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Leonardo Salari[1], Maurizio Gatta[1], Angelica Fiorillo[1,2,*], Ivana Fiore[3,4], Piero Ceruleo[5], Giuseppe Di Stefano[6], Angelica Ferracci[1,7], Mario Federico Rolfo[1] and Carmelo Petronio[8]

1 Dipartimento di Storia, Patrimonio Culturale, Formazione e Società, Università degli Studi "Tor Vergata", Roma, Italy

2 Dipartimento di Beni Culturali, Università di Bologna, Ravenna, Italy

3 Laboratorio di Archeozoologia, Sezione di Bioarcheologia, Museo delle Civiltà, Roma, Italy

4 Dipartimento di Biologia Ambientale, "Sapienza" Università di Roma, Italy

5 Via Giotto 18, Tivoli (Roma), Italy

6 Roma (Italy) - joedistefano@libero.it

7 Servizio Archeologico, Belle Arti e Paesaggio per le Province di Frosinone e Latina, Rome, Italy

8 Fondazione Roma Sapienza, Italy

**Corresponding author*

E-mail address: angelica.fiorillo@uniroma2.it

Phone: +39 3891155533

ORCID: https://orcid.org/0000-0002-8690-1277

ABSTRACT

Recent excavations in Grotta Guattari (Circeo Promontory, southern Latium, Italy), in an area that had never been investigated before, the so-called *Antro del Laghetto*, returned abundant fossil remains of cave hyena. The newly acquired chronology of Grotta Guattari speleothems has allowed us to date the hyena frequentation, and thus the bone accumulations of this part of the cave, around 65 ka (Late Pleistocene, MIS 4). Comparisons with mandibles and upper and lower jugal teeth of extinct and extant hyenas have led to the determination that the species that occupied Grotta Guattari is *Crocuta spelaea*. The cave hyena from Grotta Guattari had robust jaws and it was relatively large, with some specimens among the largest in Western Europe. Comparisons with the age at death classes of main preys of modern and Late Pleistocene predators suggest that the bone accumulations can be referred to the hunting activity by *Crocuta spelaea*, which introduced only parts of the carcasses into the cave. Comparisons with dens of modern and Late Pleistocene hyenas suggest this part of Grotta Guattari had a multiple use (storage + communal den), an occurrence already documented in other Late Pleistocene sites. Finally, some cases of cannibalism were described.

KEYWORDS: Quaternary, southern Latium, *Crocuta spelaea*, predatory behaviour, hyena dens, cannibalism.

Introduction

The Hyaenidae Gray, 1821 family comprises four living species: The striped hyena, *Hyaena hyaena*, (Linnaeus, 1758), the spotted hyena, *Crocuta crocuta* (Erxleben, 1777), the brown hyena, *Parahyaena brunnea* (Thunberg, 1820) and the aardwolf, *Proteles cristatus* (Sparrman, 1783) (Koepfli et al., 2006; Wilson & Reeder, 2005). Except for the latter, a termite-feeding specialist, the other species are known for the strength of their bite, due to a craniodental morphology adapted to cracking and crushing the bones of prey and/or scavenged carcasses.

The current distribution of the spotted hyena and the brown hyena is exclusively in sub-Saharan Africa, while the striped hyena is present both in central-northern Africa and in part of south-western Asia up to India (Mills, 1998; Wilson & Reeder, 2005).

Several species of Hyaenidae populated Eurasia during the Pleistocene. In Italy, *Chasmaporthetes lunensis* (Del Campana, 1914), *Pliocrocuta perrieri* (Croizet and Jobert, 1828) and *Pachycrocuta brevirostris* (Gervais, 1850) were present during the Early Pleistocene, while *Hyaena prisca* De Serres, Dubreuil and Jean-Jean, 1828 and various species and/or subspecies of *Crocuta* Kaup, 1828 mainly in the Middle and Late Pleistocene (Gliozzi et al., 1997; Iannucci et al., 2021; Palombo et al., 2008; Petronio et al., 2011, 2019). Fossil remains referred to *H. prisca*, whose systematic position is debated (Iannucci et al., 2021; Pérez-Claros, 2024; Turner et al., 2008; Werdelin & Solounias, 1991), are sporadic, while the vast majority of bone-cracking hyena remains has been referred to the genus *Crocuta* (e.g., Bonifay, 1971; Caloi & Palombo, 1986; Iannucci et al., 2021; Lewis & Werdelin, 2022; Palombo et al., 2008; Petronio et al., 2011, 2019; Werdelin & Solounias, 1991).

The oldest European remains referred to *Crocuta* are those of the final Early Pleistocene found in the TD4 level of Trinchera Dolina from Atapuerca (Garcia & Arsuaga, 2001) and from Cueva Negra del Estrecho del Río Quípar (Walker et al., 2020) in Spain, stratigrafically placed below the Matuyama-Brunhes geomagnetic reversal boundary. *Crocuta* remains (i.e. two incomplete

hemimandibles and an ulna) from the Casal Selce (Rome) deposits in central Italy are slightly more recent, immediately placed above the Matuyama-Bruhnes boundary (Sardella & Petrucci, 2012).

In Eurasia, *Crocuta* would have left its last occurrences around 40 ka in Central Europe and Russia (Diedrich, 2024; Stuart & Lister, 2014), and not beyond 31 ka ago in Southern Europe (Stuart & Lister, 2014). However, recent studies suggest it might have persisted until 25 ka in France (Brugal et al., 2020) and until the Last Glacial Maximum, approximately around 20 ka, in Italy (Petronio et al., 2007, 2011). More recent radiometric dating based on hyena coprolites should be considered unreliable, due to the susceptibility to contamination associated with these biological remains (Bon et al., 2012; Diedrich, 2012; Gatta et al., 2016).

According to some authors, a single species for the entire history of the genus *Crocuta* existed (i.e. *C. crocuta*) (e.g., Diedrich, 2011; Iannucci et al., 2021; Kurtén, 1957, 1968; Turner, 1984, 1990). However, studies on mitochondrial DNA have highlighted the presence of two distinct groups in European fossils, suggesting that multiple migratory waves from the same native African species were at the origin of the Eurasian Pleistocene populations (Roholand et al. 2005). Further molecular studies (Sheng et al., 2014; Westbury et al., 2020) have shown that, although indistinguishable in morphology, the European and Chinese Late Pleistocene *Crocuta* are quite distinct genetically, whereas European Late Pleistocene and extant African *Crocuta* have been viewed as conspecific, despite being quite distinct morphometrically.

Numerous *Crocuta* fossil remains, mostly African but also Eurasian, have been recently re-examined demonstrating that *C. crocuta* occurred for the first time in Africa only in the Late Pleistocene (Lewis & Werdelin, 2022). Furthermore, two different species lived in Europe, *Crocuta intermedia* (De Serres, Dubreuil and Jean-Jean, 1828) during the Middle Pleistocene and *Crocuta spelaea* (Goldfuss, 1823) in the Middle-late and Late Pleistocene (Lewis & Werdelin, 2022). This work tentatively follows the Lewis and Werdelin (2022) systematics.

Therefore, Middle Pleistocene fossil remains attributed to the different forms of *Crocuta* should be re-examined.

Recent archaeological excavations in Grotta Guattari (Circeo Promontory, central Italy) returned abundant fossil remains of cave hyena, especially teeth (Fiore et al., forthcoming; Petronio et al., 2021; Rolfo et al., 2023, 2025; Salari et al., forthcoming). This work aims to describe and discuss the aforementioned remains attributed to *C. spelaea* by comparing them with those of important Italian and Western European fossil deposits.

The cave

Grotta Guattari opens on the slopes of Monte Morrone in San Felice Circeo (southern Latium, Italy; Figure 1). The cave is an important prehistoric site known since 1939 following the fortuitous discovery of a Neanderthal skull (Blanc, 1939a), considered one of the best-preserved in the World. Two Neanderthal mandibles were also found (Blanc, 1939a; Sergi & Ascenzi, 1955). Numerous archaeological excavations were intermittently carried out inside and outside the cave until the 50s of the last century, discovering thousands of vertebrate remains and some Mousterian artifacts (Blanc & Segre, 1953; Taschini, 1979). The Neanderthal skull was initially interpreted as part of a cannibalistic ritual (Blanc, 1939a; Sergi, 1974; *inter alios*). Subsequent studies demonstrated that the modifications of the skull were carried out by hyenas and the cave was interpreted as a cave hyena den based on the gnawing traces on most of the faunal remains from the paleosurface and the abundance of coprolites (Piperno & Giacobini, 1991; Stiner, 1991a, 1991b, 1994; Toth & White, 1991).

Recent investigations have been carried out on the occasion of the eightieth anniversary of the discovery (2019), preliminarily to the construction of a new visit route of the cave by the *Soprintendenza Archeologia, Belle Arti e Paesaggio per le province di Frosinone e Latina*, with the collaboration of archaeologists from the University of Rome "Tor Vergata". The

excavations focused on areas that had never been investigated before, the so-called *Antro del Laghetto* (i.e. Chamber of the small lake) within the cave and a thick deposit outside, in front of the entrance (Rolfo et al., 2023, 2025). The analyses and study of the external area are still ongoing.

The *Antro del Laghetto*, mentioned for the first time by Blanc (1939b), opens in front of the *Antro dell'Uomo* (i.e. Chamber of Men) (Figure 1) and it has an irregular shape, elongated and narrow, with a maximum length of 9.93 m and a width of 3.6 m. The name of this chamber is clearly due to the seasonal presence, October to May, of a modest water basin powered by rising groundwater. The archaeological investigation of the *Antro del Laghetto* made it possible to study a deposit with a thickness between 0.47 m and 1.02 m and to identify and document four stratigraphic levels (Rolfo et al., 2023, 2025).The two levels (i.e. Level 2 and Level 3) identified beneath the superficial stalagmitic crust have yielded about 9300 mammal remains, of which over 1300 (14.4%) taxonomically identified, about sixty coprolites, a few human remains and some lithic artifacts (Rolfo et al., 2023, 2025; Salari et al., forthcoming). Radiometric dating of the paleosurface of the *Antro dell'Uomo* between 51 and 59 ka (Rolfo et al., 2023) substantially confirmed previous datings (Belluomini et al., 1990; Schwarcz et al., 1991), while Level 2 of the *Antro del Laghetto* provided radiometric dating around 65 ka, correlatable to the Marine Isotope Stage (MIS) 4 (Rolfo et al., 2023).

The most abundant species identified are *Cervus elaphus* Linnaeus, 1758, *C. spelaea* and *Bos primigenius* Bojanus, 1827, followed by *Sus scrofa* Linnaeus, 1758 and *Equus ferus* Boddaert, 1785 (Table 1). Further taxa, including some never identified before in Grotta Guattari such as *Felis silvestris* Schreber, 1777, *Panthera spelaea* (Goldfuss, 1810), *Equus hydruntinus* Regalia, 1907 and *Rupicapra* Blainville, 1816 sp., have also been discovered (Petronio et al., 2021; Rolfo et al., 2023, 2025; Salari et al., forthcoming). Most of the fossil remains examined show gnawing traces by a large carnivore, namely *C. spelaea* (Fiore, 2021; Fiore et al., forthcoming;

Rolfo et al., 2023, 2025). The epiphyseal ends of the long bones have been removed by the chewing activity, and in some cases the margins also retain the hollow left by tooth contact and traces of gnawing. Modifications due to the activity of this carnivore are evident also on many fallen antlers of cervids, on some human bones and on those of the cave hyena itself (Fiore et al., forthcoming; Rolfo et al., 2025). In particular, from *Antro del Laghetto* at Grotta Guattari traces of cannibalism by cave hyena have been found on various elements of *C. spelaea* of both the skull and postcranial remains. A skull fragment with the snout part missing shows zig-zag fracture margins and rounded edges, and some jaw fragments show more or less evident traces on the margins, in particular one has repeated and overlapping furrows on the mandibular branch lower edge (Rolfo et al., 2025; Fig. 12AB); some punctures were also found on the teeth. Regarding the postcranium remains, scores left by cave hyena bites are present on the atlas, coxal, humerus, ulna (Figure 2) and tibia.

Therefore, levels 2 and 3 of the *Antro del Laghetto* returned clear indications of the cave hyena occupation (Fiore et al., forthcoming; Petronio et al., 2021; Rolfo et al., 2023, 2025; Salari et al., forthcoming), as well as the paleosurface of the *Antro dell'Uomo* and the *Vano Principale* (i.e. Main chamber) (Piperno & Giacobini, 1991; Stiner, 1991a, 1991b, 1994). Furthermore, the relative abundance and distribution of coprolites have allowed us to hypothesize that the *Antro del Laghetto* was near another entrance to the cave, currently obliterated, parallel to the current one (Rolfo et al., 2023, 2025).

Finally, a peculiar aspect of this part of the cave is the large amount of *C. spelaea* remains (21.6%) which, generally, in the various Italian deposits is present with few finds compared to those of Ungulates: For example, the cave hyena remains in the nearby Grotta La Sassa (Gatta et al., 2022) and in the Mousterian levels of Grotta del Fossellone (Alhaique & Tagliacozzo, 2000) and Cava Muracci - Area 3 (Gatta et al., 2019) are respectively 7.2%, 0 .6% and 2.4%.

Material and Methods

The cave hyena remains recovered from the *Antro del Laghetto* at Grotta Guattari between 2019 and 2022 were examined in the Laboratory of Prehistoric Archeology of the University of Rome "Tor Vergata".

The fossil material was compared with osteological material, both fossil and recent, from the aforementioned Laboratory with the support of Pales and Lambert (1971). Most of the finds are very fragmented due to the destructive action carried out by the cave hyena, by trampling, typical of restricted spaces such as the caves, and by the water action due to the aforementioned rising groundwater, but several intact and some articulated bones were also found. Furthermore, a high percentage of the fossils are covered by calcium carbonate concretions (Figure 3C). However, this feature did not hinder taxonomic and anatomical identifications, albeit careful measurements were sometimes not possible. Measurements were taken with a standard calliper according to Cardoso (1993, Fig. 3), for the mandible, and Werdelin and Solounias (1991, Fig. 2), for upper and lower carnassials, whose symbologies are also adopted, and expressed in mm. The age at death was estimated according to the stage of fusion of the long bone epiphyses and tooth eruption, replacement and wear stages, with the help of Brugal et al. (1997).

The measurements taken were compared with those of living *C. crocuta* (Cardoso, 1993; Lewis & Werdelin, 2022), *C. intermedia* from Lunel-Viel (Bonifay, 1971; Lewis & Werdelin, 2022) and *C. spelaea* from Grotte de Jaurens (Ballesio, 1979; Cardoso, 1993), Oubliettes de Gargas (Cardoso, 1993), Kent's Cavern, Tornewton Cave, Wookey Hole, Goyet Caves, Grotte de Rosée and Teufelslucke (Lewis & Werdelin, 2022). Furthermore, the teeth measurements of the cave hyena from Cava Muracci and Grotta La Sassa (Gatta et al., 2019, 2022 and unpublished data) are also proposed (Table 2). The above measures are shown in tables and processed in graphs, both bivariate scattergram and logarithmic decimal (Simpson's log-ratio diagram) according to Simpson (Simpson & Roe, 1939); in the latter case, the measurements

of the hemimandibles of living *C. crocuta* taken by Cardoso (1993) were used as reference. Finally, ternary diagrams to investigate the mortality profile of the most abundant Ungulates were made following the methodology of Stiner (1990).

Abbreviations: Dental terminology for the upper teeth is: I: Incisors, C: Canine, P: Premolars, M: Molars, D: Deciduous; the lower teeth are indicated by lowercase letters; L: Length, W: Width; LpP4: Length of paracone of P4; LmP4: Length of metastyle of P4; WaP4: Anterior width of P4 (at protocone); WblP4: Width of P4 between paracone and metastyle; Ltm1: Length of trigonid of m1. Other abbreviations (mandible): Lp3-p4: Length from front of p3 to back of p4; Lc-m1: Length from front of c to back of m1; Lp2-m1: Length from front of p2 to back of m1.

Systematic Notes

Order Carnivora Bowdich, 182

Family Hyaenidae Gray, 1821

Genus *Crocuta* Kaup, 1828

Crocuta spelaea (Goldfuss, 1823)

Material: The fossil remains attributed overall to *C. spelaea* from *Antro del Laghetto* at Grotta Guattari are listed in table 3. Only many isolated teeth, some hemimandibles, a III and a IV metacarpus, a patella and a tarsal bone have been preserved intact. Therefore, the morphometric analysis focused on the hemimandibles and the upper and lower cheek-teeth, both in the alveoli and isolated. The maxillary bones are all fragmented and P1 was preserved in very few specimens (Figure 3A). Four maxillae presented P2, P3 and P4 (Figure 3B), while in the other specimens there are only one or two premolars, all permanent. Even isolated upper cheek-teeth are all permanent. The odontometric data are recorded in table 4. For the premaxillary only the

second incisor is preserved. Isolated upper incisors and canines are all permanent; the incisors are scarce, while the isolated upper canines are 23 in total.

The mandibles are also mostly fragmentary. One mandible and three hemimandibles are almost intact (Figure 3C-F), while in the others only the horizontal branch or part of it has been preserved. All bear permanent teeth, often only a few cheek-teeth, and are referable to adult individuals, except for one fragment which presents erupting p3 and p4 (Figure 3G), referable to a young adult. Even in the mandibles few incisors and canines have been preserved; isolated incisors are scarce, while isolated lower canines are 24 in total, all permanent. Among the isolated lower cheek-teeth there are also some milk teeth, including a deciduous carnassial, d4 (Figure 3H). The measurements are recorded in tables 5 and 6.

The hemimandibles and the isolated lower carnassials are classified according to Brugal et al. (1997) as follows: one each in Stages I and III, 11 in Stage IV, five in Stage V and eight in Stage VI. Taking into account the other isolated teeth, the post-cranial bones, the lateralization and the stratigraphy, the *C. spelaea* fossil remains from *Antro del Laghetto* can be referred to at least 26 individuals, of which two very young, one young, one young adult, 14 adults and eight senile individuals.

Description and comparisons: In the maxillaries the jugal teeth are closely placed together, but without overlapping; they are all permanent and are very strong. The dimensions of the teeth of cave hyena from Grotta Guattari are on average larger than those of Cava Muracci and Grotta La Sassa (Table 4).

P1 is very small, oval in shape, with a single cusp and a ridge that crosses the entire length of the tooth. P2 has a protocone flanked anteriorly by an accessory cusp. The tooth is crossed by a ridge which, in the anterior part, continues towards the lingual surface to end on a very prominent cingulum which delimits the entire internal surface.

The graph (Figure 4) shows the minimum, medium and maximum values of the length and width of P2 of cave hyena from Grotta Guattari compared with those of living *C. crocuta*, *C. intermedia* from Lunel-Viel and *C. spelaea* from different sites of Western Europe. The values of the fossil specimens are all well aligned, with the exception of Grotte de Jaurens which has a trend curve with a slightly smaller angle, similar to that of living *C. crocuta*. The average P2 value of Grotta Guattari is close to the average of *C. spelaea* of the other sites and the maximum value of living *C. crocuta*; the latter is greater than the maximum value of *C. intermedia*. The maximum P2 value of Grotta Guattari is lower only than those of Teufelslucke and Kent's Cavern.

P3 is conical in shape, much higher than P2 and slightly higher than P4. The protocone is large and occupies practically the entire surface of the tooth, the metastyle is very small and the parastyle is barely perceptible.

The graph (Figure 5) reveals a certain alignment of the living *C. crocuta* with *C. intermedia*, while a greater dispersion in the values of *C. spelaea* is noted. The average P3 value of Grotta Guattari is close to that of *C. spelaea* of the other sites and to the maximum value of extant *C. crocuta*; the latter is smaller than the maximum value of *C. intermedia*. The minimum P3 value is slightly higher than that of other Pleistocene sites, while the maximum value is slightly lower.

The upper carnassial, P4, is the largest upper tooth. It appears powerful, with a high and sharp protocone, a reduced parastyle, a high and sharp paracone, a sharp and elongated metastyle, generally longer than the paracone, the talon is projected slightly forward and forms an oblique angle with the parastyle. This last feature, together with the dimensions, excludes any possible occurrence of *H. prisca*: Indeed, in this species the length of the tooth does not exceed 35 mm and the talon forms a right angle with the parastyle (Bonifay, 1971).

The graph (Figure 6) shows the values of the teeth of the fossil specimens quite aligned, while the curve of living *C. crocuta* has a different trend, with a slightly smaller angle. In particular,

P4 of Grotta Guattari has the same alignment as Kent's Cavern, Grotte de Rosée, Goyet Caves and *C. intermedia* from Lunel-Viel, while the slope of the trend curve of Teufelslucke and Tornewton Cave is slightly steeper. The average P4 value of Grotta Guattari is close to that of *C. spelaea* of the other sites and to the maximum values of *C. intermedia* and *C. crocuta*. The maximum P4 value is very close to those of Goyet Caves, Tornewton Cave and Wookey Hole, while those of Grotte de Rosée, Teufelslucke and Kent's Cavern are larger and those of Grotte de Jaurens are smaller in size than Grotta Guattari.

The hemimandibles have a very robust appearance, with a concavity of the lower edge of the horizontal ramus with maximum development under m1, a mental foramen under the anterior part of p2, a masseteric fossa that begins under the posterior part of m1 or immediately behind it and a relatively high and ample vertical branch. The osteometric data are exposed in table 5. Even in the mandible the jugal teeth are closely placed together, but without overlapping and are very strong. The tooth sizes of cave hyena from Grotta Guattari are on average larger than those of Cava Muracci and Grotta La Sassa (Table 6).

The decimal logarithmic graph (Figure 7) shows the average value of the hemimandibles of Grotta Guattari compared with those of the hemimandibles of *C. spelaea* from Gargas and Grotte de Jaurens, *C. intermedia* from Lunel-Viel and extant *C. crocuta*. It can be appreciated that the fossil specimens differ from those of the living spotted hyena particularly due to their larger size and the robustness of the horizontal branch. The *C. intermedia* hemimandibles differ from other fossil specimens above all due to the shorter lengths and the curve trend relating to the dental row lengths. Instead, the Grotta Guattari hemimandibles are characterized by their relatively large dimensions, particularly in the height of the horizontal ramus and in the width of the vertical branch, which is slightly lower than Grotte de Jaurens and *C. intermedia*.

Similar to the upper one, but smaller in size, p2 shows a robust protoconid and ridge that ends in the center of the anterior part of the tooth.

The graph (Figure 8) highlights the values of the fossil specimens are all fairly aligned. Goyet Cave differs, particularly in terms of minimum value, and it has a trend curve with a lesser slope, similar to that of *C. crocuta*. The average p2 value of Grotta Guattari is close to the average values of *C. spelaea* of the other sites and the maximum values of *C. crocuta* and *C. intermedia*. The maximum p2 value is similar to Goyet Cave and close to those of the other sites, with Wookey Hole, Teufelslucke and Kent's Cavern expressing the highest values.

Conical in shape and taller than the other teeth, also p3 is similar to the upper one, but slightly smaller in size, with a high protoconid that occupies practically the entire surface of the tooth and, when not worn, the ridges on the anterior and posterior sides of the cone can be appreciated. The values of the graph (Figure 9) are all fairly aligned. The Grotta Guattari average is close to the *C. spelaea* averages of the other sites and the maximum value of *C. crocuta*. The maximum p3 value is among the largest, close to Kent's Cavern, Goyet Cave, Wookey Hole and Teufelslucke.

The posterior premolar, p4, is lower than the previous tooth, but with relatively high and slightly inclined backwards protoconid, low and robust paraconid and metaconid. The paraconid is smaller but still distinct from the protoconid, the metaconid is broader and with two cusps.

The graph (Figure 10) shows the fossil specimens fairly aligned and, when they are not, such as Grotta Guattari and Tornewton Cave, the trend curve is almost parallel to the main alignment. Both the average and maximum values of Grotta Guattari are among the largest, and are slightly displaced to the left indicating decidedly wide and robust teeth. This feature clearly separates *C. spelaea* of Grotta Guattari from the extant *C. crocuta* which, according to Lewis and Werdelin (2022) is characterized by the reduction of the p4 width compared to the extinct species, both African and Eurasian. However, in the graph (Figure 10) the maximum value of *C. crocuta* is greater than that of *C. intermedia*, close to the average p4 values of *C. spelaea*, but the trend curve has a lower slope.

The lower deciduous carnassial, d4, shows a sharp anterior part formed by a protoconid and paraconid of equal length, but with the former slightly taller. This is followed by a more developed talonid, proportionally to the permanent carnassial, with sharpened endoconid and hypoconid.

The permanent carnassial, m1, is the longest lower tooth. It displays a symmetrical and sharp protoconid and paraconid, extremely reduced talonid and absent or barely perceptible metaconid. These features, together with the dimensions, exclude any possible occurrence of *H. prisca*: In fact, in this species the lower carnassial length rarely exceeds 25 mm, the talonid is reduced, but more developed than in *Crocuta*, and the metaconid is strong (Bonifay, 1971). The talonid of m1 of Grotta Guattari is very small and occupies between 5.8 and 7.0% of the tooth, values on average lower than those of living *C. crocuta* and among the lowest among those of *C. spelaea* (Table 7).

The graph (Figure 11) shows the values of all specimens fairly aligned with the exception of *C. intermedia* from Lunel-Viel which presents a trend curve with a slightly smaller angle. The average m1 value of Grotta Guattari is slightly lower than those of *C. spelaea* of the other sites, close to the minimum of Grotte de Jaurens and the maximum of extant *C. crocuta*. The maximum m1 value is slightly lower than those of Kent's Cavern, Goyet Cave, Wookey Hole and Teufelslucke, close to the maximum values of Grotta de Rosée and Grotte de Jaurens, slightly higher than that of Tornewton Cave.

In summary, the cave hyena mandibles from *Antro del Laghetto* at Grotta Guattari have a shape and size closer to those of *C. spelaea* from Gargas and Grotte de Jaurens than those of *C. intermedia* from Lunel-Viel and living *C. crocuta*. Tooth sizes, both in average and in minimum and maximum values, consistently fall within the range of variability of *C. spelaea* from the Western European sites and are always larger than those of *C. intermedia* from Lunel-Viel and living *C. crocuta*. Furthermore, the cave hyena from Grotta Guattari clearly differs from *H.*

prisca both in its larger size and in its dental morphology, particularly of the upper and lower carnassials. For all these reasons, the cave hyena remains from the *Antro del Laghetto* at Grotta Guattari have been attributed to *C. spelaea*.

Discussion

Cave hyena remains are quite common in the Late Pleistocene of Western Europe, particularly in cave sites where this carnivore was often the main agent of accumulation of faunal remains (Brugal et al., 2020; Diedrich, 2024; Sauqué et al., 2017). *Crocuta spelaea* is well represented also in northern (Minieri et al., 1995; Valensi, 2009), in central (Masseti & Salari, 2012; Minieri et al., 1995; Petronio et al., 2011) and in southern Italy (Mecozzi et al., 2018; Minieri et al., 1995; Pandolfi et al., 2017; Salari et al., 2019) during the Late Pleistocene. The cave hyena is mostly represented by scant remains that rarely exceed 10% of number of identified specimens (e.g., Buca della Iena, 17.8%; Pitti & Tozzi, 1971). Perhaps also for this reason there is a lack of adequate systematic studies on this carnivore.

The sizes of the jaws and teeth of the Grotta Guattari cave hyena were compared with large samples of *C. spelaea* from several Western European sites. The above-mentioned dimensions are always on average and some specimens are among the largest, as seen in the comparisons made. Furthermore, the sizes of *C. spelaea* from Grotta Guattari are larger than those from the nearby sites of Grotta La Sassa and Cava Muracci (Tables 4 and 6), and also from other small or very small collections, such as Gabasa 1 (Blasco Sancho & Montes Ramìrez, 1997) and Labeko Koba (Altuna & Mariezkurrena, 2000) in Spain, Gudenushöhle (Döppes, 1997) in Austria, Grotta B di Spagnoli (Sala, 1978), Grave della Nostra Famiglia (Salari, 2012), Tana delle Iene (Conti et al., 2012) and “Melpignano” (Iannucci et al., 2021) in Italy. Nevertheless, our specimens have a similar or slightly smaller size than those of Buca della Iena (Pitti &

Tozzi, 1971) in Italy, Réseau Salomé (Fourvel et al., 2017), Portel-Ouest and Bizé-Tournal (Testu, 2006) in France.

Compared to *C. spelaea* from Western European sites, the cave hyena from Grotta Guattari is characterized by the robustness of the mandible, both in the height of the horizontal ramus and in the width of the vertical branch, by the robust premolars, both upper and lower, and for the lower carnassial, m1, of modest dimensions, but very sharp and with an extremely reduced talonid. The differences found do not appear to depend on chronology: For example, the size of the teeth of *C. spelaea* from Wookey Hole (MIS 5), Kent's Cavern (MIS 3) and Teufelslucke (MIS 3) are almost always among the largest, while those from Grotte de Jaurens (MIS 3) are among the smaller ones. These differences could be attributed to different environmental and climatic adaptations or the type of predation (hunting or scavenging). The particularly robust jaw and premolars of the cave hyena from Grotta Guattari seem to be connected precisely to the strength of the bite, suitable for breaking and crushing the bones, a typical behaviour of these carnivores. This suggestion agrees with the high fragmentation of the fossil remains and the strong gnawing traces on the bones.

In order to have indications of the predation behaviour, the age classes of the Ungulates, potential prey of the cave hyena, have been examined. The Grotta Guattari mammal assemblage is mainly composed of adult individuals, while senile or young specimens are scarce, except for *Palaeoloxodon antiquus* (Falconer & Cautley, 1847), attested only by a few calves and very young individuals (Rolfo et al., 2025; Salari et al., forthcoming), as currently occur in cases of predation by extant *C. crocuta* (Salnicki et al., 2001). Therefore, two ternary diagrams were made, following the methodology proposed by Stiner (1990) and recently used by Pandolfi et al. (2013), Gatta et al. (2019, 2022), and Fiorillo et al. (forthcoming). The mortality profile of the most abundant ungulate from Grotta Guattari was compared with the mortality profile of the main prey of some modern carnivores and with those found in several Late Pleistocene sites

of central and southern Italy. The most abundant species and potential prey of the cave hyena of the *Antro del Laghetto* is *C. elaphus*. Considering the antler remains, some of which fallen antlers, the red deer is represented by two main age classes: one, more numerous, of individuals aged around 3-4 years and the other with some individuals over 12 years old. However, considering the fusion of the long bone epiphyses and tooth eruption, replacement and wear stages, the red deer is represented by six young, 19 adults and three senile (Rolfo et al., 2025; Salari et al., forthcoming). The red deer population of Grotta Guattari, based on the latter age at death classes, falls into the ”living-structure“ field (Figure 12). This would suggest an accumulation of specimens that died from natural causes as already recorded in several catastrophic death assemblages from the Late Pleistocene to recent times (Pandolfi et al., 2013; Stiner, 1990). However, in the ”living-structure“ field, with a high percentage of adult individuals, there are also bone accumulations by carnivores, both modern (Figure 12A) and from archaeological and paleontological sites (Figure 12B). Nevertheless, several bone accumulations by opportunistic predators who kill the prey according to availability in the territory, such as the lions, humans and, sometimes, wolves and hyenas, are also positioned in this field (Stiner, 1990). The possible contribution of wolves and lions to the *Antro del Laghetto* deposit in Grotta Guattari has already been excluded (Fiore et al., forthcoming; Rolfo et al., 2025) based on experimental archaeozoological data and the observations of various authors (Arriaza et al., 2016; Diedrich, 2010, 2014; Egeland et al., 2008; Haynes, 1983; Pokines & Peterhans, 2007; Yravedra et al., 2011;*inter alios*), while gnawing traces and other destructive activities by hyenas are numerous (Fiore, 2021; Fiore et al., forthcoming; Rolfo et al., 2025). As for humans, only two bones with butchering traces have been found so far, which could be interpreted as human waste introduced into the cave by the hyenas along with other remains. However, the sporadic frequentation of the cave by Neanderthals cannot be excluded (Rolfo et al., 2025). Albeit, the position of the *Antro del Laghetto* at Grotta Guattari would be closer to

the cases of predation by anatomically modern humans, such as Palidoro and Grotta Polesini, than by Neanderthals, such as Grotta dei Moscerini, Grotta S. Agostino and Grotta Breuil (Figure 12B). Finally, the scavenging activity would imply a high number of senile remains, "old dominated" or at least equal to that of adult individuals (Stiner, 1990), but the cases of predation and scavenging by spotted hyena on the Gemsbok, *Oryx gazella* (Linnaeus, 1758), and Mountain zebra, *Equus zebra* Linnaeus, 1758, from Namib Desert (Namibia) (Stiner, 1990; Tilson et al., 1980) are both distant in the graph from the position of the *Antro del Laghetto* at Grotta Guattari (Figure 12A). Moreover, the mortality profile of the red deer from Grotta Guattari is close to the hunting activity of the spotted hyenas on the Thompson's Gazelle, *Eudorcas thomsonii* (Günther, 1884), from the Serengeti (Tanzania - Kenya), among the cases of modern carnivores (Figure 12A) and to the main prey from Grotta La Sassa and Cava Muracci, among the cases of predation by Pleistocene hyenas (Figure 12B). Therefore, the bone accumulation is plausibly due to hunting activity by cave hyena which consumed part of the prey on the killing site, introducing only parts of the carcasses or specific anatomical elements into the cave. On the other hand, the occurrence of fallen antlers of cervids and probably also the long bones of pachyderms can be traced back to occasional scavenging.

The three abovementioned Late Pleistocene sites are all within the Pontine Plain: Cava Muracci in the centre of the plain, Grotta La Sassa in the hills of Ausoni Mounts and Grotta Guattari near the sea, in the Circeo Promontory. The small differences in the mortality profiles of the main prey of these three sites could relate to the different use of the three caves by the cave hyenas.

The widespread and holistic analyses of fossiliferous deposits produced by *C. spelaea* and comparisons with modern spotted hyenas of Africa allowed palaeontologists to recognise three main types of dens during the Late Pleistocene (Diedrich, 2014; Palomares et al., 2022):

1. “Cub raising den” or “Breeding den”: This typology of den is intended to wean newborns up to 1.5 years old. This peculiar den is usually of small size, sufficient to shelter only the mother with her offspring and easy to defend from predators but also other hyenas. Material evidence to denote this den usually is the high percentage of young and very young hyena individuals, together with numerous nibbling sticks, severe gnawing on prey remains and a high percentage of small/medium size prey.
2. “Communal den” or “Feeding shelter”: It is the most common type of den, inhabited by juveniles up to senile individuals, but bone remains mainly belong to adult/senile and display cannibalistic modifications. Prey remains are abundant, mainly belong to medium/large size prey and are severely gnawed, often fragmented up to be anatomically and taxonomically not identifiable. The widespread presence of coprolites, commonly used by these carnivores to mark their territory, is a basic feature to correctly interpret this typology of site.
3. “Storage den” or “Prey depot”: It is not a proper den as a hiding place to store preys that will not be eaten immediately. These hiding places are most common where food availability is not granted, such as in inhospitable regions or during adverse climates, such as the cold oscillation of the Late Pleistocene. The interpretation of these deposits is mainly based on the abundance of bone remains characterised by articulated body parts with slight or absent gnawing. The presence of few hyena remains, mostly adult or senile, and sporadic coprolites also indicate the origin of these deposits.

However, these patterns are to be considered general indicators since even among modern spotted hyenas are not always observed the same behaviours. Moreover, cave sites were probably frequented several times, perhaps with a different use, within a short time during the Late Pleistocene.

Cava Muracci (Areas 1-2-3) can be reliably identified as a cub raising den during MIS 3 based on the abovementioned parameters. The small bone assemblage (about 2000 remains), including small and medium-size mammals, has a high percentage of young specimens (Fiorillo et al., forthcoming; Gatta et al., 2019). Furthermore, only four individuals of *C. spelaea* have been discovered, one adult and three young, with evident cannibalistic traces. Gnawing modifications are also widespread on all other remains, suggesting heavy exploitation of soft tissues and trabecular bones. Nibbling sticks, toy bones gnawed by cubs to ease the development of teeth, are also common. Finally, the cave was small and with a vertical access, uneasy to access for predators.

Grotta La Sassa is a karst cave inhabited by cave hyenas and hibernating brown bears during a short timeframe of late MIS 3. The Late Pleistocene layers returned a rich fossil assemblage of about 4700 remains belonging to 87 individuals of at least 23 different taxa (Gatta et al., 2022). Cave hyena is represented by 8 individuals, newborns are absent while adults and senile represent the 75% and young-adults the 25% of total individuals. Preys are mostly represented by adults (> 50% of MNI) of large mammals. However, a very high percentage of the 77.3% could not be identified at the species/genus level due to the severe fragmentation. Taphonomic analysis revealed diffuse gnawing traces on 53% of total remains and a significant underrepresentation of epiphyses. Bone fragments partially digested and regurgitated, a well-known action among adult hyenas, are also very common. Finally, numerous hyena coprolites have been dropped to reclaim their spaces from nearby bears (Gatta et al., 2022), a behaviour already documented in other Pleistocene cave sites shared with other carnivores and in living hyenas (Bearder & Randall, 1978; Diedrich, 2012, 2014, 2015; Gatta et al., 2022; Horwitz & Goldberg, 1989). All these evidences strongly suggest an interpretation of the site as a communal den.

Grotta Guattari is a complex site whose paleontological evidence does not clearly suggest a specific type of den. The cave is constituted of several rooms, narrow passages, niches and multiple entrances certainly frequented by *C. spelaea* for several millennia during the Late Pleistocene. However, in-depth data is currently available only from the *Antro del Laghetto* (Fiore et al., forthcoming; Rolfo et al., 2023, 2025; Salari et al., forthcoming), therefore the interpretation is based on only a small part of the site and must be considered preliminary. The mammal assemblage recovered is extremely rich (> 9000 remains), albeit only 14.4% of remains could be taxonomically identified. The at least 25 taxa identified mostly belong to large mammals in their prime age (≈ 80% of the total) while young and senile specimens are present in significantly lower percentages. *Crocuta spelaea* is attested by 26 individuals, 14 of whom are adult and eight senile. All these features seem to clearly define a communal den. Nevertheless, the area returned a relatively low number of coprolites and a significant number of articulated body parts and spare bones without gnawing modifications, which are indicators of a storage den. All these evidence suggests the cave has an intermediate classification (storage + communal den), an occurrence already documented in other Late Pleistocene sites (Diedrich, 2011, 2014), which could be due to multiple indistinguishable frequentations or to behavioural variability of the clan that inhabited the cave.

The *Antro del Laghetto* at Grotta Guattari, finally, returned several cave hyena remains with obvious traces of cannibalism, i.e. traces of gnawing made by the hyena itself. Cannibalism among hyenas is a frequent behaviour probably scavenged, also attested at other Late Pleistocene European sites (Diedrich, 2020).

Conclusion

The study of the cave hyena remains recovered from the *Antro del Laghetto* deposit in Grotta Guattari leads to the determination that the species that occupied this part of the cave around

65 ka (Late Pleistocene, MIS 4) is *Crocuta spelaea*. This determination was reached through a detailed morphometric analysis of the mandibles and lower and upper jugal teeth of recovered Hyenids and the comparison with data from various Middle and Late Pleistocene deposits of Western Europe.

Crocuta spelaea from Grotta Guattari was relatively large in size, larger than those from the nearby sites of Grotta La Sassa and Cava Muracci, and also from other Italian and European localities, with some specimens among the largest in Western Europe. Moreover, the cave hyena from Grotta Guattari is characterized by the robustness of the mandible, both in the height of the horizontal ramus and in the width of the vertical branch, by the robust premolars, both upper and lower, suitable for breaking and crushing the bones of prey and/or of scavenged carcasses.

For these reasons, the numerous cave hyena remains from the *Antro del Laghetto* at Grotta Guattari are of extraordinary importance and represent an essential reference point for any morphometric comparison of this species.

Furthermore, *C. spelaea* is the main agent of accumulation of the mammal assemblage from *Antro del Laghetto*, as attested by the numerous gnawing traces on the bone remains, including some human bones and those of the cave hyena itself. This, together with the analysis of the age at death classes of the main prey and the predator, and the comparisons with the dens of the extant spotted hyena and the Pleistocene cave hyena, has allowed us to hypothesize some behaviours of the cave hyena in the Circeo Promontory and the Pontine Plain in the Late Pleistocene, during the final phases of MIS 4. On the one hand, the bone accumulations are probably mainly due to the hunting activity of cave hyenas that consumed part of the prey at the place of killing, introducing only parts of the carcasses into the cave, even if the occurrence of fallen deer antlers and perhaps also long bones of pachyderms can be traced back to a scavenger behaviour. On the other hand, *C. spelaea* used the *Antro del Laghetto* at Grotta

Guattari both as a storage and as a communal den, an intermediate and mixed use well documented in other Late Pleistocene cave hyena dens of Europe.

Data Availability Statement

The data that support the findings of this study are available from the corresponding author, A.F., upon reasonable request.

Acknowledgements

We thank Francesco Di Mario and Antonio Borrani of the *Soprintendenza Archeologia, Belle Arti e Paesaggio per le province di Frosinone e Latina* for the study permit, and Cristina Lemorini for the analyses Hirox 3D Digital Microscope at LTFAPA of the Department of Scienze dell'Antichità, "Sapienza" University of Rome. We also thank the editor, Mark T. Young, and two anonymous reviewers for all valuable comments and suggestions.

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Taxon	L. 2		L. 3		Total	
	NISP	**%**	**NISP**	**%**	**NISP**	**%**
Lepus sp.	5	0.6	1	0.2	6	0.4
Canis lupus	7	0.9	3	0.6	10	0.7
Vulpes vulpes	15	1.8	7	1.3	22	1.6
Ursus spelaeus			3	0.6	3	0.2
Ursus arctos	11	1.3	19	3.7	30	2.2
Mustelidae	1	0.1			1	0.1
Felis silvestris	2	0.2			2	0.1
Panthera spelaea	1	0.1	1	0.2	2	0.1
Panthera pardus	3	0.4			3	0.2
Crocuta spelaea	163	20.0	125	24.1	288	21.6
Palaeoloxodon antiquus	2	0.2	5	1.0	7	0.5
Elephantidae	8	1.0			8	0.6
Stephanorhinus cf. *S. hemitoechus*	2	0.2	1	0.2	3	0.2
Rhinocerotidae	5	0.6			5	0.4
Equus ferus	55	6.7	25	4.8	80	6.0
Equus hydruntinus			8	1.5	8	0.6
Sus scrofa	55	6.7	39	7.5	94	7.0
Megaloceros giganteus	37	4.5	14	2.7	51	3.8
Cervus elaphus	230	28.2	113	21.8	343	25.7
Dama dama	40	4.9	20	3.9	60	4.5
Capreolus capreolus	2	0.2	4	0.8	6	0.4
Cervidae	30	3.7	33	6.4	63	4.7
Bos primigenius	135	16.5	98	18.9	233	17.5
Capra ibex	3	0.4			3	0.2
Rupicapra sp.	1	0.1			1	0.1
Caprinae	3	0.4			3	0.2
Total identified specimens	816	100	519	100	1335	100
Identified specimens	816	18.8	519	10.5	1335	14.4
Indeterminate bones	3513	81.2	4443	89.5	7956	85.6
TOTAL	**4329**	**100**	**4962**	**100**	**9291**	**100**

Table 1. Grotta Guattari (Late Pleistocene, Latium): Number of identified specimens (NISP); L.: Level; (by Rolfo et al. 2025).

Site	Country	Age	References
Lunel-Viel	Hérault, France	Middle Pleistocene, MIS 9-8	Bonifay 1971; Cardoso 1993; Brugal et al. 2020
Wookey Hole	Somerset, United Kingdon	Late Pleistocene, MIS 5	Lewis & Werdelin 2022
Tornewton Cave (*Hyaena* Stratum)	Devon, United Kingdon	Late Pleistocene, MIS 5	Hodge et al. 2016; Lewis & Werdelin 2022
Grotta Guattari (*Antro del Laghetto*)	Latium, Italy	Late Pleistocene, MIS 4	Rolfo et al. 2023, 2025; this work
Kent's Cavern	Devon, United Kingdon	Late Pleistocene, MIS 3	Stuart & Lister 2014; Lewis & Werdelin 2022
Teufelslucke	Lower Austria, Austria	Late Pleistocene, MIS 3	Lewis & Werdelin 2022
Cava Muracci	Latium, Italy	Late Pleistocene, MIS 3	Gatta et al. 2019; this work
Grotta La Sassa	Latium, Italy	Late Pleistocene, MIS 3	Gatta et al. 2022; this work
Grotte de Jaurens	Corrèze, France	Late Pleistocene, MIS 3	Ballesio 1979; Cardoso 1993; Brugal et al. 2020
Goyet Caves	Namur, Belgium	Late Pleistocene, MIS 3	Peigné et al. 2009; Lewis & Werdelin 2022
Oubliettes de Gargas	Hautes-Pyrénées, France	Late Pleistocene	Cardoso 1993
Grotte de Rosée	Engis, Belgium	Late Pleistocene	Lewis & Werdelin 2022

Table 2. Sites and chronology of Quaternary species of *Crocuta* in Western Europe used for comparisons in this study. MIS: Marine Isotope Stage.

Skeletal elements	n.
Skull	18
Maxillary/Premaxillary	11
Upper teeth	76
Hemimandible	26
Lower teeth	103
Indeterminate teeth	5
Atlas	4
Axis	3
Vertebrae	11
Scapula	0
Humerus	1
Radius	0
Ulna	10
Carpal bones	0
Metacarpus	3
Pelvis	1
Femur	3
Patella	2
Tibia	2
Fibula	0
Talus	0
Calcaneus	0
Tarsal bones	1
Metatarsus	3
Phalanx I	1
Phalanx II	4
Phalanx III	0
TOTAL	**288**

Table 3. Grotta Guattari (Late Pleistocene, Latium): Skeletal elements of *Crocuta spelaea* from *Antro del Laghetto*.

	Grotta Guattari					Cava Muracci (3)					Grotta La Sassa				
	n.	min	max	mean	s.d.	n.	min	max	mean	s.d.	n.	min	max	mean	s.d.
L P2	10	16.2	19.6	18.06	1.043	1			15.40		5	16.3	18.4	17.18	0.776
W P2	10	12.4	15.2	13.52	0.985	1			12.40		5	11.7	12.8	12.34	0.488
L P3	14	23.4	26.6	24.59	0.854	3	21.8	24.1	23.20	1.229	7	22.3	25.8	23.86	1.450
W P3	14	16.6	19.6	18.22	1.028	3	16.8	18.1	17.50	0.656	7	15.4	17.8	16.56	0.920
L P4	21	37.6	44.0	40.65	1.678	2	36.7	37.2	36.95	0.354	5	38.2	39.8	38.92	0.729
LpP4	21	12.4	20.0	15.35	2.111	2	12.8	14.6	13.70	1.273	5	12.0	15.2	13.56	1.144
LmP4	21	13.8	21.0	17.31	1.456	2	16.1	16.2	16.15	0.071	5	15.4	17.8	16.80	1.039
LaP4	18	20.3	23.8	22.45	1.035	2	20.4	20.4	20.40	0	5	18.2	20.4	19.32	0.965
LblP4	20	11.2	14.0	12.68	0.761	2	11.3	12.5	11.90	0.849	5	11.8	13	12.64	0.477

Table 4. Measurements (mm) of upper teeth of *Crocuta spelaea* from Grotta Guattari, Cava Muracci and Grotta La Sassa (Latium, Italy); n.: number of measurements; min: minimum; max: maximum; s.d.: standard deviation.

Measurements	GG hemi 1	GG hemi 2	GG hemi 3	GG hemi 4	GG hemi 5	GG hemi 6	GG hemi 7	GG hemi 8	GG hemi 9	GG hemi 10	GG hemi 11	GG mean	GG s.d.
Lp3-p4	45.2	44.6	44.8	43.5	44.4		45.3	45.0				44.69	0.612
Lc-m1	113.0	112.3	113.0	114.0		109.6						112.38	1.668
Lp2-m1	90.1	86.5	87.2	87.5	87.5	87.8	90.2	89.0	89.2			88.33	1.329
1	189.0	202.0	184.0	190.0								191.25	7.632
2	194.0	206.0										200.00	8.485
3	193.0	198.0	189.0									193.33	4.509
4	90.0	89.0										89.50	0.707
5	57.5	53.8	55.0	51.5	51.5	52.5	57.5		49.0	51.2		53.28	2.925
6	43.0	41.5	40.0	44.2		42.0	43.2	35.4	39.5		40.4	41.02	2.629
7	66.5	78.2	76.0	73.7	74.5							73.78	4.416
8	49.3	51.6	53.5	48.0	48.0	49.5	48.5	47.5	47.5	44.0	42.5	48.17	3.063

Table 5. Measurements (mm) of hemimandibles of *Crocuta spelaea* from Grotta Guattari. Lp3-p4: length from front of p3 to back of p4; Lc-m1: length from front of c to back of m1; Lp2-m1: length from front of p2 to back of m1; 1: maximum length from Condylar process to Infradental; 2: length from the Angular process to the Infradental; 3: length from the high posterior point of the vertical branch to the Infradental; 4: height of vertical branch from base of Angular process to Coronion; 5: height of the horizontal branch to back of m1; 6: height of the horizontal branch in front of p2; 7: distance from mesial edge of Condylar process to back of m1; 8: height of the horizontal branch between p3 and p4; GG: Grotta Guattari; hemi: hemimandible; s.d.: standard deviation.

	Grotta Guattari					Cava Muracci (3, 7)					Grotta La Sassa				
	n.	min	max	mean	s.d.	n.	min	max	mean	s.d.	n.	min	max	mesn	s.d.
L p2	22	15.7	18.1	17.12	0.587	3	15.1	16.2	15.53	0.586	3	15.8	16.7	16.43	0.551
W p2	22	11.0	13.8	12.35	0.650	3	10.6	11.6	11.27	0.577	3	11.6	12.2	11.87	0.306
L p3	26	20.2	25.4	22.43	1.293	3	20.8	21.6	21.30	0.436	2	23.2	23.2	23.20	0.000
W p3	26	14.7	19.2	16.62	1.250	3	15.5	16.2	15.80	0.361	2	16.2	16.8	16.50	0.424
L p4	27	20.8	25.1	23.00	0.993	3	21.8	23.2	22.27	0.808	4	21.6	24.3	22.98	1.282
W p4	27	13.4	17.2	15.09	0.833	3	14.2	15.0	14.47	0.462	4	15.2	15.7	15.45	0.289
L m1	23	29.2	34.2	31.07	1.314	4	29.8	31.3	30.53	0.695	4	29.4	30.2	29.80	0.365
Ltm1	23	26.9	32.2	28.89	1.367	4	27.2	29.8	28.53	1.226	4	26.8	27.8	27.28	0.411
W m1	21	12.4	14.8	13.47	0.610	4	13.2	13.8	13.38	0.287	4	13.6	14.2	13.85	0.252

Table 6. Measurements (mm) of lower teeth of *Crocuta spelaea* from Grotta Guattari, Cava Muracci and Grotta La Sassa (Latium, Italy); n.: number of measurements; min: minimum; max: maximum; s.d.: standard deviation.

Species/Site	min %	max %
Crocuta spelaea		
Wookey Hole	9.9	10.8
Tornewton Cave	8.9	9.8
Grotta Guattari	5.8	7.0
Kent's Cavern	4.7	9.5
Teufelslucke	8.8	10.0
Cava Muracci	4.8	8.7
Grotta La Sassa	7.9	8.8
Goyet Caves	9.9	13.0
Grotte de Rosée	8.9	9.5
Crocuta crocuta	6.9	9.6

Table 7. Length of the talonid of lower carnassial vs length of lower carnassial (%). Data from Lewis and Werdelin (2022) and this work; min: minimum; max: maximum.

Figure captions

Figure 1. A-B) Geographic location of Grotta Guattari (San Felice Circeo, central Italy) and some other sites quoted in the text; C) Map of Grotta Guattari with names of every trench and excavation area since 1939. Areas investigated between 2018-2023, i.e. *Antro del Laghetto*, in purple.

Figure 2. Grotta Guattari (San Felice Circeo, central Italy), Late Pleistocene, *Crocuta spelaea*: 1) localisation of ulna fragment on the complete element; 2) ulna fragment from *Antro del Laghetto*; 3) microscopic magnification of the gnawing (photo by Hirox 3DM by I. Fiore).

Figure 3. Grotta Guattari (San Felice Circeo, central Italy), Late Pleistocene, *Crocuta spelaea*: left maxillary A1) in occlusal view, A2) in lingual view; B) right maxillary in labial view; scale bar 5 cm; mandible C1) in labial view, C2) in occlusal view; left hemimandibles D1), E1 and F1) in lingual view, D2), E2 and F2) in labial view; scale bars 5 cm; right hemimandible fragment G1) in labial view, G2) in lingual view; scale bar 3 cm; lower deciduous carnassial H1) in lingual view, H2 in labial view; scale bar 2 cm (photos by M.F. Rolfo and L. Salari).

Figure 4. Scattergram of maximum length vs maximum width of the minimum, mean and maximum of upper P2 of cave hyaena from Grotta Guattari compared with the minimum, mean and maximum dimensions of *Crocuta spelaea* from several sites of the Late Pleistocene of Western Europe, *C. intermedia* from Lunel Viel and living *C. crocuta*. Number of measures in brackets; data from Bonifay (1971), Ballesio (1979), Cardoso (1993), Lewis and Werdelin (2022) and this work.

Figure 5. Scattergram of maximum length vs maximum width of the minimum, mean and maximum of upper P4 of cave hyaena from Grotta Guattari compared with the minimum, mean and maximum dimensions of *Crocuta spelaea* from several sites of the Late Pleistocene of Western Europe, *C. intermedia* from Lunel Viel and living *C. crocuta*. Number of measures in

brackets; data from Bonifay (1971), Ballesio (1979), Cardoso (1993), Lewis and Werdelin (2022) and this work.

Figure 6. Scattergram of maximum length vs maximum width of the minimum, mean and maximum of upper carnassial, P4, of cave hyaena from Grotta Guattari compared with the minimum, mean and maximum dimensions of *Crocuta spelaea* from several sites of the Late Pleistocene of Western Europe, *C. intermedia* from Lunel Viel and living *C. crocuta*. Number of measures in brackets; data from Bonifay (1971), Ballesio (1979), Cardoso (1993), Lewis and Werdelin (2022) and this work.

Figure 7. Simpson's log-ratio diagrams comparing the mean dimensions of the hemimandible of *Crocuta spelaea* from Grotta Guattari (n. 11 hemimandibles), Grotte de Jaurens (n. 13), Oubliettes de Gargas (n. 1) and *C. intermedia* from Lunel Viel (n. 13). Standard: *C. crocuta* (0, n. 13). Data from Bonifay (1971), Ballesio (1979), Cardoso (1993) and this work. Lp3-p4: length from front of p3 to back of p4; Lc-m1: length from front of c to back of m1; Lp2-m1: length from front of p2 to back of m1; 1: maximum length from Condylar process to Infradental; 2: length from the Angular process to the Infradental; 3: length from the high posterior point of the vertical branch to the Infradental; 4: height of vertical branch from base of Angular process to Coronion; 5: height of the horizontal branch to back of m1; 6: height of the horizontal branch in front of p2; 7: distance from mesial edge of Condylar process to back of m1; 8: height of the horizontal branch between p3 and p4.

Figure 8. Scattergram of maximum length vs maximum width of the minimum, mean and maximum of lower p2 of cave hyaena from Grotta Guattari compared with the minimum, mean and maximum dimensions of *Crocuta spelaea* from several sites of the Late Pleistocene of Western Europe, *C. intermedia* from Lunel Viel and living *C. crocuta*. Number of measures in

brackets; data from Bonifay (1971), Ballesio (1979), Cardoso (1993), Lewis and Werdelin (2022) and this work.

Figure 9. Scattergram of maximum length vs maximum width of the minimum, mean and maximum of lower p3 of cave hyaena from Grotta Guattari compared with the minimum, mean and maximum dimensions of *Crocuta spelaea* from several sites of the Late Pleistocene of Western Europe, *C. intermedia* from Lunel Viel and living *C. crocuta*. Number of measures in brackets; data from Bonifay (1971), Ballesio (1979), Cardoso (1993), Lewis and Werdelin (2022) and this work.

Figure 10. Scattergram of maximum length vs maximum width of the minimum, mean and maximum of lower p4 of cave hyaena from Grotta Guattari compared with the minimum, mean and maximum dimensions of *Crocuta spelaea* from several sites of the Late Pleistocene of Western Europe, *C. intermedia* from Lunel Viel and living *C. crocuta*. Number of measures in brackets; data from Bonifay (1971), Ballesio (1979), Cardoso (1993), Lewis and Werdelin (2022) and this work.

Figure 11. Scattergram of maximum length vs maximum width of the minimum, mean and maximum of lower carnassial, m1, of cave hyaena from Grotta Guattari compared with the minimum, mean and maximum dimensions of *Crocuta spelaea* from several sites of the Late Pleistocene of Western Europe, *C. intermedia* from Lunel Viel and living *C. crocuta*. Number of measures in brackets; data from Bonifay (1971), Ballesio (1979), Cardoso (1993), Lewis and Werdelin (2022) and this work.

Figure 12. Ternary diagrams showing the mortality profile of *Cervus elaphus* from Antro del Laghetto at Grotta Guattari compared with mortality profiles of main preys of A) extant large carnivores and B) Late Pleistocene sites of central and southern Italy (data by Stiner 1990; Pandolfi et al. 2013; Gatta et al. 2019, 2022 and Fiorillo et al. forthcoming).