



New material of hyaenids (Mammalia, Carnivora) from Olduvai Gorge, Tanzania (Early Pleistocene)

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KEY WORDS - *Hyaenidae*, *Hyaena*, *Crocota*, *Early Pleistocene*, *Olduvai*, *Tanzania*.

ABSTRACT - *The Hyaenidae are today a small carnivoran family including only four monospecific genera, although their paleodiversity was very high from the Miocene to the Pleistocene, with a paleobiogeographic distribution spanning Eurasia, Africa and North America. The living species Crocota crocuta, Parahyaena brunnea and Proteles cristatus are limited to the African Continent, while the distribution of Hyaena hyaena includes northern, central and eastern Africa and southwestern Asia. The paleontological record suggests that forms very similar to the extant ones lived in Africa at least from the late Pliocene. Here we report new hyaenid craniodental material from the renowned site of Olduvai Gorge, in northern Tanzania. The fossils were found in three different Olduvai localities (FC West, MCK East and Loc. 64 in Naisiusiu area), within layers spanning stratigraphically from Bed I to Upper Bed II (Early Pleistocene). We refer the remains to Hyaena sp., Crocota cf. ultra and Crocota sp., supporting the occurrence of at least two hyenas (the smaller and slenderer Hyaena and the large and robust Crocota) in the Olduvai Bed I-II carnivore guild.*

RIASSUNTO - [Nuovo materiale di ienidi (Mammalia, Carnivora) dalla Gola di Olduvai, Tanzania (Pleistocene Inferiore)] - *Gli Hyaenidae sono oggi una piccola famiglia di carnivori comprendente solo quattro generi monospecifici, ma la loro paleodiversità è stata molto alta tra il Miocene e il Pleistocene, con una distribuzione paleobiogeografica che spaziava in Eurasia, Africa e Nord America. Le specie viventi Crocota crocuta, Parahyaena brunnea e Proteles cristatus sono ristrette al continente africano, mentre l'areale di Hyaena hyaena comprende l'Africa settentrionale, centrale e orientale e l'Asia sudoccidentale. Il record paleontologico suggerisce che forme molto simili a quelle attuali fossero già presenti in Africa almeno dal Pliocene superiore. In questo lavoro, descriviamo nuovo materiale craniodentale di ienidi dal noto sito della Gola di Olduvai, in Tanzania settentrionale. I fossili sono stati rinvenuti in tre differenti località della Gola (FC West, MCK East e Loc. 64 nell'area di Naisiusiu), all'interno di livelli che abbracciano stratigraficamente un intervallo compreso tra il Bed I e l'Upper Bed II (Pleistocene Inferiore). I resti vengono riferiti a Hyaena sp., Crocota cf. ultra e Crocota sp., supportando così la presenza di almeno due iene (la più piccola e snella Hyaena e la grossa e robusta Crocota) nell'associazione a carnivori dei Bed I-II di Olduvai.*

INTRODUCTION

Olduvai Gorge in northern Tanzania (Fig. 1) is recognized as one of the most important paleontological and archeological sites in the world. The huge amount of fossils and stone tools found in the Olduvai stratigraphic succession (Fig. 1) allows to reconstruct almost uninterrupted the evolution of East African ecosystems in the last two million years, as well as some crucial phases of early human evolution. Much of the fame of Olduvai Gorge is due to the research activity of Mary and Louis Leakey, who have worked at the site for more than thirty years. Among their most important findings are Olduvai Hominid (OH) 5 and OH 7, representing respectively the holotypes of *Paranthropus boisei* (Leakey, 1959) and *Homo habilis* Leakey, Tobias and Napier, 1964, which were the first ancient hominin fossils discovered in East Africa (Blumenschine et al., 2012).

Many international scientific projects are currently carried out in Olduvai Gorge, including that of the University of Perugia School of Paleoanthropology. This was started in 2011 as the first Italian field project at Olduvai and is aimed at the surface collection (Fig. 2),

preliminary restoration and cataloguing of paleontological and archeological remains from various sites of the Gorge, in order to save them by human-induced and natural destructive agents.

Here we describe new hyaenid skull remains collected during the 2014 and 2015 field seasons from Early Pleistocene layers of three different sites of Olduvai Gorge.

Institutional abbreviations

LCCO: Leakey Camp Collection Olduvai, Tanzania; NMDS: National Museum and House of Culture, Dar es Salaam, Tanzania; UPOP: University of Perugia Olduvai Project.

THE HYAENIDAE: FOSSIL RECORD AND EVOLUTIONARY HISTORY

The family Hyaenidae includes only four living species, each assigned to its own genus: the spotted hyena *Crocota crocuta* (Erxleben, 1777), the striped hyena *Hyaena hyaena* (Linnaeus, 1758), the brown

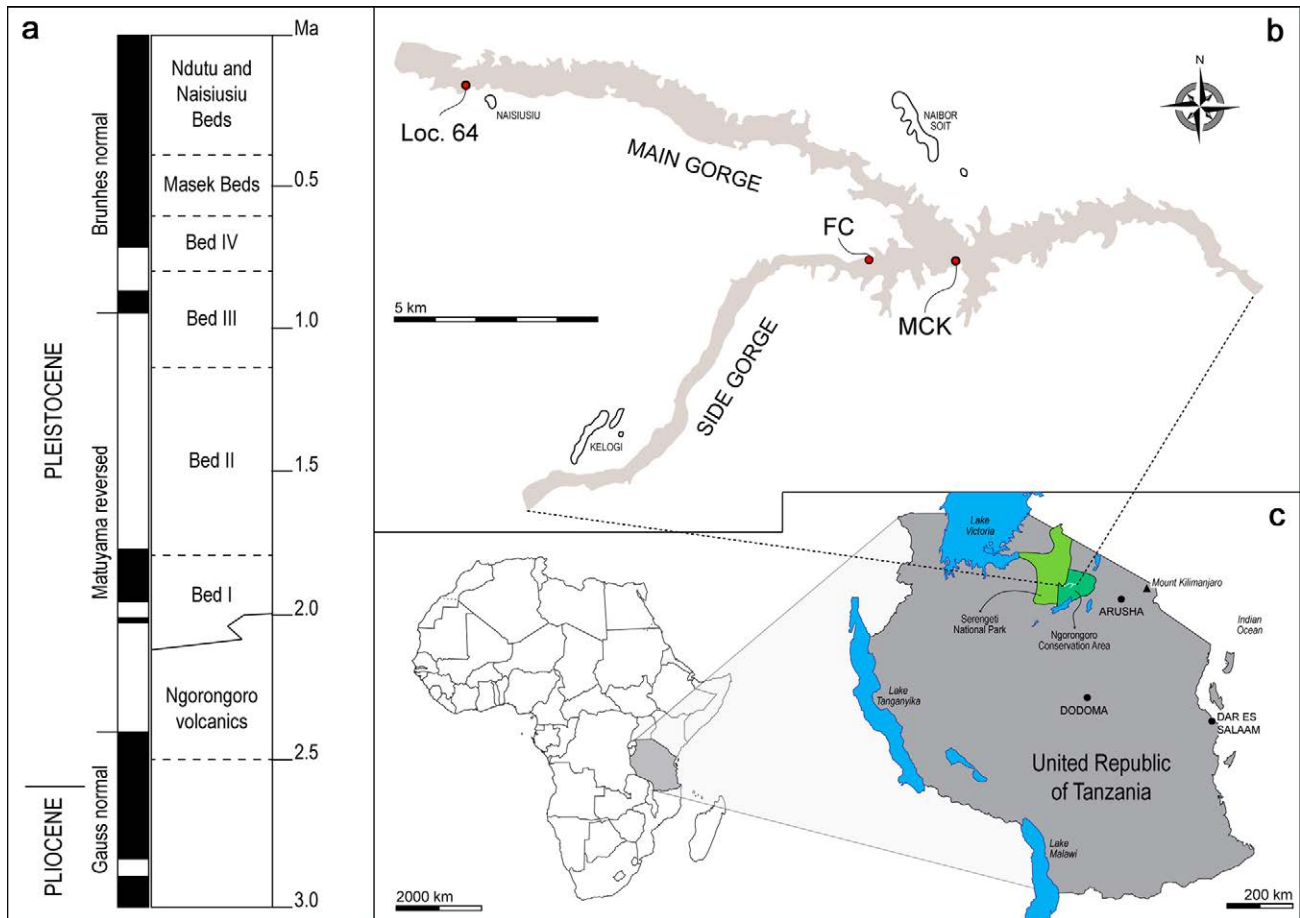


Fig. 1 - The site of Olduvai Gorge, Tanzania. a) Stratigraphy (redrawn from Hay, 1976); b) outline map (redrawn from Hay, 1976), with location of the three localities in which the fossils described in the paper were found in 2014-2015; c) location of Olduvai Gorge within the Ngorongoro Conservation Area, northern Tanzania. Online version in color.

hyena *Parahyaena brunnea* (Thunberg, 1820), and the aardwolf *Proteles cristatus* (Sparrman, 1783). The taxonomic status of the genus *Parahyaena* is discussed, as sometimes it is regarded as a subgenus of *Hyaena* (Kingdon & Hoffmann, 2013). This is mostly attributed to the limited knowledge on the phylogeny of hyaenids. According to the traditional view, the genus *Proteles* would be basal to the clade including *Crocota* and the sister taxa *Hyaena* and *Parahyaena*, thus supporting the inclusion of the two taxa in the same genus. On the contrary, some studies (Werdelin & Solounias, 1991) recognize a greater affinity between the brown hyena and the spotted hyena, confirming the taxonomic validity of the genus *Parahyaena*. Later molecular studies on Hyaenidae (Jenks & Werdelin, 1998; Koepfli et al., 2006) support the traditional view, recognizing the basal status of *Proteles* and the sister-taxon relationship between the brown hyena and the striped hyena, which form a clade closely related to *Crocota*. Despite the sister-taxon relationship of *Parahyaena* and *Hyaena*, the depth of time since their split (and the number of fossil taxa assigned to each genus) has led some (e.g., Werdelin & Solounias, 1991) to advocate for retaining the two genera as separate (i.e., they are sister-taxa today, but only because the entire family has so few living members).

Contrary to what is commonly thought, no living hyaenid species is an exclusive scavenger. Although in

fact carcasses are the primary energy source for the striped hyena and especially the brown hyena, their feeding habits are very opportunistic and also include many other food sources such as insects, fruit and small-medium prey (Kingdon & Hoffmann, 2013). On the other hand, the spotted hyena is an efficient pack hunter, capable to kill large prey such as wildebeests, buffalos and zebras (Kingdon & Hoffmann, 2013). Finally, the aardwolf feeds almost exclusively on termites (Holekamp & Kolowski, 2009).

The morphology and adaptations of the four living taxa are the remnants of the great diversity that has characterized the Hyaenidae in the geological past. Whereas their current distribution is limited to Africa and - only for *H. hyaena* - Asia, from the Miocene to the Pleistocene members of this family were common in the whole Eurasia and Africa, and in North America with the only genus *Chasmaporthetes* Hay, 1921 (Gilbert et al., 2008; Holekamp & Kolowski, 2009). The hyaenids appear in the fossil record in the early Miocene of Europe, while the earliest occurrence in Africa dates back to the middle Miocene of Morocco (Werdelin & Solounias, 1991; Werdelin & Turner, 1996; Kingdon & Hoffmann, 2013). Werdelin & Solounias (1991) divide the Hyaenidae into two main morphological groups: the “hyaenid” taxa (i.e., taxa with morphology and ecology similar to the extant *Hyaena*, *Parahyaena* and *Crocota*) and “non-hyaenid”



Fig. 2 - Field survey work at Site FC West, Olduvai Gorge, Tanzania. The contact between Bed II and Bed III is marked up. Online version in color.

taxa (i.e., basal canid-like taxa, including the living *Proteles*). The highest diversity of the “non-hyaenid” group is recorded in the Turolian Mammal Age (late Miocene), with more than 20 species recognized across the Old World. Their diversity then drastically decreases in the Plio-Pleistocene, probably related to the radiation of canids. On the contrary, the diversification of the “hyaenid” taxa proceeds gradually until the Villafranchian, followed by a slow decline leading to the extant species.

From a cladistic point of view, all the primitive, small- to medium-sized canid-like taxa constitute the hyaenid basal stem group (Werdelin & Solounias, 1991). This clade includes taxa such as *Plioviverrops* Kretzoi, 1938, which retain reduced body size comparable to those of the modern mongooses and civets, with dental adaptations to omnivory and insectivory (Werdelin & Solounias, 1991; Holekamp & Kolowski, 2009). A general trend of body size increase is registered in more derived taxa such as *Ictitherium* Roth & Wagner, 1854 (Werdelin, 1988) and *Hyaenictitherium* Zdansky, 1924 (De Bonis et al., 2005), which in some cases reach the size of the living striped hyena. This clade also includes - although doubtfully (Koepfli et al., 2006) - the genus *Proteles*, whose evolutionary history is almost unknown. The molecular data (Koepfli et al., 2006) suggest that this genus splits from the other Hyaenidae in the earliest late Miocene

(approx. 10.6 Ma), but the oldest fossil species, *Proteles amplidentus* Werdelin & Solounias, 1991, is from the middle early Pleistocene of South Africa (Werdelin & Solounias, 1991), while some doubtful material is reported in the middle Pliocene of Laetoli, Tanzania (Werdelin & Deghani, 2011). The hyaenid taxa more derived than *Hyaenictitherium* are grouped (Werdelin & Solounias, 1991) into two monophyletic clades, both characterized by a general trend of body size increasing. The first clade is formed by active hunters with adaptations to cursoriality, such as *Lycyaena* Hensel, 1862, *Hyaenictis* Gaudry, 1861 and *Chasmaporthetes*. The second clade includes taxa in which the dentition shows a strong bone-cracking functional component, to the detriment of the shearing one. In particular, these hyenas show broad third upper and lower premolars, sagittally oriented carnassials and reduced or absent distal molars, and these characters are often associated to very strong mandibles and crania with vaulted forehead (Werdelin & Solounias, 1990, 1991). Members of this group are the living *Hyaena*, *Parahyaena* and *Crocota*, as well as extinct genera such as *Pliocrocota* Kretzoi, 1938, *Pachycrocota* Kretzoi, 1938 and *Adcrocota* (Kretzoi, 1938). Bone-cracking hyenas are particularly widespread in Eurasia and Africa during the Plio-Pleistocene (Petter & Howell, 1989; Werdelin & Solounias, 1991; Werdelin & Turner, 1996; Werdelin & Kurtén, 1999). The only Miocene taxon, *Adcrocota*, seems to have not reached sub-Saharan Africa, leaving free the bone-cracking niche in the carnivore guild (Kingdon & Hoffmann, 2013). All the extant species appear to have originated in Africa between 15 and 7 Ma (Koepfli et al., 2006).

SYSTEMATIC PALEONTOLOGY

Class MAMMALIA Linnaeus, 1758

Order CARNIVORA Bowdich, 1821

Family HYAENIDAE Gray, 1821

Genus *Hyaena* Brisson, 1762

Hyaena sp.

(Figs 3-4, Suppl. Video 1)

Material - Fragment of cranium, including the caudoventral portion of the left maxilla and the rostradorsal portion of the left jugal (Leakey Camp paleontological collections, Olduvai Gorge, Tanzania, UPOP14#39).

Locality - Western part of Site FC (Fuch’s Cliff; Leakey, 1965: 102), northern part of the Side Gorge, Olduvai Gorge, Tanzania (Figs 1-2).

Stratigraphy and age - Middle Bed II, Early Pleistocene (Figs 1-2).

Description - The preserved part of the cranium (Fig. 3) consists of the ventral orbital border (i.e., the rostradorsal portion of the left jugal) and the caudoventral portion of the left maxilla (Fig. 4) broken between the distal wall of the mesial root of the P³ and the root of the M¹. The ventral orbital outline is rounded and the border of the orbit is slightly protruding with respect to the jugal

lateral surface. A large infraorbital foramen with oval section lies rostroventrally to the orbit and very close to it. The infraorbital canal emerges on the medial side of the maxilla at the level of the contact between the P³ and P⁴. In ventral view, the roots of the P³, P⁴ and M¹ are in situ, indicating that the three teeth were broken during post-diagenetic processes. The P³ distal root is very large and rounded, with a small groove on the anterior margin; a similar groove is visible also on the distal wall of the P³ mesial root, which is missing. The P⁴ is three-rooted. The long mesiolingual root denotes the presence of a prominent protocone. The small M¹ was probably two-rooted, but only the labial root is preserved, lying distolingually to the P⁴.

Remarks - The morphology of UPOP14#39 is comparable to that of the extant *H. hyaena* (Fig. 4). In particular, UPOP14#39 and *H. hyaena* show the presence of a well-developed M¹, which is on the contrary very small or absent in *C. crocuta* (Kingdon & Hoffmann, 2013). The presence of a relatively large M¹ is also actually considered as a diagnostic character for the extinct *C. ultra*

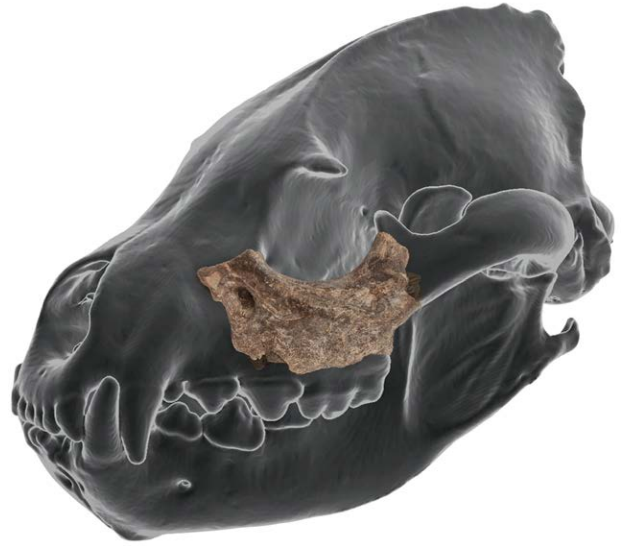


Fig. 4 - Digital model of UPOP14#39 (*Hyaena* sp.) placed in the correct anatomical position on the digital model of a cranium of modern *Hyaena hyaena*. Online version in color.

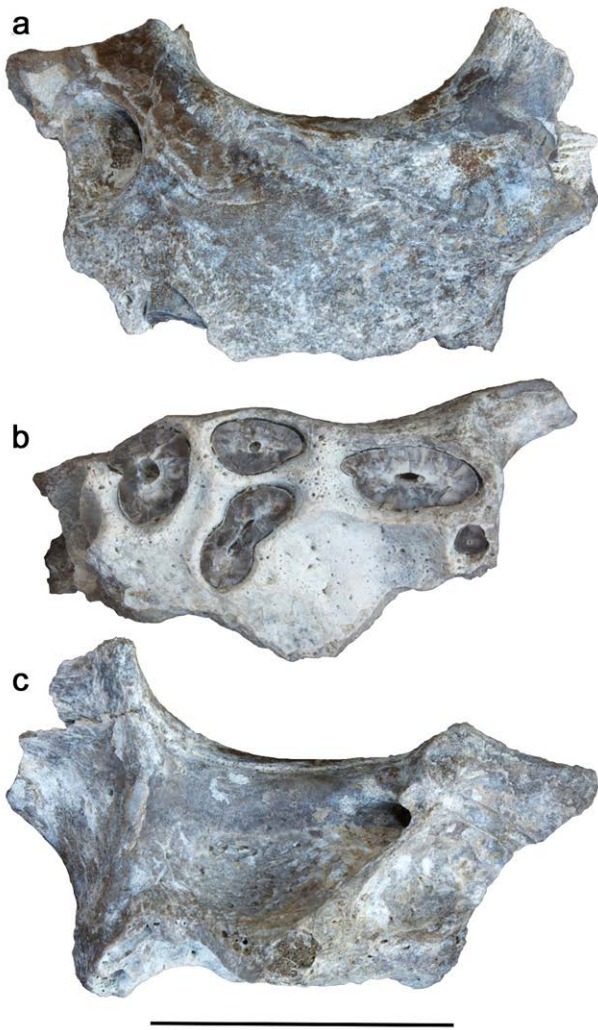


Fig. 3 - *Hyaena* sp. (UPOP14#39) from Site FC West, Olduvai Gorge (Tanzania). Fragment of cranium in a) left lateral view; b) ventral view; c) right lateral view. Scale bar corresponds to 3 cm. Online version in color.

Ewer, 1954 (Kurtén, 1956), but the general morphology and size (see below) of UPOP14#39 allow to not referring it to the latter taxon.

UPOP14#39 resembles *H. hyaena* also from the biometric point of view (Tab. 1; see in particular the distance between the ventral orbital border and the P⁴ alveolus and that between the orbit and the infraorbital foramen, which are very close to the values measured for *H. hyaena*).

The extant striped hyena, *H. hyaena*, is recorded in Africa from about 1.9 Ma and is preceded by the ancestral *H. makapani* Toerien, 1952, which appears at about 3.5 Ma (Werdelin & Lewis, 2005). The occurrence of *H. hyaena* in Olduvai Bed I-II is reported by Petter (1973) and Werdelin & Peigné (2010). The latter authors also report unspecified findings of *Hyaena* sp. from Bed IV. Given the poor state of preservation, we also identify UPOP14#39 as *Hyaena* sp.

Genus *Crocuta* Kaup, 1828

Crocuta cf. *ultra* Ewer, 1954
(Fig. 5, Suppl. Video 2)

Material - Left dentary with P₃-M₁ (Leakey Camp paleontological collections, Olduvai Gorge, Tanzania, UPOP15#01).

Locality - Eastern part of Site MCK (Margaret Cropper Korongo; Leakey, 1965: 105), middle part of the Main Gorge, close to the junction with the Side Gorge, Olduvai Gorge, Tanzania (Fig. 1).

Stratigraphy and age - Upper Bed II, Early Pleistocene (Fig. 1).

Description - The mandible (Fig. 5) is broken between the mesial edge of the canine alveolus and the caudal end

Cranium and upper teeth	<i>Hyaena</i> sp.	<i>Crocota crocuta</i>					<i>H. hyaena</i>
	UPOP 14#39	LCCO Crocuta 4	LCCO Crocuta 5	LCCO Crocuta 6	LCCO Crocuta 7	LCCO Crocuta 8	LCCO Hyaena 1
Length of the orbit (inner)	31.4	37.6	33.7	30.7	33.7	34.5	28.1
Height of maxilla below the ventral border of orbit	22.9	35.4	31.3	18.6	26.3	38.4	22.5
Min distance between orbit and infraorbital foramen	8.1	13.7	15.6	9.8	10.9	14.9	9.8
Infraorbital foramen height	11.0	11.7	9.6	13.1	12.5	13.5	10.9
P ³ breadth (alveolar)	<i>10.1</i>	<i>15.0</i>	<i>12.0</i>	<i>13.0</i>	<i>14.0</i>	<i>10.0</i>	<i>11.5</i>
P ⁴ labial length (alveolar)	25.1	34.2	30.8	33.8	33.3	30.8	28.8
P ⁴ lingual length (alveolar)	26.4	38.0	34.1	37.4	37.3	32.6	31.5
P ⁴ max breadth (alveolar)	16.7	17.2	16.2	17.0	17.1	16.5	16.3
P ⁴ protocone max length (alveolar)	5.7	6.5	6.1	7.3	6.4	5.9	6.2
P ⁴ max breadth behind protocone (alveolar)	7.2	10.3	9.4	9.9	9.7	7.0	9.0
P ⁴ min breadth behind protocone (alveolar)	6.7	7.6	7.8	7.7	8.7	6.6	8.5
M ¹ length (alveolar)	4.1	-	-	-	-	-	3.5

Tab. 1 - Selected measurements (mm) of the cranium and upper teeth of *Hyaena* sp. (UPOP14#39) from Site FC West, Olduvai Gorge (Tanzania), compared to the living *Crocota crocuta* and *Hyaena hyaena*. LCCO Crocuta 6 is a juvenile individual. Estimated measurements are in italics.

of the corpus. The rostral part of the masseteric fossa is visible and does not reach the M₁. The preserved part of the symphysis reaches caudally the mid part of the P₂ alveolus. The canine is freshly broken and the root is in situ. The cheek teeth are closely crowded together. The P₂ is missing while the P₃-M₁ are well preserved. The P₃ and

P₄ are very similar in size and shape, with a high pyramidal main cusp. The P₃ has not a mesial accessory cusp but only a low swelling adjacent to the main cusp. The distal accessory cusp is blunt and low. On the contrary, the P₄ has both a very low mesial accessory cusp and a well-developed distal accessory cusp. The M₁ is large and long. The paraconid is larger than the protoconid and the talonid is well developed, bearing a distinct labial cusplid.

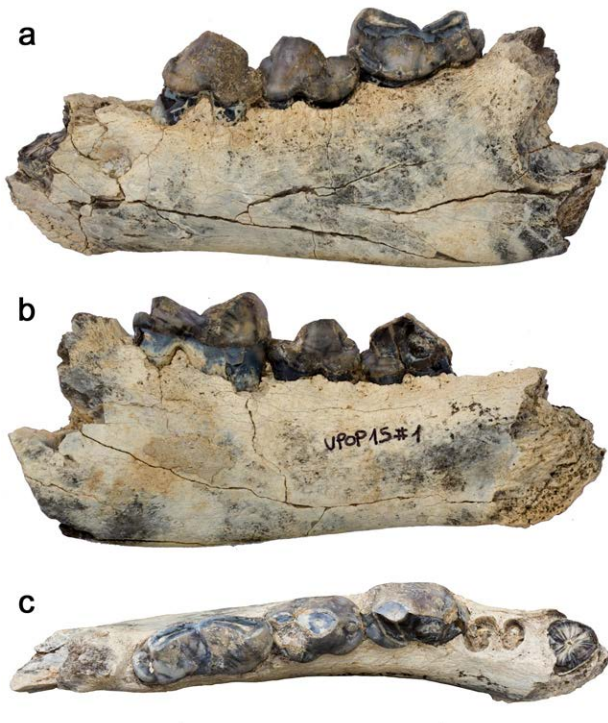


Fig. 5 - *Crocota* cf. *ultra* (UPOP15#01) from Site MCK East, Olduvai Gorge (Tanzania). Left dentary in a) labial view; b) lingual view; c) dorsal view. Scale bar corresponds to 5 cm. Online version in color.

Remarks - The African evolutionary history of the spotted hyenas is not clear (Werdelin & Lewis, 2005). In addition to the living species *C. crocuta*, at least three other species are known in the African fossil record: *C. dietrichi* Petter & Howell, 1989, *C. ultra* and the recently described *C. eturono* Werdelin & Lewis, 2008. Some authors (e.g., Turner, 1990) stated that *C. dietrichi* and *C. ultra* could fit in the variability range of *C. crocuta*, but these species should be considered valid according to Werdelin & Lewis (2005). *Crocota ultra* is the only species reported in Olduvai Bed I-II (Petter, 1973; Werdelin & Peigné, 2010).

The morphometric measurements collected on UPOP15#01 (Tab. 2) fall within the range of both *C. ultra* and living *C. crocuta*, but the morphology of the specimen fits well with the original description of the former species by Ewer (1954). For this reason, UPOP15#01 is here identified as *Crocota* cf. *ultra*.

Genus *Crocota* Kaup, 1828

Crocota sp.
(Figs 6-7, Suppl. Video 3)

Material - Crushed left dentary broken in two parts (labeled as a and b), with roots of P₄-M₁ (Leakey Camp paleontological collections, Olduvai Gorge, Tanzania, UPOP15#31).

Mandible	<i>Crocota cf. ultra</i>	<i>Crocota sp.</i>	<i>Crocota ultra</i>						<i>Crocota crocuta</i>						<i>H. hyaena</i>
	UPOP 15#01	UPOP 15#31	NMDS 5349	NMDS 63/3131	NMDS 64/7642	NMDS 57/1510	NMDS 59/263	NMDS 61/7577	LCCO Crocuta 1	LCCO Crocuta 2	LCCO Crocuta 3	LCCO Crocuta 4	LCCO Crocuta 5	LCCO Crocuta 6	LCCO Hyaena 1
Max height	42.5	-	-	-	-	-	-	-	44.3	41.5	41.2	46.4	42.5	31.1	30.8
Height behind canine	31.1	-	-	-	-	-	-	-	35.1	33.0	30.9	35.6	30.0	28.3	24.3
Height behind M ₁	42.5	-	-	-	43.3	32.2	34.0	47.0	44.3	41.5	41.2	46.4	42.5	31.1	30.8
Breadth at P ₄	15.8	-	-	-	-	-	-	-	15.9	15.0	15.0	17.6	15.8	13.0	14.0
Length of diastema	5.6	-	-	-	-	-	-	-	7.3	7.6	10.6	9.5	9.5	3.6	5.3
Check tooth length (alveolar)	77.1	-	-	-	-	-	-	-	78.3	77.6	78.4	82.5	77.7	75.4	69.2
C _{mand} length	15.3	-	-	-	14.0	-	-	14.9	17.0	14.6	14.7	17.0	13.3	14.7	13.1
C _{mand} breadth	9.9	-	-	-	11.5	-	-	10.5	12.6	12.2	11.3	12.3	11.0	10.6	10.0
P ₂ length	13.0	-	-	-	-	-	13.1	14.4	13.6	14.2	14.0	15.1	13.2	13.5	14.3
P ₂ max breadth	-	-	-	-	-	-	8.8	10.3	9.3	10.0	9.4	10.2	9.1	9.4	8.3
P ₃ length	19.4	-	-	18.9	19.5	19.6	19.5	19.4	20.5	19.6	19.7	21.6	18.4	20.0	18.7
P ₃ max breadth	13.1	-	-	13.3	13.8	14.0	13.1	13.8	13.5	13.4	14.0	14.4	12.8	13.3	10.8
P ₄ length	20.1	-	20.9	-	20.1	21.5	19.8	21.2	20.2	22.8	21.4	22.7	20.3	21.6	20.3
P ₄ max breadth	12.4	-	12.1	-	12.8	12.7	12.4	13.0	11.7	12.3	11.5	12.6	10.8	12.0	10.8
M ₁ length	28.0	-	-	-	26.7	-	26.6	25.9	26.4	26.2	26.9	28.1	26.0	27.1	20.0
M ₁ max breadth	11.6	-	-	-	11.8	-	11.7	12.0	10.8	10.8	10.5	11.6	11.2	11.3	10.1
Breadth of mandibular condyle	-	+38.0	-	-	-	-	-	-	40.8	38.4	39.6	45.2	41.6	27.0	28.0
Height of mandibular condyle	-	18.0	-	-	-	-	-	-	16.2	14.8	14.2	18.4	15.4	10.7	12.4

Tab. 2 - Selected measurements (mm) of the mandible and lower teeth of *Crocota cf. ultra* (UPOP15#01) from Site MCK East and *Crocota sp.* (UPOP15#31) from Loc. 64, Naisiusiu area, Olduvai Gorge (Tanzania), compared to fossil *Crocota ultra* from Olduvai and living *Crocota crocuta* and *Hyaena hyaena*. LCCO Crocuta 6 is a juvenile individual. Estimated measurements are in italics.

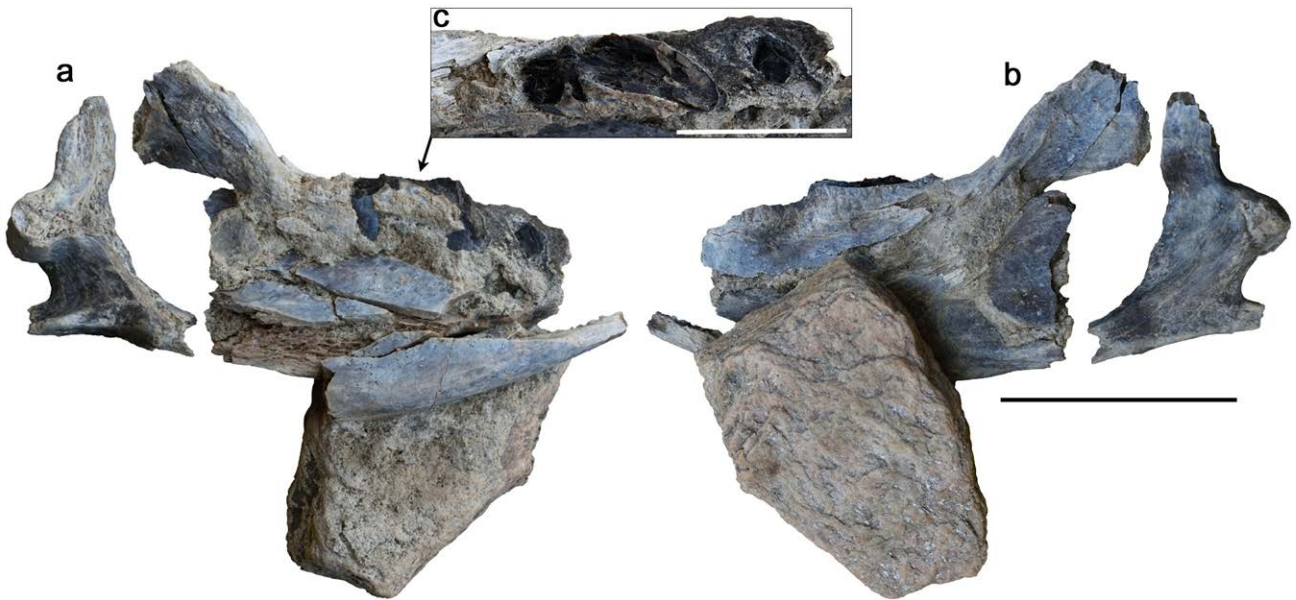


Fig. 6 - *Crocuta* sp. (UPOP15#31) from Loc. 64, Naisiusiu area, Olduvai Gorge (Tanzania). Left dentary in a) lingual view; b) labial view; c) close-up of the teeth in occlusal view. Scale bars correspond to: a, b) 5 cm; c) 3 cm. Online version in color.

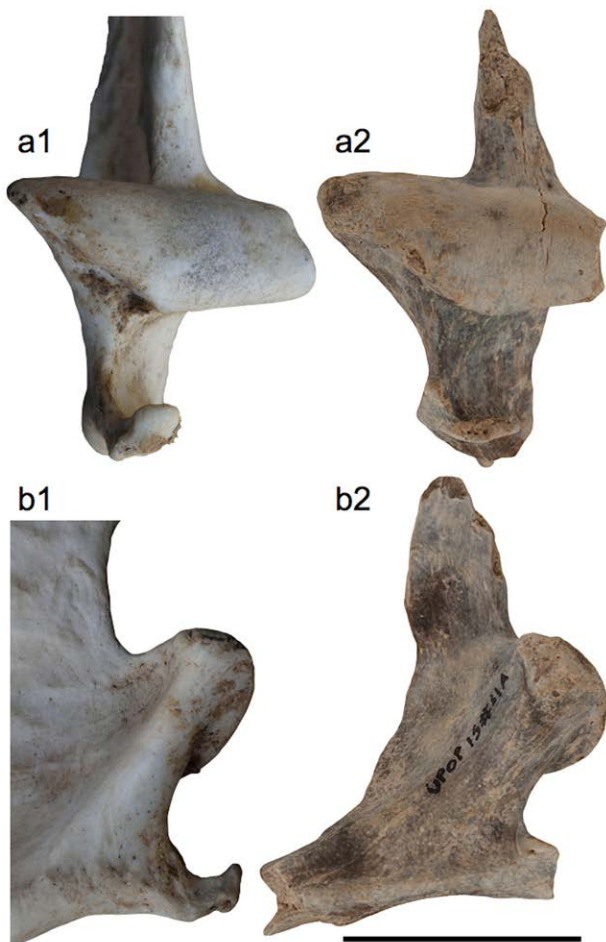


Fig. 7 - Comparative condylar morphology of *Crocuta crocuta* (a1-b1) and *Crocuta* sp. UPOP15#31 (a2-b2): a1-a2) caudal views; a2-b2) labial views. Scale bar corresponds to 3 cm. Online version in color.

Locality - Naisiusiu area, Geological Locality 64 (Hay, 1976), western part of the Main Gorge, Olduvai Gorge, Tanzania (Fig. 1).

Stratigraphy and age - Bed I, Early Pleistocene (Fig. 1).

Description - The specimen (Fig. 6) is very damaged and crushed laterally, broken in two parts, one including the corpus with roots of P_4 - M_1 and the first part of the ramus, the other including the condylar and angular processes. A piece of pinkish granite was left attached to the labial surface so as not to further endanger the stability of the fossil. In labial view, the masseteric fossa is visible and does not reach the M_1 as in UPOP15#01. In occlusal view, the distal root of P_4 and the root of M_1 are in situ. Even if fragmented, the M_1 appears long and laterally compressed. Posteriorly, the condylar process is large and strong, enlarging dorsoventrally in the medial portion (Fig. 7). The angular process is slender and its ventral tip is curved in a medial direction in caudal view.

Remarks - The general morphology of UPOP15#31 (e.g., very long and laterally compressed lower carnassial, dorsoventral enlargement of the medial portion of the condyle, distance between the condylar and angular processes) resembles that of a hyaenid (Figs 6-7) and not that of other carnivorans of the same size. For example, in pantherine cats such as the lion *Panthera leo* (Linnaeus, 1758), the M^1 is shorter and laterally larger, the mandibular condyle is laterally broader and the angular process more massive. In the light of the size of the condylar process (Tab. 2), which is considerably broader than that of *H. hyaena*, we identify UPOP15#31 as *Crocuta* sp. (Fig. 7).

CONCLUSIONS

The study of the carnivore guild in hominin-bearing paleontological sites such as Olduvai Gorge, is of great importance to help reconstructing the paleoecological context and to infer information about the interactions between the hominins and carnivores. These interactions are well studied at Olduvai from two different points of view: hominin-carnivore competition for prey and carcasses (Blumenschine, 1995; Pante et al., 2012) and predation pressure on paleolandscapes (Njau & Blumenschine, 2012). The Hyaenidae are a very interesting group to investigate, given their strong ecological impact on the present and past ecosystems, including their possible interactions with early hominins.

Fossil carnivorans are quite rare at Olduvai compared to other mammal groups and often represented by not sufficiently complete material to allow precise taxonomic determinations (Leakey, 1965). At least 20 Carnivora species belonging to five-six families (Herpestidae, Felidae, Hyaenidae, Canidae, Viverridae and dubitatively Mustelidae, listed in order of species diversity) are reported from Olduvai Bed I and II (Petter, 1973; Werdelin & Peigné, 2010). The new craniodental fossils presented in this paper is added to the poor hyaenid material described so far (Leakey, 1965; Petter, 1973), confirming the co-occurrence of at least two genera, *Crocota* and *Hyaena*, in the lower part of the Olduvai succession (undescribed material of the cursorial hyena *Chasmaporthetes* cf. *australis* from Bed I is also reported by Werdelin & Peigné, 2010). The probable sympatry between the large and robust *Crocota* and the small and slender *Hyaena* in the Olduvai Bed I-II carnivore guild is mirrored today in many African ecosystems, where the spotted hyena and the striped hyena share the same habitats (Holekamp & Kolowski, 2009; Kingdon & Hoffmann, 2013).

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