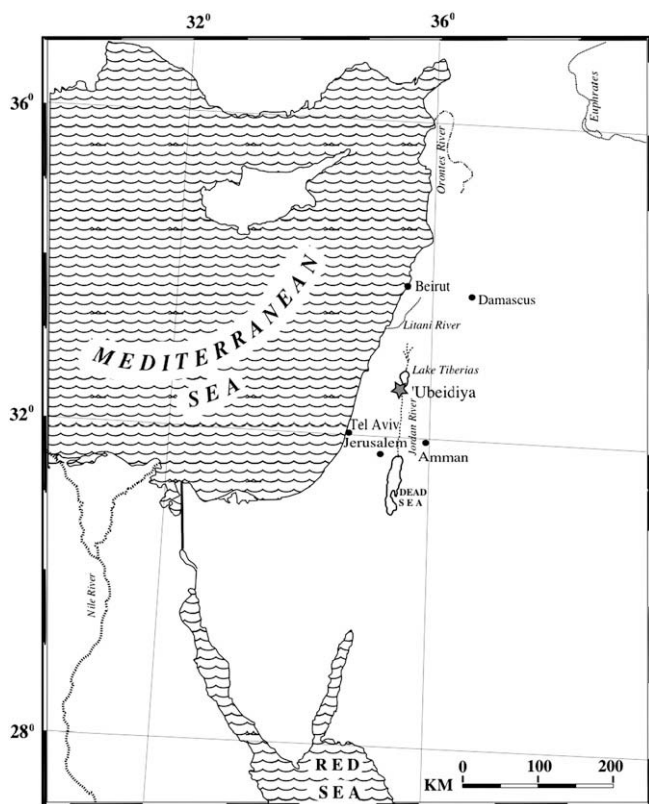


Figure 1. Location of the site of 'Ubeidiya.

The stratigraphic sequence has been divided into four members (from lower to upper): Li (Limnic Inferior), Fi (Fluvatile Inferior), Lu (Limnic Upper), and Fu (Fluvatile Upper), and suggested a general paleo-ecological reconstruction of the deposits (Picard and Baida, 1966a,b; Bar-Yosef and Tchernov, 1972). The changing lithology indicated the presence of a lake into which a river or a major wadi debouched, forming a delta (Mallol, 2006). This paleo-lake is now called lake 'Ubeidiya. The four members have been interpreted to represent the alternating regressions and transgressions of the lake (Mallol, 2006). The tool types of the lithic assemblages included bifaces and trihedrals, thus corresponding to the definition of the Early Acheulian (Bar-Yosef and Goren-Inbar, 1993; Shea and Bar-Yosef, 1998).

No radiometric dates are available for the 'Ubeidiya Formation itself. Therefore, estimated dates for the fossil bearing strata rely on the location of the formation within the Quaternary stratigraphy of the Jordan Valley, paleomagnetic analyses, and long ranging bio-chronological correlations. The lava flows of the Cover Basalt form the base of the sequence of the Jordan Valley and were K/Ar dated around the Sea of Galilee to 5–3.3 Ma (Mor, 1993; Heinmann and Braun, 2000). The 'Erq el Ahmar Formation, which overlies the Cover Basalt and underlies the 'Ubeidiya Formation, has been assigned to the Pliocene. Paleomagnetic studies have shown that the 'Erq el Ahmar Formation includes both normal and reverse polarities (Braun et al., 1991; Verosub and Tchernov, 1991) and the normal is correlated with the Olduvai Subchron dated from 1.96–1.78 Ma (Ron and Levi, 2001). Paleomagnetic studies of the 'Ubeidiya Formation itself have indicated reversed polarity and thus, it must antedate the Brunhes/Matuyama boundary (Opdyke et al., 1983; Braun et al., 1991; Verosub and Tchernov, 1991). 'Ubeidiya is directly overlain by the mainly alluvial-colluvial deposits known as the Naharayim Formation (Picard, 1943; Heinmann and Braun, 2000). The Yarmouk Basalt, which overlies 'Ubeidiya, has been

radiometrically dated to  $0.79 \pm 0.17$  Ma and serves as an upper boundary for the formation (Braun et al., 1991; Heinmann and Braun, 2000). Hence the 'Ubeidiya Formation is positioned securely within the Matuyama Chron (i.e., between c. 1.78–0.8 Ma). Tchernov (1987), based on long distance faunal correlations, estimated an age of 1.4–1.0 Ma for the 'Ubeidiya Formation.

## Methodology

An inventory of the specimens by species and strata, specifying fossils corresponding to the old and the new collections, as well as published and unpublished material, is given in Appendix 1. Morphometric measurements were taken with digital calipers and are recorded to the nearest 0.1 mm. Abbreviations are L = length, W = width, Ltrig = length trigonid, PTD = proximal transverse diameter, PAPD = proximal antero-posterior diameter, MTD = transverse diameter at the diaphysis, MAPD = antero-posterior diameter at the diaphysis, DTD = distal transverse diameter, and DAPD = distal antero-posterior diameter.

Faunal material was compared to the fossil material retrieved from the following sites: Venta Micena, Fuente Nueva-3, and Barranco León (Museum Prehistory and Paleontology, Orce, Spain), Cueva Victoria (Archaeological Museum, Cartagena, Spain), Atapuerca (Insitute of Human Paleoecology and Social Evolution, University of Tarragona, Spain), Le Vallonnet (Museum of Menton, France), Olivola, Upper Valdarno, and Pirro Nord (Museo di Paleontologia University of Florence, and Department of Earth Sciences, University of Rome "La Sapienza", Italy), Apollonia (Department of Earth Sciences, University of Thessalonika, Greece), Dmanisi and Ahkalkalaki (Georgian National Museum, Tbilisi, Georgia), Geshen Benot Ya'akov and Evron Quarry (Department of Ecology, Systematics, and Evolution, Hebrew University of Jerusalem, Israel), Pinjor and Tatrot Formation, India (Natural History Museum, London), Buia (National Museum of Eritrea), Hadar and Omo (National Museum of Ethiopia), Koobi Fora and West Turkana (Kenya), and Olduvai (Tanzania; National Museum of Kenya), Ain Brimba (Tunis), and Ain Boucherit and Ain Hanech (Algeria; National Museum of Natural History, Paris). Abbreviations for institutions and sites used in the text are: VM = Venta Micena; Ata = Atapuerca; UB = 'Ubeidiya; and IGF = Museo di Paleontologia, University of Florence. All faunal material from 'Ubeidiya is housed in the paleontological collection of the Department of Evolution, Systematics and Ecology at The Hebrew University of Jerusalem.

## Systematic paleontology

### Felidae

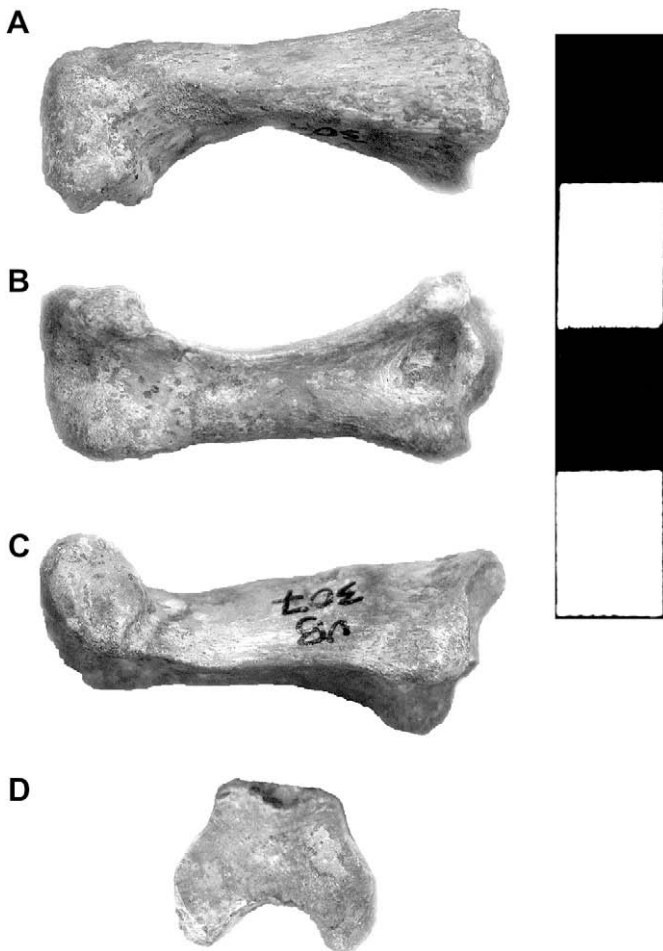
*Megantereon cf. M. whitei* Broom, 1937. Previous identifications as *Megantereon cf. M. megantereon* Croizert and Jobert, 1928 by Haas (1966) and as *Megantereon cf. M. cultridens* Croizert and Jobert, 1928 by Balleisio (1986) were based on an incomplete, upper right non-crenulated crown of a canine (UB 80) from stratum II 23. The measurements are width 8.0 mm and length 19.5 (Haas, 1966, their Pl. VI, Fig. 5).

A left lower canine (UB 14) from stratum II 24 may be assigned to *Megantereon* as well, although the mesial and distal faces of the

Table 1

Measurements of the middle phalanx UB 307 of *Megantereon cf. whitei* from 'Ubeidiya and the unpublished specimen of *M. whitei* VM90-C3-3A15-15 from Venta Micena (Spain).

	L	PTD	PAPD	MTD	MAPD	DTD	DAPD
UB-307	31.68	12.60	11.3	6.54	7.46	11.68	9.24
VM90-C3-3A15-15	33.27	12.87	10.2	7.56	8.1	12.54	9.03



**Figure 2.** UB-307, middle phalanx of *Megantereon* sp. cf. *M. whitei*: a) dorsal view; b) ventral view; c) lateral view; d) proximal view.

crown are badly preserved due to friction with the upper 3rd incisor and canine. The measurements are width 11.1 mm and length 9.9 mm.

A second phalanx UB 307 (Table 1; Fig. 2) has been identified as *Megantereon*. The anatomy is typical for a felid middle phalanx, but it is elongated compared to the morphology exhibited by the genus *Panthera*, especially extant *P. leo* or *P. pardus*. The articular surface of the proximal end is projected in the dorsal area and has two deep depressions for the articulation with the trochlea of the proximal phalanx. The diaphysis is horizontally curved, ventrally convex, has a triangular section, is antero-posteriorly compressed in the distal area, and has deep depressions in the proximal and distal regions of the ventral face. The trochlea, on the distal end is ventrally divided and laterally oriented. This specimen exhibits morphological and metrical similarities to one unpublished middle phalanx of *Megantereon whitei* (VM90-C3-3A15-15) from the site of Venta Micena, Spain (Table 1).

Unfortunately, the collection of 'Ubeidiya specimens attributed to *Megantereon* is very small. Thus, the determination of the specific species is difficult, especially in light of the absence of any diagnostic element. Moreover, the taxonomic status of the Plio-Pleistocene genus *Megantereon* is problematic. The origin of the genus *Megantereon* is controversial. Berta and Galiano (1983) proposed an early Pliocene North American origin for the genus. Turner (1987) suggested that both middle to late Pliocene and early Pleistocene specimens ascribed to this genus corresponded to a single highly plastic taxon, *Megantereon cultridens*, ranging throughout Eurasia

and Africa. The alternative view identifies two lineages, a Pliocene Eurasian lineage, *M. cultridens*, and a Pliocene-Pleistocene African lineage, *M. ekidoit*—*M. whitei*. The latter species dispersed into Eurasia from Africa during the Plio-Pleistocene transition at around 1.8 Ma replacing *M. cultridens* in the fossil record. The *M. ekidoit*—*M. whitei* lineage can be identified in Africa as early as the onset of the Pliocene. The species *M. ekidoit* was described from the South Turkwell hominid site (3.5 Ma) located in the Turkana Basin (Werdelin and Lewis, 2000, 2002). It has been suggested that this species is a primitive form of *M. whitei* (Palmqvist, 2002; Palmqvist et al., 2007).

The oldest Eurasian record of *M. whitei* is at the Georgian site of Dmanisi (Martínez-Navarro and Palmqvist, 1995), together with the earliest human evidence outside Africa (Gabunia and Vekua, 1995; Lordkipanidze et al., 2005, 2007). But *M. whitei* has also been identified in Venta Micena (Spain), Pirro Nord (Italy), and Apollonia-1 (Greece; Martínez-Navarro, 1991, 1992a,b; Martínez-Navarro and Palmqvist, 1995, 1996; Rook et al., 2004). Also, it is probably present in Untermassfeld, Germany, where it has been identified as *M. cultridens adroveri* (Hemmer, 2001). This subspecies, first described at Venta Micena (Pons-Moyà, 1987), is a junior synonym of *M. whitei* (Martínez-Navarro and Palmqvist, 1995; Palmqvist et al., 2007). A small sized *Megantereon* sp. is also found in the far southeast of Asia, in Java (Indonesia; Kurtén, 1962; De Vos and Aziz, 1987). The principal differences between *M. whitei* and *M. cultridens* are the proportional reduction of the splanchnocranium, with a shorter premolar series and longer upper canine in the African species. From an ecomorphological perspective, this would suggest that *M. whitei* is a more specialized hyper-carnivore than *M. cultridens* (Martínez-Navarro and Palmqvist, 1995, 1996; Palmqvist et al., 2007).

Although precise identification of the 'Ubeidiya specimens is not possible at this time, the small size of the specimens and the morphological similarities between the second phalanx to that of Venta Micena, suggest a tentative identification to the species described by Broom (1937), *Megantereon whitei*. Moreover, no record of *M. cultridens* has been found in any early Pleistocene site of western Asia and Europe (Martínez-Navarro and Palmqvist, 1995, 1996; Palmqvist et al., 2007).

*Panthera* cf. *P. gombaszoegensis* Kretzoi, 1938. Balleisio (1986) identified two large felid specimens as *Panthera gombaszoegensis*: a left 4<sup>th</sup> metacarpal (Balleisio, 1986, their Pl. V, Fig. 1) from stratum II-36 (UB 167) and a left proximal phalanx (UB 28) from stratum II-23. The 4<sup>th</sup> metacarpal from 'Ubeidiya (UB 167) has the two proximal articular surfaces for the 3<sup>rd</sup> metacarpal divided by a shallow sulcus, as appears in the extant species of the genus *Panthera* (Balleisio, 1986). Morphologically, this specimen is distinct from *Megantereon cultridens* from the late Pliocene site of Senèze, France, which has a deep sulcus. Moreover, the maximum length of UB 167 is 97.1 mm, which is larger than the Senèze specimen that is 83 mm long (Balleisio, 1986). We compared the specimen UB 167 with the unpublished left 4<sup>th</sup> metacarpal VM90-C3-3A15-15 of *M. whitei* from Venta Micena (corresponding to the same hand of the phalanx cited above). The *M. whitei* metacarpal has different proportions, the orientation of the two proximal surfaces is more oblique, and the sulcus dividing them is more marked. This suggests that the 'Ubeidiya specimen should be assigned to the genus *Panthera* rather than *Megantereon*.

The origin and dispersal of the different species of the genus *Panthera* remains unclear (Hemmer, 2000). The genus *Panthera* originated in Africa, and is known from the Tanzanian deposits of Laetoli dated to 3.5 Ma (Barry, 1987). The specimens from Laetoli show mixed characteristics of lion, leopard, and tiger that attest to their ancestral phylogenetic position. During the early Pleistocene,

two large feline species are known from Africa and Europe, and one of these may be the one present at 'Ubeidiya. The first is the fossil jaguar *Panthera gombaszoegensis*, which is known from Europe as early as 2.0 Ma. It is found at Olivola, Italy (ca. 2.0 Ma; Del Campana, 1913); Tegelen, The Netherlands (ca. 1.8–2.0 Ma; Koenigswald, 1960; O'Regan and Turner, 2004); and Dmanisi, Georgia (ca. 1.8 Ma; Vekua, 1995, 2001), and persists until the early-middle Pleistocene transition of Atapuerca Gran Dolina, Spain (ca. 0.8 Ma; García García, 2003). The second, *Panthera leo*, has been identified by Petter (1973) in Africa at Olduvai Beds I and II.

Comparison of the postcranial morphometrics is difficult, especially since data for fossil lions are rare. Using comparative data for both fossil and modern lion populations, *Panthera leo* and *Panthera gombaszoegensis* differ in maximum length of their 4<sup>th</sup> metacarpal. The sample of nine fossil and modern specimens of *Panthera leo* suggests that the 4<sup>th</sup> metacarpal is longer ( $105.6 \pm 5.74$  mm) than a sample of five specimens of *Panthera gombaszoegensis* ( $89.34 \pm 10.92$  mm; student  $t$ -test =  $-3.1$ ,  $df = 5.36$ ,  $p$ -value  $< 0.025$ ).

The 'Ubeidiya specimen UB 167 (Table 2) does not differ significantly from either the *Panthera gombaszoegensis* population (single specimen  $t$ -test =  $0.649$ ,  $df = 4$ ,  $p$ -value =  $0.55$ ) or from *Panthera leo* populations (single specimen  $t$ -test =  $-1.405$ ,  $df = 8$ ,  $p$ -value =  $0.2$ ). These results do not allow conclusive taxonomic assignment, but the affinities of faunal assemblage which correspond to the early Pleistocene and the absence of lions in other Eurasian assemblages until the middle Pleistocene (the oldest record of *Panthera leo* in Eurasia is at the site of Isernia La Pineta in Italy at 0.6 Ma [Sala, 1990]), suggests that the most probable identification of this taxon is *Panthera* cf. *P. gombaszoegensis*.

*Lynx* sp. Ballesio (1986) identified the 'Ubeidiya specimens as *Lynx* sp., based on the anatomy of the canine crown and the absence of the metaconid in the lower carnassial, which is substituted by a developed cingulum in the base of the crown.

Ballesio (1986) compared the specimens from 'Ubeidiya to those of the late Pliocene European *Lynx issiodorensis* (from Perrier, Etouaires, and Sant-Vallier, in France and Upper Valdarno, in Italy), *Lynx* sp. from Yushé (China), the French middle Pleistocene *Lynx spelaea* (from L'Escale and Lunel-Viel), and *Lynx thomasi* from Morocco, suggesting that all fossil *Lynx* specimens are larger than those from 'Ubeidiya. We compared the 'Ubeidiya specimens to the measurements of *Lynx issiodorensis* ssp. ex aff. *spelaeus* from the early Pleistocene site of Untermassfeld, Germany (Hemmer, 2001), which are also larger than the 'Ubeidiya specimens. Ballesio (1986) suggested that these specimens were also similar in size to the extant *Caracal caracal*, present in Africa and the Indian Subcontinent, but notes that in the *caracal* as in the serval (*Leptailurus serval*), the grooves of the canines are less marked. The South African fossil serval *Leptailurus spelaeus* from Sterkfontein are similar in size to those of the extant species *Leptailurus serval*, and which is smaller than the form from 'Ubeidiya.

Anatomically, the specimens from 'Ubeidiya appear to represent a form of *Lynx*. This species seems different from its homologous of the European Villafranchian *Lynx issiodorensis*, although we cannot discard its possible relation to the extant Afro-Indian lineage of *Caracal caracal*. This hypothesis may be further supported by the taxonomic affiliation of *Lynx issiodorensis*. Recently, Morales et al. (2003) reclassified all the European Pliocene forms previously determined as *Lynx issiodorensis* to *Caracal issiodorensis* based on several dental and postcranial anatomical characteristics. The most parsimonious explanation is that this late Pliocene form is the ancestor of both *Caracal* and *Lynx*.

*Felis* sp. The fossil record of small felids is very scarce. Only one distal end of right humerus from the stratum II-36 was attributed to *Felis* sp. by Ballesio (1986) and no new material has been found.

The small cats are known from the early Pliocene (i.e., *Felis* aff. *silvestris* from the site of Layna, Spain; Morales et al., 2003), but the record is very scarce in the early Pleistocene assemblages. The species *Felis lunensis*, from the latest late Pliocene Italian site of Olivola, is close to *Felis silvestris* (Ficcarelli and Torre, 1965; Kurtén, 1965), as is the species from Poggio Rosso in the Upper Valdarno cited as *Felis silvestris lunensis* (Mazza et al., 2004). The oldest clear record ascribed to *Felis silvestris* is at the site of Vallonnet, France (Moullé et al., 2005) and at the Spanish karstic site of Cueva Victoria, unpublished material reveals the presence of a small felid with similar anatomy and size to *Felis silvestris*.

#### Hyaenidae

*Crocota crocota* Erxleben, 1777. No new material of *Crocota crocota* has been found. All the published hyaenid fossil material from 'Ubeidiya was classified as *Crocota crocota* by Ballesio (1986). The metric data (Ballesio, 1986) and the anatomy of the dentition match that of the extant African hyena of Ethiopian origin, *Crocota crocota*. The premolars are robust, especially the P3's (upper and lower), but less so than in the latest Pliocene and early Pleistocene Eurasian well-known large, super carrion-eater hyena *Pachycrocota brevirostris*. The most relevant anatomical characteristic of the *Crocota* dentition is the trigonid of the lower carnassial (M<sub>1</sub>), it is proportionally long and has no metaconid.

The size of the 'Ubeidiya specimen is smaller than in *Pachycrocota brevirostris* (Howell and Petter, 1980; Julià and De Villalta, 1984; Martínez-Navarro, 1992a) from all sites of Eurasia to which it has been compared (Shansi, Nihowan, Choukoutien-1, Siwaliks, Sangiran, Upper Valdarno, Sainzelles, Süßenborn, Stranska Skala, Gombaszog, Apollonia; Incarcial, Cueva Victoria, and Venta Micena). The 'Ubeidiya specimen is similar to the extant and fossil African *Crocota crocota* from the late Pliocene site of Omo and the early Pleistocene site of Olduvai (Ballesio, 1986), but smaller than the early Pleistocene North African site of Ain Hanech, Algeria (Arambourg, 1979) and the middle Pleistocene European

**Table 2**

Measurements of the Mc- IV UB-167 and other specimens of *Panthera gombaszoegensis* and *P. anthera leo*.

Species	Site	Length	PTD	PAPD	MTD	MAPD	DTD	DAPD	Ref.
UB 167	Ubeidiya	97.1	17.9	21.2	12.1	11.9	18.1	18.6	This study
<i>P. gom</i>	Dmanisi DM 2002	106.6	13.1	20	11	11.7	16.6	18.1	Vekua, 2001
<i>P. leo</i>	TD - 8 Ata94 t.29	100	19.6		14.2		18.8		García García, 2003
<i>P. gom</i>	Olivola IGF 4347	78.7	16		11.6		14.7		García García, 2003
<i>P. leo</i>	(Kenya) ♀ 12319	102.6	16.7		12		18.2		García García, 2003
<i>P. leo</i>	(Kenya) ♀	98	16.8		12.1		17.2		García García, 2003
<i>P. leo</i>	$n = 18$	104.8 (90.4–113.5)							
<i>P. pardus</i>	$n = 16$	66.3 (58–80)							
<i>P. leo spelaea</i>	Lezetxiki, Spain	125.8							García García, 2003

sites of Mosbach and Petralona (Ballesio, 1986). The late Pleistocene European *Crocota spelaea* is the largest form of the genus.

'Ubeidiya is the only early Pleistocene site of Eurasia, with late Villafranchian fauna, older than 0.9–1.0 Ma where *Crocota crocuta* is clearly recorded. A reference to this species is made at the Pabbi Hills, in the Pinjor Formation of the Upper Siwaliks, northern Pakistan, where it is published based on two mandibular and one maxillary fragments (from locality 73) and a P4 (from locality 68) dated 1.2–1.4 Ma (Turner, 2004; Dennell et al., 2006); however, all the teeth from these sites ascribed to this species are from older individuals with heavily worn crowns that have no well preserved cuspids. Curiously, they are found in an assemblage with well-represented and anatomically diagnostic material of *Pachycrocota brevirostris*. In all the other sites of this continent, from the Iberian Peninsula to China and Indonesia, the large recorded hyenid is *Pachycrocota brevirostris*. Also, although the presence of *Crocota* was described at the early Pleistocene site of Akhalkalaki, Georgia (Vekua, 1986), personal observation by one of us (B.M.N.) concludes that these specimens may be identified as *Pachycrocota brevirostris*.

The oldest unequivocal record of *Crocota crocuta* in Western Europe is at the sites of Gran Dolina of Atapuerca (TD 4–5), Spain, in the early-middle Pleistocene transition around 0.8 Ma, where it appears together with the last record of *Panthera gombaszoegensis* on the continent (García García, 2003), and Ponte Galeria (Italy) also around 0.7–0.8 Ma (Sardella, 2004). In younger deposits, *Crocota crocuta* dominates the Eurasian carnivore assemblages.

### Canidae

This is the best-preserved and represented family of the Order Carnivora in the 'Ubeidiya assemblage. Most of the fossil material classified by Ballesio (1986) was ascribed to the late Villafranchian middle size species from the Upper Valdarno *Canis arnensis* and a few specimens were ascribed to the large size species *Canis* sp. (size *C. falconeri*).

*Canis mosbachensis* Soergel, 1925. Previous analysis identified the common canid to *Canis arnensis* Del Campana, 1913 (Ballesio, 1986). Although the measurements of the specimens from 'Ubeidiya (Tables 3 and 4) are within the range of variability of *Canis arnensis*, they are not morphologically similar. They have been compared to the *Canis arnensis* type specimens from the late Pliocene sites of the Italian Upper Valdarno and differ in their anatomy. They have been assigned to the species described by Soergel (1925) at the German site of Mosbach, *Canis mosbachensis*. The taxon is the same as the middle-large size canid taxon from the early Pleistocene European sites of Venta Micena, Spain and Pirro Nord, Italy, which was previously ascribed to *Canis arnensis* (Rook and Torre, 1996). The same species is also present at Vallonnet, France (Moullé, 1992); Untermassfeld, Germany (Sotnikova, 2001); and many other sites in Europe.

There are some anatomical differences between *Canis arnensis* from the late Pliocene sites of Italy and the small form represented in the Eurasian early-middle Pleistocene *Canis mosbachensis* (Martínez-Navarro, 2002): A) In *Canis arnensis*, the talonid of the lower carnassial ( $M_1$ ) presents two different and isolated cuspids (hypoconid and entoconid), but in *Canis mosbachensis* both cuspids are linked by a sinuous crest. B) In the labial face at the posterior boundary of the  $M_1$  trigonid, *Canis mosbachensis* shows a small crest that starts in the basal area and goes to the vertex of the protoconid, but in *Canis arnensis* this crest is not present. C) *Canis mosbachensis* shows two small tubercles between the metaconid and the entoconid in the lingual face of the  $M_1$ , and neither of them are present in *Canis arnensis*. D) In the  $M_2$ , *Canis arnensis* shows four very well isolated cuspids, two in the trigonid (protoconid and metaconid) and two in the talonid (hypoconid and entoconid) which is proportionally large; but the species *Canis mosbachensis* never presents the entoconid, and it is replaced by a cingular boundary, the talonid is shorter than in *Canis arnensis*, and the  $M_2$  shows a well-pronounced cingular antero-external border, which is not present in *Canis arnensis*. E) In the  $M^1$  of *Canis arnensis*, the protocone is linked with the

**Table 3**  
Measurements of the upper dentition of *Canis mosbachensis*.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
UB-76													12.1	4.5	24.8	10	13.3	15.6	7.7	11.6
UB-55	4.3	4.9																		
UB-46	4.6	5.3																		
UB-90	5.2	5.1																		
UB-38			4.2	4.7																
UB-152			4.2	4.7																
UB-105					5.3	9.4														
UB-40					5.3	8.4														
UB-110					6	6.1														
UB-93					7.2	9.9														
UB-41							8.1	5.1												
UB-103							7.5	5												
UB-34							7.7	4.5												
UB-17							8.5	5.4												
UB-62											4.6									
UB-102												4.3								
UB-127														3.6						
UB-52														5.2						
UB-128															18.8					
UB-44															21	10.3				
UB-146																				
UB-109																		13	16	
UB-53																				7.5
UB-36																				7.4
UB-150																				9.5
UB-186																				6.4
																				6.8
																				10
																				6.2
																				11.3

Measurement abbreviations: 1 = I<sup>1</sup>L; 2 = I<sup>1</sup>W; 3 = I<sup>2</sup>L; 4 = I<sup>2</sup>W; 5 = I<sup>3</sup>L; 6 = I<sup>3</sup>W; 7 = CL; 8 = CW; 9 = P<sup>1</sup>L; 10 = P<sup>1</sup>W; 11 = P<sup>2</sup>L; 12 = P<sup>2</sup>W; 13 = P<sup>3</sup>L; 14 = P<sup>3</sup>W; 15 = P<sup>4</sup>L; 16 = P<sup>4</sup>W; 17 = M<sup>1</sup>L; 18 = M<sup>1</sup>W; 19 = M<sup>2</sup>L; 20 = M<sup>2</sup>W.

**Table 4**Measurements of the lower dentition of *Canis mosbachensis*.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
UB-43	2.6	3.5																			
UB-85			3.5	5																	
UB-1255			4.7	4.8																	
UB-85			5.2	5.9																	
UB-87					4.7	4.7															
UB-270					5.2	5.4															
UB-50							7.7	5.2													
UB-47							7.3	4.9													
UB-94							8.2	5.2													
UB-75							8.3	6.5													
UB-98									69.5												
UB-66												4									
UB-37										4.2											
UB-45												5.6									
UB-98											9.6	4.1									
UB-305											11	4.7		5.4							
UB-48											11.4	4.3									
UB-149											9.5	4.3									
UB-71														5.1							
UB-56														5.2							
UB-79											10.2	4.3	11.8	5.4							
UB-77																8.8					
UB-13															23.2	8.3	14.8				
UB-306																8	15.1				
UB-290													11.4	4.6		7.5	13.2				
UB-268													11.7	5.6	20	7.8	13.9				
UB-81																		8.6	7.5		
UB-54																		9.1	6.5		
UB-60																				5.3	4.6

Measurement abbreviations: 1 = I<sub>1</sub>L; 2 = I<sub>1</sub>W; 3 = I<sub>2</sub>L; 4 = I<sub>2</sub>W; 5 = I<sub>3</sub>L; 6 = I<sub>3</sub>W; 7 = CL; 8 = CW; 9 = P<sub>1</sub>-M<sub>3</sub>L; 10 = P<sub>2</sub>L; 11 = P<sub>3</sub>L; 12 = P<sub>3</sub>W; 13 = P<sub>4</sub>L; 14 = P<sub>4</sub>W; 15 = M<sub>1</sub>L; 16 = M<sub>1</sub>W; 17 = M<sub>1</sub> Ltrig; 18 = M<sub>2</sub>L; 19 = M<sub>2</sub>W; 20 = M<sub>3</sub>L; 21 = M<sub>3</sub>W.

parastyle and the metastyle by a well defined crest, and the paraconule and metaconule are well marked in it; the hypocone is externally well marked and it forms a small cingular external crest, which disappears in the anterior border of the paraconule and in the posterior border of the metaconule; in the external face, the cingulum is not pronounced; but the most important differences in this element between *Canis arnensis* and *Canis mosbachensis* are that in the first, the protocone and the metaconule are well marked and the hypocone is less prominent than in the second; this anatomy is directly related to the talonid morphology of the lower carnassial M<sub>1</sub>. The size of the postcranial elements identified to this canid from 'Ubeidiya all fall within the variability of a middle size dog.

Although *Canis mosbachensis* has been interpreted to be an evolved form of the late Pliocene *Canis etruscus* or an ancestor of the late middle and late Pleistocene extant *Canis lupus*, this species has no clear anatomical relationship with any of these species. The ethology of this species seems similar, by its dental structure and size, to that of the extant jackals, being omnivorous scavengers.

*Lycaon lycaonoides Kretzoi, 1938*. A big right upper canine of large size canid from stratum II 23 has been identified as *Canis* sp. (size *Canis falconeri*) by Ballesio (1986). Other dental specimens from the same stratum have been found during this revision: a complete M<sub>2</sub>, a talonid of M<sub>1</sub>, and probably one I<sub>3</sub>, from stratum II 24. The large size of all the specimens, the presence in the lower carnassial talonid of a large and isolated hypoconid together with a small and isolated entoconid, and the second lower molar with three peaks, two in the trigonid (protoconid and metaconid) and one in the talonid (hypoconid), suggest identification to the lineage of the extant tetradactyl African wild painted hunting dogs, the genus *Lycaon*.

The systematics of these large hypercarnivorous canids, well known in the late Pliocene of Eurasia and the early Pleistocene of

Eurasia and Africa, are rather controversial with a lot of synonyms obscuring the real interpretation of the fossil forms (i.e., *Canis falconeri*, *Canis [Xenocyon] falconeri*, *Xenocyon lycaonoides*, *Xenocyon gigas*, *Xenocyon rosi*, *Xenocyon* sp., *Cuon sthelinii*, *Cuon rosi*, *Canis africanus*, *Canis atrox*, and *Canis antonii*; cf. Rook, 1994).

Martínez-Navarro and Rook (2003) revised the fossil record of this lineage in the Old World, from the late Pliocene until the present. The authors grouped all the forms in the genus *Lycaon*, based on anatomical, ethological, and ecological characteristics, proposing a gradual evolution from the late Pliocene species until the extant species, and simplifying the systematics in three chronospecies: *Lycaon falconeri*, for the late Pliocene forms of Eurasia, *Lycaon lycaonoides*, for the early Pleistocene and the beginning of the middle Pleistocene of Eurasia and Africa, and *Lycaon pictus*, for the middle-late Pleistocene and extant African form. The anatomy of the 'Ubeidiya specimens, the left M<sub>1</sub> talonid UB 89 and the left M<sub>2</sub> UB 82, corresponds to the typical early Pleistocene chronospecies *Lycaon lycaonoides*.

It is quite common to find both species of canids, *Canis mosbachensis* and *Lycaon lycaonoides*, in most of the European and Asian late Villafranchian faunal assemblages of the early Pleistocene, such as Venta Micena, Cueva Victoria (Spain); Vallonnet (France); Pirro Nord (Italy); Apollonia-1 (Greece); Untermassfeld (Germany); Lakhuti (Tajikistan); or as in this case, at 'Ubeidiya. Both canids are absent from Dmanisi (Georgia), where only one canid species is recorded, *Canis etruscus* (Vekua, 1995) the typical large size canis-like dog of the late Pliocene European and western Asian assemblages. The presence of this species, *Canis etruscus*, and the absence of the early Pleistocene taxa *Lycaon lycaonoides* and *Canis mosbachensis* serves as a good biochronological marker for this Georgian site, which has been dated to ca. 1.77 Ma (Lordkipanidze et al., 2005, 2007).

*Lycaon lycaonoides*, which is a species of Eurasian origin, dispersed into Africa around the Plio-Pleistocene boundary

(Martínez-Navarro and Rook, 2003), following a contrary route to the hominins. It is found in Ain Hanech, where it has been referred to *Canis atrox* (Arambourg, 1979), but also in the East and the South of the continent, including Olduvai Beds I and II, ascribed to *Canis africanus* (Ewer, 1965) and Kromdraai A (Turner, 1986).

*Vulpes cf. V. praeglacialis*, Kormos, 1932. This taxon was previously identified as *Vulpes* sp. by Ballesio (1986). This small fox is represented by four dental specimens in stratum II 23 of 'Ubeidiya. Although it is not possible to say more about the anatomy, its small size (P3 = L:7.6, W:3.0; P4 = L:11.4, W:5.0) appears similar to the early-middle Pleistocene fox described by Kormos (1932), *Vulpes praeglacialis*.

This species, which probably evolved from the late Pliocene form *Vulpes alopecoides*, is present in most of the early and early middle Pleistocene of Europe, from Venta Micena (Spain) until the lower levels of L'Aragò sites (Tautavel, France). Another form of *Vulpes* is also cited at the North African site of Ain Hanech (Arambourg, 1979), where a mandible was published as *Vulpes*

*atlantica*. Unfortunately, no metric or anatomical comparisons are possible for this taxon.

*Ursidae*

*Ursus etruscus* Cuvier, 1812. The only described species of this family at 'Ubeidiya is the classical European *Ursus etruscus*. Comparison with other specimens from the late Pliocene sites of Saint Vallier and Senèze (France); Tegelen (The Netherlands); Villarroya, La Puebla de Valverde, and Almenara (Spain); Upper Valdarno (Italy); the early Pleistocene site of Venta Micena (Spain; Ballesio, 1986; Torres Pérez-Hidalgo, 1992); and Dmanisi (Georgia; Vekua, 1995) place the 'Ubeidiya population within the variability of this species.

Two new, and probably synonymous, early Pleistocene species of *Ursus* connecting the etruscoid form (*Ursus etruscus*) with the arctoid form (*Ursus arctos*) have been recently described. One is from the site of Gran Dolina of Atapuerca (Spain), *Ursus dolinensis* (García and Arsuaga, 2001), and another is from Untermaßfeld

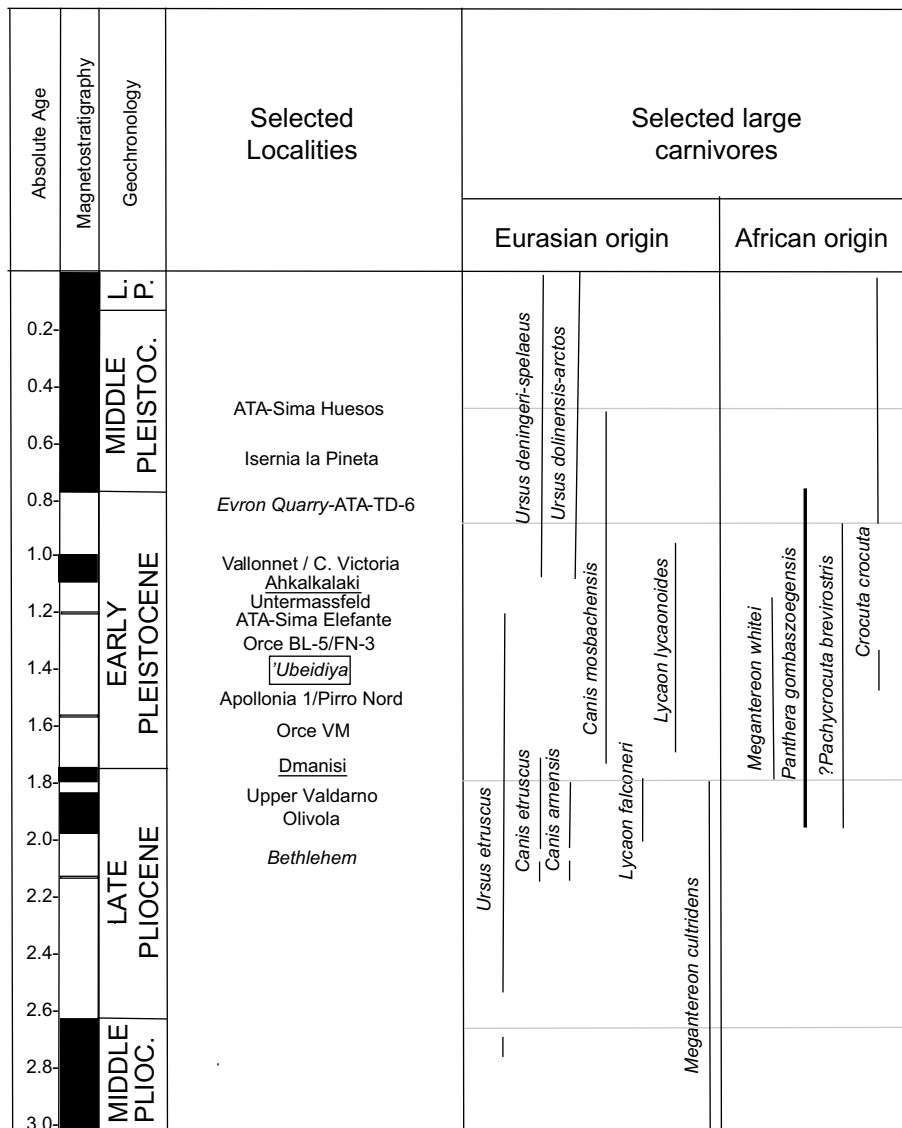


Figure 3. Biochronologic chart of the middle-late Pliocene and Pleistocene selected large carnivores in different sites of the Levantine Corridor (in italic), the Caucasian Region (underlined), and Europe (the other). 'Ubeidiya falls in the chronology between 1.2 and 1.5 Ma. (? = means that it is not totally clear the African origin of these species).

(Germany), *Ursus rodei* (Musil, 2001). Also, an archaic form of *Ursus deningeri* was described at Vallonnet, France (Moullé, 1992). This latter species is typical in most of the European middle Pleistocene sites.

The comparison of the ursid specimens from 'Ubeidiya with *Ursus dolinensis* shows that the specimens do not differ metrically, but exhibit several anatomical differences, especially of the mandible. The holotype of *Ursus dolinensis* (García and Arsuaga, 2001; their Fig. 1z) has a larger retromolar space than the specimen UB 78 (Ballesio, 1986, their Pl. 1, Fig. 1); however, the ascending ramus is more vertically oriented and the maseteric fossae is better delimited in the 'Ubeidiya specimen. We concur with the identification of Ballesio (1986) that the ursid species present at 'Ubeidiya falls within the variability of *Ursus etruscus* and is, together with the specimens from Pietrafitta (Italy; Mazza and Rustioni, 1992) and Venta Micena (Spain; Torres Pérez-Hidalgo, 1992), one of the last representatives of this species.

## Discussion

The revision of the fossil collection of large carnivores from 'Ubeidiya indicates the presence of the following species: *Megantereon* cf. *M. whitei*, *Panthera* cf. *P. gombaszoegensis*, *Lycaon lycaonoides*, *Canis mosbachensis*, and *Vulpes* cf. *V. praeglacialis*. The following taxa were previously identified and their identification has been sustained: *Lynx* sp., *Felis* sp., *Crocuta crocuta*, and *Ursus etruscus*. This faunal list, together with the other taxa identified at 'Ubeidiya (Haas, 1966; Tchernov, 1986; Belmaker, 2002; Martínez-Navarro et al., in prep.), represents a mixed Ethiopian and Holarctic assemblage representative of an early Pleistocene large mammal community. The presence of African fauna in the Levantine Rift Valley is consistent with the northward extension of the tropical "Sudanese" climate characterized by tropical biota similar to those of the African savanna homeland of early hominins (Por, 2004).

The revised large carnivore guild has implications for the biochronology of the site and biogeographic patterns relating to the dispersal of taxa from Africa to Eurasia during the early Pleistocene. Paleomagnetic studies have placed the 'Ubeidiya Formation securely within the Matuyama Chron (i.e., between ca. 1.78–0.8 Ma). Within this time frame, the biostratigraphic data from the faunal assemblage has suggested a date between 1.4–1.0 Ma (Tchernov, 1987). The revised list provided in this paper allows us to estimate with better resolution both a maximum and minimum age of the 'Ubeidiya Formation fossil bearing layers. A lower limit for the age of the site is supported by evidence from the middle and large size canids, *Lycaon lycaonoides* and *Canis mosbachensis*. The presence of a canid guild which is younger than that of Dmanisi (*Canis etruscus*) suggests that 'Ubeidiya must postdate 1.77 Ma. Furthermore, the presence of *Ursus etruscus* is, together with the specimens from Pietrafitta (Italy; Mazza and Rustioni, 1992) and Venta Micena (Spain; Torres Pérez-Hidalgo, 1992), one of the last representatives of this species and thus provides an upper limit for the age of the 'Ubeidiya formation at ca. 1.2–1.3 Ma.

A more refined biochronological age for the formation is provided by the presence of the species *Megantereon* cf. *M. whitei* at 'Ubeidiya. *Megantereon whitei* replaced *Megantereon cultridens* in western Asia and Europe around the Plio-Pleistocene boundary. The latest record of *Megantereon cultridens* in Europe is at Upper Valdarno (Italy) inside the normal Olduvai Subchron, and the earliest record outside Africa of *Megantereon whitei* is at Dmanisi together with the oldest hominins in Eurasia, dated to 1.77 Ma. No record of *Megantereon cultridens* in western Asia or Europe is documented during the early Pleistocene. Then, the presence of *Megantereon whitei* at 'Ubeidiya can serve as a good biochronological marker (Martínez-Navarro and Palmqvist, 1995,

1996; Palmqvist et al., 2007). The latest record in Europe of this species is ca. 1.0–1.1 Ma at Untermassfeld, Germany (Hemmer, 2001), but its last record in East Africa is ca. 1.5–1.6 Ma (Howell and Coppens, 1976; Leakey et al., 1976). The presence of this taxon at 'Ubeidiya thus supports the date between 1.77 and 1.1 Ma for the site. Therefore the chronological position of 'Ubeidiya based on the carnivore guild is between ca. 1.6–1.5 to 1.3–1.2 Ma, older by ca. 100–200 kya than previous estimates (Tchernov, 1987).

The biochronological results are consistent with results obtained by recent paleomagnetic studies. Two short normal paleomagnetic episodes found within the Fi member were assigned to the Gilsa (1.575–1.567 Ma) and Cobb Mountain (1.215–1.190 Ma) short polarity events (Sagi, 2005). Thus, suggesting a date of ca. 1.55 to 1.2 Ma for the fossil bearing strata (Fig. 3).

## Conclusions

Analysis of the large carnivore assemblage in 'Ubeidiya and revision of earlier collections from this site indicated a revised identification of five taxa: *Megantereon* cf. *M. whitei* (previously *M. cultridens*), *Panthera* cf. *P. gombaszoegensis* (previously *P. gombaszoegensis*), *Canis mosbachensis* (previously *C. arnensis*), *Lycaon lycaonoides* (previously *Canis* sp. size of *C. falconeri*), and *Vulpes* cf. *V. praeglacialis* (previously *Vulpes* sp.).

The biochronological analysis narrows the age range for the fossil bearing strata at 'Ubeidiya and the Early Acheulian industry in the Jordan Valley to 1.5–1.2 Ma and is 100–200,000 years earlier than previously estimated.

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## Appendix 1. Inventory of the large carnivores in 'Ubeidiya (1960–1999)

The specimens corresponding to the old collections, previously published by Haas (1966) and Ballesio (1986), are referred to these publications and the new unpublished specimens have no reference.

*Megantereon* cf. *M. whitei* Broom, 1937

*Stratum II-23*: UB 80 crown of a right upper canine (Haas, 1966, their Pl.VI, Fig. 5; Ballesio, 1986); *Stratum II-24*: UB 14 left lower canine; *No stratigraphic data*: UB 307 left middle phalanx.



*Panthera cf. P.gombaszoegensis* Kretzoi, 1938

*Stratum II-23*: UB 28 left 1st phalanx (1st finger; [Ballesio, 1986](#)); *Stratum II-36*: UB 167 left 4th metacarpal ([Ballesio, 1986](#), their Pl. V, Fig. 1).

*Lynx* sp.

*Stratum I-15*: UB 122 left P<sub>4</sub>; *Stratum I 15-16*: UB 121 distal end of right humerus (broken; [Ballesio, 1986](#)); *Stratum I-16*: UB 123 left talus; *Stratum II-23*: UB 261 distal end of right humerus ([Haas, 1966](#), their Pl.V, Fig.8), UB 29 left upper canine ([Ballesio, 1986](#)), UB 65 distal fragment of left P<sub>4</sub> ([Ballesio, 1986](#)), UB 31 left M<sub>1</sub> ([Ballesio, 1986](#), their Pl. V, Fig. 3), UB 260 left lower canine ([Haas, 1966](#), their Pl.VI, Fig.6), UB 30 fragment of left hemimandible; *Stratum II-24*: UB 91 right calcaneum ([Ballesio, 1986](#)); *Stratum II-36*: UB 142 left tibia fragmented at the distal end ([Ballesio, 1986](#), their Pl. V, Fig. 4); *Stratum II-37*: UB 161 left lower canine ([Ballesio, 1986](#), their Pl. V, Fig. 6); *No stratigraphic data*: UB Proximal left radius ([Ballesio, 1986](#), their their Pl. V, Fig. 5).

*Felis* sp.

*Stratum II-36*: UB 141 distal end of a right humerus ([Ballesio, 1986](#)); *No stratigraphic data*: UB proximal end of right tibia ([Haas, 1966](#), their Pl. VI, Fig. 4).

*Crocota crocuta* Erxleben, 1777

*Stratum II-23*: UB 68 left I<sub>3</sub>, UB 70 right I<sub>3</sub> (identified as a right lower I<sub>3</sub> of *Ursus etruscus* in [Ballesio, 1986](#)); *Stratum II-24*: UB 25 left P<sub>4</sub> ([Ballesio, 1986](#), their Pl. VI, Fig. 4), UB 86 Distal right humerus ([Ballesio, 1986](#), their Pl. VI, Fig. 5); *Stratum II-36*: UB 294 right P<sup>4</sup> ([Ballesio, 1986](#), their Pl. VI, Fig. 1), UB 293 right M<sub>1</sub> ([Ballesio, 1986](#), their Pl. VI, Fig. 3), UB 147 metastyle of left P<sup>4</sup>, UB 144 left P<sup>3</sup> ([Ballesio, 1986](#), their Pl.VI, Fig. 2 figured in [Ballesio](#) as a right upper P<sub>3</sub>); *Stratum II-26*: UB 296 left P<sub>3</sub> ([Haas, 1966](#), their Pl.V, Fig. 6), UB 295 right P<sub>4</sub> ([Haas, 1966](#), their Pl. V, Fig. 7); *Stratum III-20*: UB 12 metastyle fragment of right P<sup>4</sup>; *Stratum III-22d*: UB 4 fragment of a canine.

*Canis mosbachensis* Soergel, 1925

*Stratum I-15 LF*: UB 130 left mandibular fragment without teeth and with the P<sub>1</sub>-P<sub>4</sub> alveolus ([Ballesio, 1986](#)), UB 126 left upper canine crown ([Ballesio, 1986](#)), UB 131 left M<sub>1</sub> ([Ballesio, 1986](#)), UB 5827 talon of left P<sup>3</sup>; *Stratum I-15-16*: UB 186 left M<sup>2</sup>, UB 127 distal fragment of right P<sup>3</sup> ([Ballesio, 1986](#)); *Stratum I-16*: UB 133 distal fragment of metapodial, UB 134 distal fragment of a right humerus ([Ballesio, 1986](#)), UB 129 left P<sup>4</sup> without the deuterocone ([Ballesio, 1986](#)), UB 128 right P<sup>4</sup> ([Ballesio, 1986](#)); *Stratum I-26*: UB 97 left mandible with the alveolus C-M<sub>3</sub> ([Ballesio, 1986](#), their Pl 3, Fig. 2), UB 98 left mandible with P<sub>3</sub>, UB 108 fragment of right M<sup>1</sup> ([Ballesio, 1986](#)), UB 107 fragment of a right M<sup>1</sup> ([Ballesio, 1986](#)), UB 105 left I<sup>3</sup> ([Ballesio, 1986](#)), UB 103 upper left canine ([Ballesio, 1986](#)), UB 106 talonide of a right M<sub>1</sub> ([Haas, 1966](#)), UB 102 distal fragment of a right P<sup>2</sup> ([Ballesio, 1986](#)), UB 104 distal fragment of a left radius, UB 100 proximal right ulna; *Stratum II-23*: UB 79 left hemimandibular fragment with P<sub>3</sub>-P<sub>4</sub> and alveolus of P<sup>2</sup> ([Ballesio, 1986](#)), UB 49 proximal fragment of a right ulna ([Ballesio, 1986](#)), UB 92 distal fragment of a right humerus ([Haas, 1966](#): their Pl. V Fig. 1), UB 77 fragment of right M<sub>1</sub> (paraconid; [Ballesio, 1986](#)), UB 85 left I<sub>2</sub>, UB 87 right I<sub>3</sub>, UB 56 distal fragment of a right P<sub>4</sub> ([Ballesio, 1986](#)), UB 90 left I<sup>1</sup>, UB 48 left P<sub>3</sub> ([Ballesio, 1986](#)), UB 55 left I<sup>1</sup> ([Ballesio, 1986](#)), UB 46 left I<sup>1</sup> ([Ballesio, 1986](#)), UB 60 left M<sub>3</sub> ([Ballesio, 1986](#)), UB 61 left

lower canine ([Ballesio, 1986](#)), UB 50 right lower canine ([Ballesio, 1986](#), Pl. III, Fig. 3), UB 47 left lower canine ([Ballesio, 1986](#)), UB 62 left fragment of P<sup>3</sup> ([Ballesio, 1986](#)), UB 59 left I<sup>1</sup> ([Ballesio, 1986](#)), UB 52 distal fragment of left P<sup>3</sup>, UB 84 right M<sub>3</sub>, UB 93 right I<sup>3</sup>, UB 53 right M<sup>2</sup> ([Ballesio, 1986](#)), UB 57 proximal end of left ulna, UB 81 right M<sub>2</sub> ([Ballesio, 1986](#)), UB 54 right M<sub>2</sub> ([Ballesio, 1986](#)), UB 51 distal fragment of left P<sup>4</sup> ([Ballesio, 1986](#)), UB 83 distal fragment of right P<sup>4</sup> ([Ballesio, 1986](#)), UB 58 talone of left M<sub>1</sub>, UB 1255 left I<sub>3</sub>?, UB 73 distal fragment of left P<sub>4</sub>, UB 71 fragment of a right P<sub>4</sub>, UB 75 left lower canine; *Stratum II 23-24*: UB 72 left calcaneum; *Stratum II-24*: UB 43 left I<sub>1</sub> ([Ballesio, 1986](#)), UB 37 distal fragment of left P<sub>2</sub> ([Ballesio, 1986](#)), UB 41 upper right canine ([Ballesio, 1986](#)), UB 40 left lower canine ([Ballesio, 1986](#)), UB 35 fragment of left M<sup>2</sup>, UB 44 right P<sup>4</sup> ([Ballesio, 1986](#), Pl. III, Fig. 6), UB 38 crown of left I<sup>2</sup> ([Ballesio, 1986](#)), UB 45 distal fragment of left P<sub>3</sub>, UB 66 distal fragment of left P<sub>3</sub> ([Ballesio, 1986](#)), UB 36 right M<sup>2</sup> ([Ballesio, 1986](#)), UB 39 fragment of left M<sup>2</sup>, UB 67 fragment of left upper canine ([Ballesio, 1986](#)), UB 34 upper left canine ([Ballesio, 1986](#)), UB 33 fragment of right talus ([Ballesio, 1986](#)), UB 76 fragment of left palate with P<sup>4</sup>-M<sup>2</sup> ([Ballesio, 1986](#), Pl. II, Fig. 4); *Stratum II 25*: UB 109a fragment of a right M<sup>1</sup>, UB 109b fragment of a right M<sup>2</sup> (both specimens belong to the same individual); *Stratum II-26*: UB 94 crown of left lower canine, UB 268 fragment of a left hemimandible with P<sub>4</sub>-M<sub>1</sub>, UB 270 left I<sub>3</sub>; *Stratum II-28*: UB 290 fragment of a right hemimandible with P<sub>4</sub>-M<sub>1</sub>; *Stratum II-36*: UB 148 proximal fragment of a right ulna ([Ballesio, 1986](#)), UB 152 right I<sub>2</sub> ([Ballesio, 1986](#)), UB 153 1st phalanx ([Ballesio, 1986](#)), UB 151 distal fragment of left P<sup>4</sup> ([Ballesio, 1986](#)), UB 150 left M<sup>2</sup> ([Ballesio, 1986](#)), UB 146 right M<sup>1</sup> ([Ballesio, 1986](#), their Pl. III, Fig.1), UB 6701 fragment of a right P<sub>1</sub>, UB 149 left P<sub>2</sub> ([Ballesio, 1986](#)), UB 168 left humerus ([Ballesio, 1986](#), their Pl. II, Fig. 3); *Stratum III-20*: UB 110 left I<sub>3</sub>; *Stratum III-22*: UB 18 distal end of a left humerus; *Stratum III-22f*: UB 17 right upper canine; *No stratigraphic data*: UB 303 right hemimandibular fragment with alveolus of canine-P<sub>4</sub> ([Ballesio, 1986](#)), UB 304 right talus ([Ballesio, 1986](#)), UB 306 left M<sub>1</sub> fragment, UB 305 fragment of a right hemimandible with P<sub>3</sub>-P<sub>4</sub> ([Haas, 1966](#), their Pl. V, Fig. 2).

*Lycaon lycaonoides* Kretzoi, 1938

*Stratum II-23*: UB 89 talonid of a left M<sub>1</sub>, UB 82 left M<sub>2</sub>, UB 88 crown of a right upper canine ([Ballesio, 1986](#), their Pl. III, Fig. 7); *Stratum III-23*: UB 1 right upper canine; *No stratigraphic data*: UB 278 right I<sub>3</sub>.

*Vulpes cf. V. praeglacialis*, Kormos, 1932

*Stratum II-23*: UB 10 right P<sup>4</sup> ([Ballesio, 1986](#), their Pl. I, Fig. 6), UB 8 right P<sub>3</sub> ([Ballesio, 1986](#)), UB 11 fragment of right M<sub>1</sub> ([Ballesio, 1986](#)), UB 9 fragment of right M<sub>1</sub> ([Ballesio, 1986](#)).

*Ursus etruscus* Cuvier, 1812

*Stratum I-15*: UB136 left M<sub>2</sub> ([Ballesio, 1986](#), their Pl. I, Fig. 4), UB 137 right M<sup>2</sup> ([Ballesio, 1986](#), their Pl. I, Fig. 2); *Stratum I-15-16*: UB 138 talon of left M<sup>2</sup> ([Ballesio, 1986](#), their Pl. I, Fig. 3), UB 135 distal end of 1st metacarpal, UB 125 right calcaneum ([Ballesio, 1986](#), their Pl. I, Fig. 5), UB 113 right P<sub>4</sub>, UB 300 talone of right M<sub>2</sub> ([Ballesio, 1986](#)); *Stratum I-16*: UB 139 mesial fragment of a right M<sup>1</sup> ([Ballesio, 1986](#)), UB 140 1st phalanx; *Stratum I-26*: UB 96 left I<sub>3</sub>; *Stratum II-24*: UB 78 fragment of left hemimandible with talonide of M<sub>1</sub>, M<sub>2</sub>, and M<sub>3</sub> ([Ballesio, 1986](#), their Pl. I, Fig. 5); *Stratum II-34*: UB 160 fragment of right hemimandible with M<sub>2</sub> and M<sub>3</sub> ([Ballesio, 1986](#), their Pl. II, Fig. 2); *Stratum III-12*: UB 302 fragment of upper left canine ([Ballesio, 1986](#), their Pl. II, Fig. 1); *Stratum II-36(?)*: UB Left lower canine ([Haas, 1966](#), their PL. II, Fig. 1).

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