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General Palaeontology, Systematics, and Evolution (Vertebrate Palaeontology)

### The Late Pleistocene faunal assemblage from Cava Muracci (Latium, Italy): Palaeoenvironmental implications for coastal central Italy during MIS 3

*Assemblage faunique du Pléistocène supérieur de Cava Muracci (Latium, Italie). Implications paléoenvironnementales pour l'Italie centrale côtière pendant le stade MIS 3*

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#### ABSTRACT

Palaeoenvironmental information on Marine Isotope Stage 3 (MIS 3) coastal Latium is sparse, mainly based on studies of isolated faunal assemblages or long pollen records from lake sediments, often of insufficient resolution to aid in palaeoenvironmental reconstruction. This study describes in detail the Late Pleistocene faunal assemblage from layers SU11 and SU12 of Cava Muracci (Cisterna di Latina, central Italy), the first of which is a partially-preserved hyena den. The first multi-disciplinary palaeoenvironmental reconstruction of coastal Latium between 34–44 ka BP, a critical time span for the presence of the latest Neanderthals and the arrival of Anatomically Modern Humans (AMH), is provided combining palaeoecological inferences from a previous pollen study of hyena coprolites with the palaeontological study described here. The results indicate a temperate climate and a landscape characterised by the coexistence of at least three habitats within a short distance between the coastline and the inland mountains, suitable for a wide variety of species.

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#### RÉSUMÉ

Les informations paléoenvironnementales sur le Latium côtier au stade isotopique marin 3 (MIS 3) sont sporadiques et basées principalement sur des études d'assemblages fauniques isolés ou sur les séquences polliniques des sédiments lacustres, qui ont souvent une résolution insuffisante pour une reconstruction paléoenvironnementale fiable.

##### Mots clés :

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Reconstitution environnementale  
*Crocota crocuta*  
Méditerranée

Cette étude se concentre sur l'assemblage faunique du Pléistocène supérieur des niveaux stratigraphiques SU11 et SU12 de Cava Muracci (Cisterna di Latina, Italie centrale), dont le premier est un repaire de hyènes, partiellement préservé. Nous présentons ici la première reconstitution paléoenvironnementale pluridisciplinaire du Latium côtier entre 34 et 44 ka BP, une période critique pour la présence des derniers Néandertaliens et l'arrivée de l'AMH. Cet article combine les inférences paléoécologiques d'une étude pollinique précédente effectuée sur des coprolithes de hyène, avec l'étude paléontologique présentée ici pour la première fois. Les résultats indiquent un climat tempéré et un paysage caractérisé par la coexistence d'au moins trois habitats proches du littoral et des montagnes intérieures, favorable à la présence d'une grande variété d'espèces.

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## 1. Introduction

The Pontine Plain is mainly known for Neanderthal discoveries in several caves of the Monte Circeo (Blanc, 1939a, 1939b, 1940a; Blanc and Segre, 1953) but several other Pleistocene fossiliferous sites have been discovered and studied (Table 1). Although the region has been widely investigated since the last century, studies have been mainly aimed at the analysis of archaeological data in relation to archaeological site function based on stand-alone analyses, while a more detailed understanding of the palaeoenvironmental setting is still lacking.

Previous environmental studies in the Pontine Plain have focussed on the Holocene period and pollen records extending back to Late Glacial or Marine Isotope Stage 3 (MIS 3) are limited (Barbieri et al., 1999; Chiarini et al., 2007; Haagsma, 1993; Sevink et al., 2013; Van Joolen, 2003; Veenman, 1996). The general interpretation of the climate during the Last Glacial is one of considerable variability, with dry and cold conditions alternating with warm and humid oscillations, a feature widely recognised in Mediterranean Europe (Allen et al., 2000; Sanchez-Gofñi et al., 2002). The global causes of the abrupt and repeated climate changes of this period are usually considered to be specific events, such as the Dansgaard–Oeschger events (Dansgaard et al., 1993), the Heinrich event 4 (H4) (Birner et al., 2016; Hemming, 2004) and severe changes to the amount of rainfall (Luetscher et al., 2015). Climate oscillations, probably related to the mentioned events (Allen et al., 2000; Watts et al., 1996), are known to have caused the rapid succession of seven regional tree fluctuations known as “Lazio Complex” in central Italy (Follieri et al., 1998). Although Latium is characterised by a peculiar climate regionalism, the variability of MIS 3 has certainly affected this region. However, a local environmental reconstruction to assess its effects in the Pontine Plain is missing.

Palaeoenvironmental and climate reconstruction of the Pontine Plain during the Late Pleistocene has been mainly based on lacustrine sediments situated rather far from the area under investigation such as: Lago di Lagaccione; Lago di Vico; Stracciacappa and Valle di Castiglione (Follieri et al., 1988, 1989, 1998; Giardini, 2007; Magri, 1999; Magri and Sadori, 1999). Nevertheless, such environmental reconstructions also show slight variations between sites in the same region, due to particular local landscape conditions. In this regard, the Pontine Plain has a distinctive landscape, very different in geomorphology and climate from

surrounding areas, which makes the environmental reconstruction based on distant lake sediments unsuitable. In this paper, we analyse the faunal assemblages of a promising site, Cava Muracci (Cisterna di Latina, Latium) (hereafter CM) and the related environmental implications, integrating the results with previously published pollen analyses of hyena coprolites from the same site (Gatta et al., 2016). Our aim is to offer a detailed palaeoenvironmental reconstruction of the Pontine Plain during MIS 3.

## 2. Palaeontological background and stratigraphic setting

### 2.1. Cava Muracci–Cisterna di Latina

The palaeontological site of Cisterna di Latina, Latium (hereafter CM) (41°35'53.4 “N 12°51'23.4” E) is located in the Pontine Plain, a 240-km<sup>2</sup>-wide region 100 m a.s.l. (De Santis et al., 1975), characterised by a mosaic of adjacent environments, 22 km inland from the present Tyrrhenian shoreline of South-West Latium (Fig. 1), on an extensive travertine surface at the base of the Lepini Mountains. The archaeological potential of this area was known in the past, since discoveries of both Upper Pleistocene and Holocene deposits were brought to light by quarrying already in the mid-1900s and again in the early 1990s (Rubini, 2003; Segre and Ascenzi, 1956). Nevertheless, the investigations have always only consisted of surface collections of artefacts without further study of their contextual associations.

In 2012, the fortuitous discovery of seven new caves following quarrying activities and their subsequent investigation yielded more than 2000 faunal remains, over 100 coprolites and a small collection of Mousterian and Aurignacian lithic artefacts (Gatta and Rolfo, 2017; Gatta et al., 2016). All the investigated areas yielded archaeological and palaeontological finds, albeit preservation of deposits and finds was extremely variable. All the sites are underground caves or sinkholes with vertical entry points and their sizes vary significantly from travertine cracks to small caves. Their distribution along the entire perimeter of the quarry suggests an intensely frequented area during the Late Pleistocene.

Area 3 is of particular interest. Despite the extensive destruction of the structure by quarrying activities, this single cave chamber, around 20 m<sup>2</sup>-wide, has yielded a multi-layered, well-preserved stratigraphy (Fig. 2) and the largest amount of finds in the quarry. The deposit,

**Table 1**

Main Pleistocene fossiliferous sites of the Pontine Plain.

**Tableau 1**

Principaux sites fossilifères du Pléistocène de la plaine pontine.

Site Name	Chronology	Bibliography	
Nettuno	Isernia F. U.	MIS 15	Mancini et al., 2008
Campoverde	Vitinia F. U. - Melpignano F. U.	MIS 7–MIS 5	Mazza et al., 1992; Petronio et al., 2011
Canale delle Acque Alte (also known as Canale Mussolini)	Melpignano F. U.	MIS 5–MIS 3	Blanc, 1935a, 1935b, 1940b; Farina, 2011
Cava della Catena - Terracina	Ingarano F. U.	MIS 4/3	Meli, 1894; Blanc, 1935b
Monte Circeo ( <i>Coelodonta antiquitatis</i> )	Ingarano F. U.	MIS 4/3/2	Palmarelli and Palombo, 1981
Monte Circeo Caves (i.e., Grotta del Fossellone, Grotta delle Capre, Grotta Barbara, Grotta Breuil, Grotta Elena, Grotta Guattari and others)	Ingarano F. U.	MIS 3/2	Blanc, 1937, 1938, 1939a, 1939c, 1954. For the faunal assemblages: Cusani Politi, 1976; Caloi and Palombo, 1987, 1989, 1991; Alhaique et al., 1996, 1998a, 1998b; Kotsakis, 1991; Ruffo and Zarattini, 1991; Stiner, 1991a, 1991b; Recchi, 1995
Riparo Salvini - Terracina	Ingarano F. U.	MIS 2	Bietti, 1984; Cassoli and Guadagnoli, 1987; Alessio et al., 1994; Recchi, 1995; Alhaique and Di Camillo, 2007; Tang and Kotsakis, 2008
Grotta della Cava - Sezze	Ingarano F. U.	MIS 2	Segre Naldini, 1984; Petronio et al., 2011

composed of four main layers, has been carefully excavated. SU11, a 45–100 cm-thick, compact layer of clay and clasts, is the most important layer. It contained abundant mammal remains, coprolites and sporadic lithic artefacts dating to the late Pleistocene, between 34,810 BP and 44,054 BP (Gatta et al., 2016). Beneath this layer, sealed by clasts and conglomerates, there was a different but undated clay layer (SU12) containing extremely rare lithic artefacts but several remains of small vertebrates. A *terminus post-quem* for this industry is offered by the underlying SU13, a tephra layer dated through  $^{40}\text{Ar}/^{39}\text{Ar}$  method to  $70 \pm 2$  ka (Gatta et al., 2017). The lowermost layer (SU14) is a very hard palaeosoil, probably reworked by water, as indicated by manganese patination. A few very fragmented bone remains and extremely rare lithic artefacts were discovered.

The morphology of the coprolites and the numerous bones showing gnaw marks of a large carnivore allowed a preliminary interpretation of layer SU11 as a layer frequented by hyenas, probably a den (Gatta and Rolfo, 2017; Gatta et al., 2016). The abundance and good preservation of the finds also permitted a set of multidisciplinary analyses, some of which are still ongoing, which greatly added to our understanding of this site and the surrounding area (Gatta and Rolfo, 2017; Gatta et al., 2016, 2017).

Sixteen coprolites recovered from SU11 have been chemically processed and microscopically analysed at Sapienza University of Rome in 2016 (Gatta et al., 2016), providing new insights into the local Late Pleistocene vegetation of coastal Latium (Fig. 3 and Gatta et al., 2016). The pollen spectrum reflects a mosaic landscape: Poaceae, Amaranthaceae, *Artemisia* and *Plantago* indicate steppe and grasslands plants, suggesting both dry and humid conditions within a short distance. The coexistence of mixed environments is also confirmed by mesophilous and thermophilous trees that indicate the presence of woodland areas, together with *Typha*, which suggests the presence of marsh environments. The climate indicated is cold and arid, while the presence of angiosperm trees may indicate

a patchy environment or warm and humid oscillations of the MIS3 (Gatta et al., 2016).

### 3. Material and methods

#### 3.1. Excavation

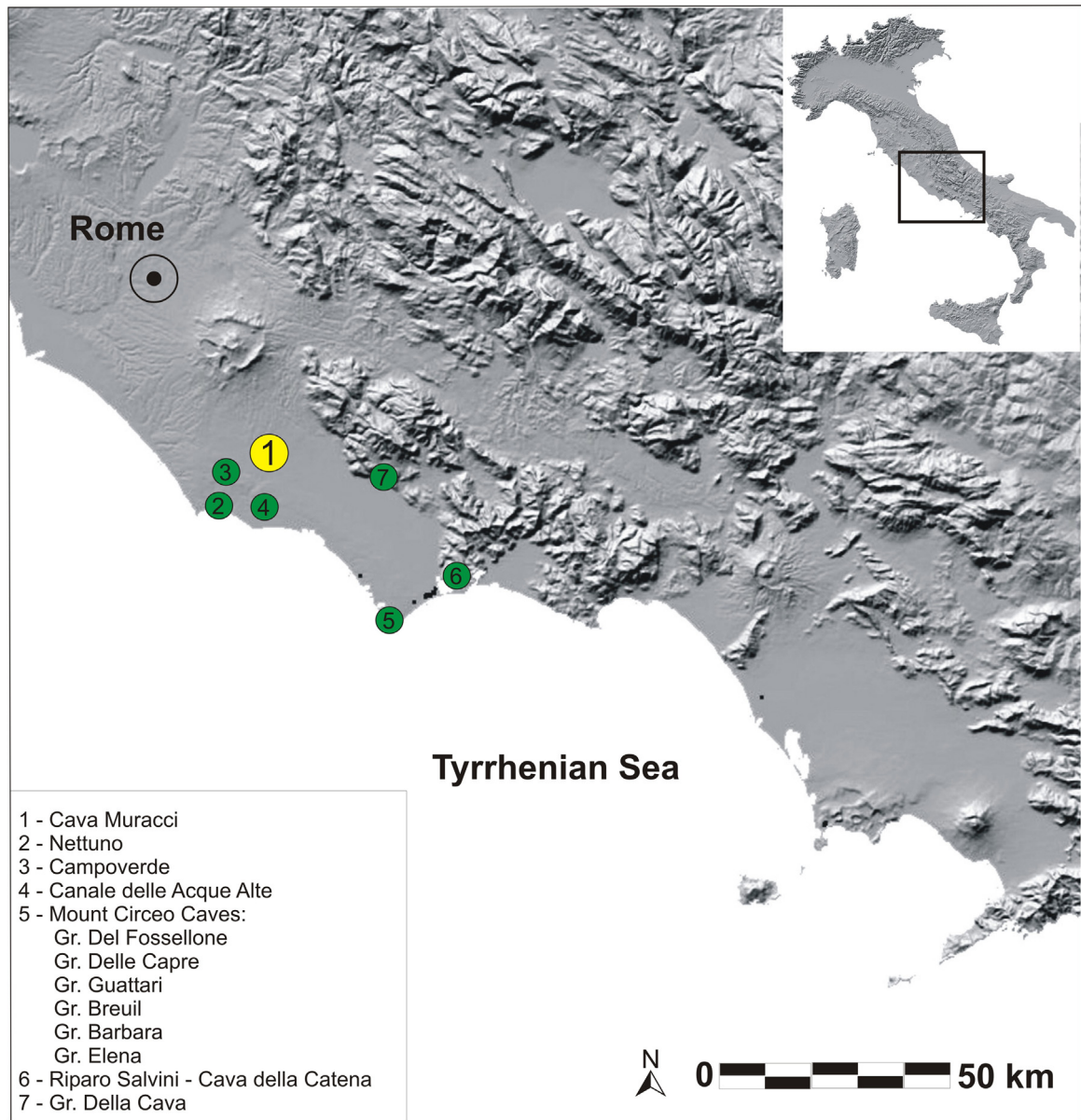
The faunal remains here presented have been excavated between 2012 and 2016 and are currently stored at the Laboratory of Prehistory, Department of History, Culture and Society, University of Rome Tor Vergata. A find number was assigned to each bone, which was recorded with its grid coordinates and depth within a  $1 \times 1$ -m excavation grid system. The soil was fully sieved with a 2-mm mesh in the field to ensure the recovery of microfauna and small macrofaunal bone fragments.

#### 3.2. The palaeontological study

This study involved 1466 fossil bones of macromammals, of which 656 (48.7%) were classified by taxon (Table 2). The number of remains belonging to small vertebrates (Fig. 4) from SU11 and SU12 amounts to several hundreds but only 61 could be assigned to genus or, more rarely, to species. All specimens described below are from layer SU11 unless indicated otherwise.

The aim of the faunal analysis was to provide information on each taxon and to infer palaeoenvironmental conditions to compare with the pollen study. To achieve these aims a detailed study of the fossil remains was undertaken, which included: (i) taxonomic analysis; (ii) taphonomic analysis; (iii) number of identified specimens (NISP) and estimates of minimum number of individuals from SU11 (MNI); (iv) estimates of age class at death.

The fossil remains were compared with osteological material, both fossil and recent, stored in the Department of Earth Sciences of the University of Rome “Sapienza”, in the Department of Sciences of the “Roma Tre” University and in the Museo Nazionale Preistorico Etnografico “Pigorini” of



**Fig. 1.** Location of Cava Muracci site (Cisterna di Latina, central Italy) and the main late Pleistocene sites of the Pontine Plain.

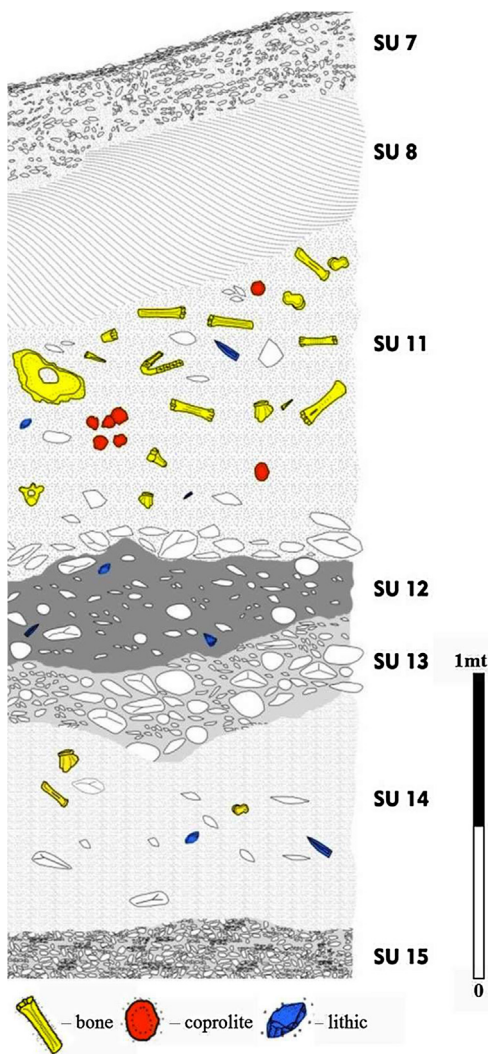
**Fig. 1.** Localisation du site de Cava Muracci (Cisterna di Latina, Italie centrale) et des principaux sites du Pléistocène supérieur de la plaine pontine.

Rome. The measurements of macromammal remains were taken with a standard calliper according to the [von den Driesch \(1976\)](#) methodology; the measurements and photos of microvertebrates were obtained with a Leica MZ6 microscope and a Leica Application Suite software version 2.6.0 R1.

The minimum number of individuals was calculated taking into consideration the side of each bone and the most frequent skeletal element from only one side; the results were integrated with the analysis of the metrical characters, sex and age profiles of the other skeletal elements. The estimated age of death was calculated according to the stage of fusion of the long bone epiphyses and

tooth eruption, replacement and wear stages, in particular according to [Barone \(1974, 1981\)](#) for present-day domestic cattle (as a proxy for *Bos primigenius*) and domestic horses (as a proxy for *Equus ferus*), [Hillman-Smith et al. \(1986\)](#) for *Ceratotherium simum* and [Goddard \(1970\)](#) for *Diceros bicornis* (as a proxy for *Stephanorhinus hemitoechus*; see [Pandolfi et al., 2013](#)), [Bull and Payne \(1982\)](#) for *Sus scrofa*, [Mariezkurrena \(1983\)](#) for *Cervus elaphus* and [Pappa et al. \(2005\)](#) for *Crocota crocuta*.

Taphonomic observations were performed taking into account several studies on the bone surface modifications made by extant large carnivores (e.g., [Arriaza et al., 2016](#); [Egeland et al., 2008](#); [Haynes, 1983](#); [Hill, 1989](#); [Sala et al.,](#)



**Fig. 2.** Stratigraphy of Area 3 from Cava Muracci: SU 7, modern external walking surface of the quarry composed of soil and gravel; SU 8, travertine ceiling of the cave; SU 11, highly consolidated red-brown clay soil with abundant remains of large mammals, small vertebrates, coprolites and rare lithics; SU 12, reddish brown layer with frequent small vertebrates and rare lithic artefacts; SU 13, greyish green layer of highly consolidated volcanic tephra and pyroclastic products; SU 14, reddish layer with extremely rare lithic and faunal remains; SU 15: travertine natural floor of the cave.

**Fig. 2.** Stratigraphie du secteur 3 de Cava Muracci : US 7, surface moderne extérieure de marche de la carrière composée de terre et de gravier ; US 8, plafond de travertin de la grotte ; US 11, sol argileux rouge brun fortement consolidé avec des restes abondants de grands mammifères, de petits vertébrés, de coprolithes et rares restes d'industrie lithique ; US 12, niveau brun rougeâtre riche en petits vertébrés et avec quelques rares objets lithiques ; US 13, niveau vert grisâtre de téphra volcanique très consolidé et de produits pyroclastiques ; US 14, niveau rougeâtre pauvre en restes lithiques et fauniques ; US 15, sol naturel de travertin de la grotte.

2014; Sutcliffe, 1970; Yravedra Sainz et al., 2011, 2012). Taphonomic observations were integrated by a ternary diagram made to investigate the mortality profile of the aurochs population (the most abundant ungulate taxon) to eventually support the hypothesis of a hyena-den accumulation, following the methodology of Stiner (1990), later adopted also by Pandolfi et al. (2013).

**Table 2**

Cava Muracci (Cisterna di Latina, central Italy), late Pleistocene. Number of identified specimens (NISP) from SU11 and SU12. For *A. italicus* only specimens with diagnostic characters (not based only on size) are considered.

**Tableau 2**

Cava Muracci (Cisterna di Latina, Italie centrale), Pléistocène supérieur. Nombre de spécimens identifiés (NISP) provenant d'US11 et US12. Pour *A. italicus*, nous avons considéré seulement les spécimens ayant des caractères diagnostiques (qui ne se basent pas uniquement sur la taille).

	NISP	%
Osteichthyes indet.	1	0.14
<i>Bufo bufo</i>	1	0.14
<i>Bufo</i> gr. <i>B. viridis</i>	1	0.14
<i>Rana</i> (s.l.) sp. 1	3	0.42
<i>Rana</i> (s.l.) sp. 2	1	0.14
<i>Podarcis</i> sp.	6	0.84
<i>Anguis veronensis</i>	6	0.84
<i>Natrix natrix</i>	5	0.70
<i>Hierophis viridiflavus</i>	2	0.28
Aves indet.	2	0.28
<i>Arvicola italicus</i>	16	2.23
<i>Microtus (Terricola) savii</i>	5	0.70
<i>Microtus (Microtus) arvalis</i>	5	0.70
<i>Myodes glareolus</i>	3	0.42
<i>Apodemus</i> gr. <i>sylvaticus-flavicollis</i>	3	0.42
<i>Glis glis</i>	1	0.14
<i>Lepus</i> sp.	18	2.5
<i>Canis lupus</i>	2	0.3
<i>Mustela nivalis</i>	1	0.1
<i>Meles meles</i>	1	0.1
<i>Crocuta crocuta</i>	17	2.4
<i>Equus ferus</i>	194	27.1
<i>Stephanorhinus hemitoechus</i>	1	0.1
<i>Sus scrofa</i>	2	0.3
Cervidae	9	1.3
<i>Capreolus capreolus</i>	1	0.1
<i>Cervus elaphus</i>	114	15.9
<i>Dama dama</i>	23	3.2
<i>Bos primigenius</i>	273	38.1
Total identified specimens	717	100.0
Identified specimens	717	47.0
Indeterminate bones	810	53.0
Total	1527	100.0

Environmental reconstructions are based on studies of the ecology and biogeographical distribution of modern taxa, particularly Boitani et al. (2003), Lanza et al. (2007a), Amori et al. (2008) and Corti et al. (2011) for living species, and previous palaeoenvironmental reconstructions (e.g., Conti et al., 2010, 2012; Pandolfi et al., 2013 and references therein) for extinct species.

Abbreviations: *L* = Length; *MC* = Metacarpal; *MT* = Metatarsal; *n* = number of specimens.

#### 4. Systematic notes and ecological indications

Osteichthyes indet.

Bony fishes are represented by a single vertebra in SU11.

*Bufo bufo* (Linnaeus, 1758)

A single presacral vertebra (procoelous, with very low neural crest, cylindrical transverse apophyses; see Bailon, 1991, 1999) belongs to the common toad *Bufo bufo*. Fossils belonging to *B. bufo* have been present in Italy since the late Miocene (Bartolini et al., 2014; Corbino, 2015; Curcio

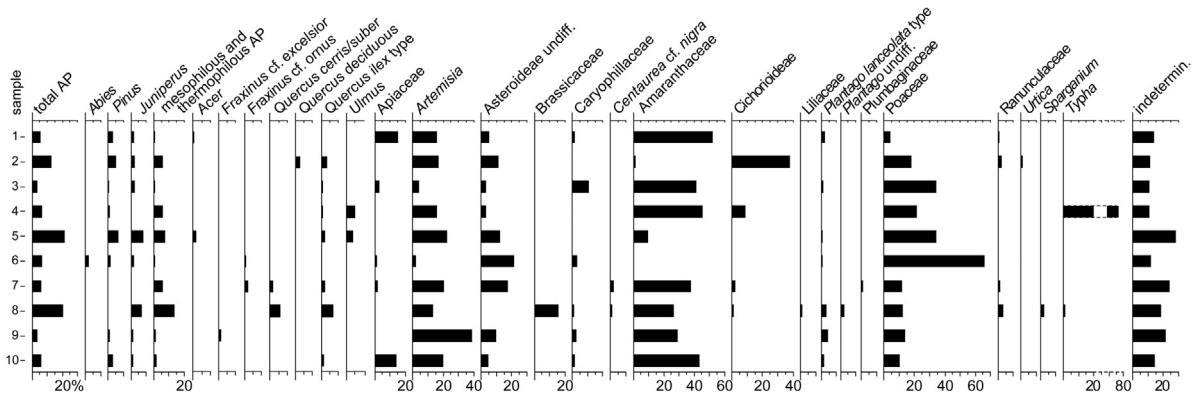


Fig. 3. Pollen diagram of hyena coprolites from SU11 of Area 3 at Cava Muracci (Cisterna di Latina, central Italy).

Fig. 3. Diagramme pollinique des coprolithes de hyène de l'US11 du secteur 3 à Cava Muracci (Cisterna di Latina, Italie centrale).

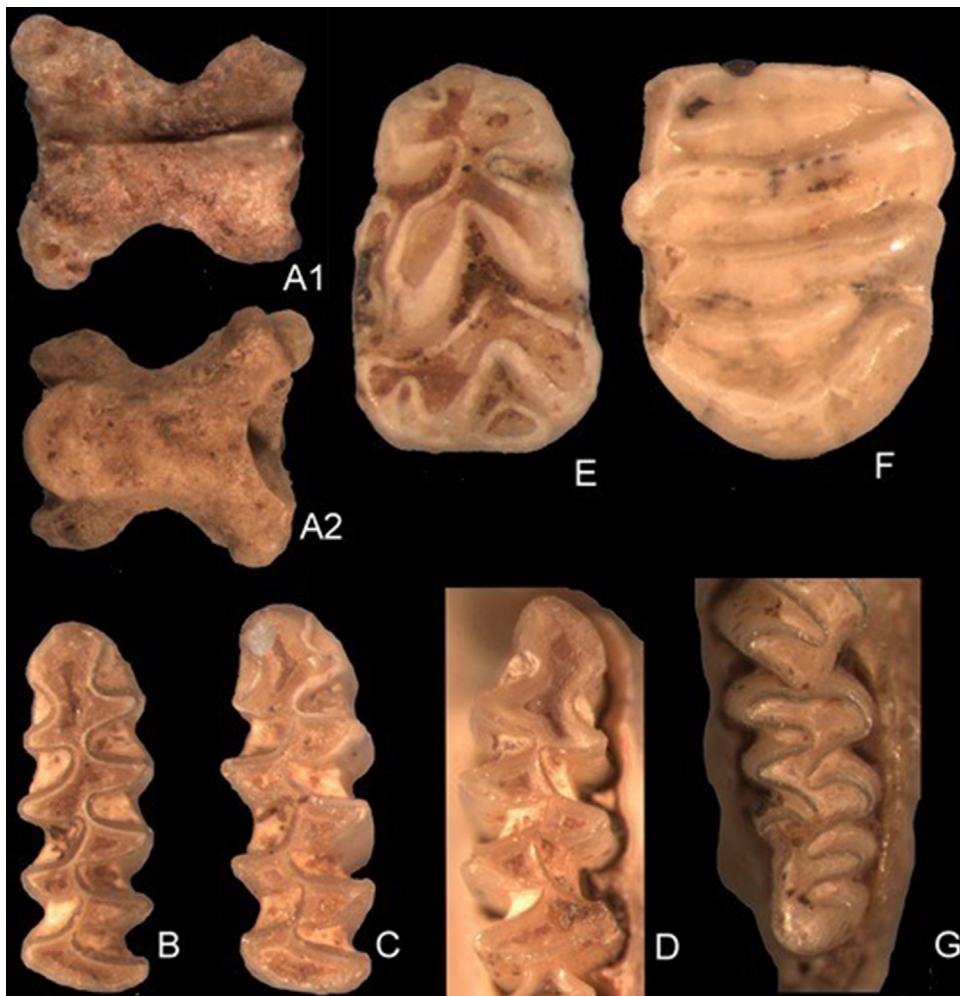


Fig. 4. Cava Muracci (Cisterna di Latina, central Italy), late Pleistocene. A. *Anguis veronensis*, dorsal vertebra, (A1) dorsal view, (A2) ventral view ( $L = 3.46$  mm) (SU11). B. *Microtus (Terricola) savii*, m1 left, occlusal view ( $L = 2.48$  mm) (SU11). C. *Microtus (Microtus) arvalis*, m1 left, occlusal view ( $L = 2.74$  mm) (SU12). D. *Arvicola amphibius*, m1 right, occlusal view ( $L = 3.93$  mm) (SU12). E. *Apodemus gr. sylvaticus-flavicollis*, m1 left, occlusal view ( $L = 1.60$  mm) (SU11). F. *Glis glis*, m3 left, occlusal view ( $L = 2.53$  mm) (SU11). G. *Myodes glareolus*, M3 right, occlusal view ( $L = 1.75$  mm) (SU11).

Fig. 4. Cava Muracci (Cisterna di Latina, Italie centrale), Pléistocène supérieur. A. *Anguis veronensis*, vertèbre dorsale, (A1) vue dorsale, (A2) vue ventrale ( $L = 3,46$  mm) (US11). B. *Microtus (Terricola) savii*, m1 gauche, vue occlusale ( $L = 2,48$  mm) (SU11). C. *Microtus (Microtus) arvalis*, m1 gauche, vue occlusale ( $L = 2,74$  mm) (SU12). D. *Arvicola amphibius*, m1 droite, vue occlusale ( $L = 3,93$  mm) (SU12). E. *Apodemus gr. sylvaticus-flavicollis*, m1 gauche, vue occlusale ( $L = 1,60$  mm) (SU11). F. *Glis glis*, m3 gauche, vue occlusale ( $L = 2,53$  mm) (SU11). G. *Myodes glareolus*, M3 droite, vue occlusale ( $L = 1,75$  mm) (SU11).

et al., 2007; Delfino, 2002 with references; Holman, 1998). The common toad lives in various environments, including arid ones (Böhme et al., 2007).

#### *Bufo* gr. *B. viridis* (Laurenti, 1768)

The only urostyle (fragment of the proximal part, small, with a low equilateral-triangle-shaped neural channel, separated articular pits; see Bailon, 1991, 1999; Ratnikov, 2001) identified belongs to a member of the group of green toads. The species of this group, classified until a few years ago in the genus *Bufo*, are now assigned to the genus *Bufo* (see Dubois and Bour, 2010). Currently, green toads are represented by *Bufo balearicus* Boettger (*Bufo lineatus* Nini in Balletto et al., 2007) in the area of CM and, presumably, the urostyle belongs to this species. However, this single specimen does not feature any diagnostic characteristics suitable to enable its assignment to one of the three species of the genus *Bufo* present in Italy. For this reason, we prefer to classify it as *Bufo* gr. *B. viridis*. The *B. viridis* group has been present in Italy since the late Miocene (Corbino, 2015; Curcio et al., 2007; Delfino, 2002 with references; Delfino et al., 2011; Holman, 1998). Green toads prefer rather damp open spaces (Balletto et al., 2007).

#### *Rana* (s.l.) sp. 1 and *Rana* (s.l.) sp. 2

Three other specimens belong to a rather small-sized frog (a fragment of maxillary with several teeth and without dermal ornamentation, the distal part of a humerus and the proximal part of a urostyle). The urostyle, with a high neural crest and well distinct articular pits (see Bailon, 1999), clearly belongs to a species of the genera *Rana* or *Pelophylax*. The other specimens, although still in need of a more specific classification, do not contradict an attribution to the same genus. The presence of another taxon cannot be excluded. Since it is not possible to certainly assign these fossils to the genera *Rana* or *Pelophylax*, the specimens are determined as *Rana* (s.l.) sp. 1. A single fragment of large humerus, belonging to a female (SU12), was classified as *Rana* (s.l.) sp. 2 because it belongs to a different species (much bigger) of *Rana* or *Pelophylax*.

Members of the genus *Rana* (s.l.) have been present in Italy since the late Miocene (Bartolini et al., 2014; Curcio et al., 2007; Delfino, 2002, 2004; Holman, 1998; Kotsakis et al., 2011). The species of the genus *Pelophylax* are known as water frogs because they spend much of the summer living in aquatic habitats; on the other hand, the pond frogs (genus *Rana*) can be found more often on dry land as long as there is sufficient humidity (Lanza et al., 2007b).

#### *Podarcis* sp.

A few remains (one fragment of maxillary and five dorsal vertebrae) belong to one species of a small lizard of the genus *Podarcis* (all but one collected in SU11). Their size excludes the attribution of these remains to other genera of the family Lacertidae. However, these fossils do not allow a classification beyond the genus level.

*Podarcis* is present in some fossil assemblages of Pleistocene and Holocene age in Italy (Corbino, 2015;

Delfino, 2002 with references; Kotsakis et al., 2011). Any palaeoecological inference is impossible without the attribution to a species.

#### *Anguis veronensis* Pollini, 1818

Six preloacal vertebrae (Fig. 4A1 and A2) belong to a slow worm, an anguid known from a few Italian fossiliferous deposits of Plio-Pleistocene age. They are procoelous, with dorso-ventrally flattened condyle and cotyle and a flat ventral surface. The lateral margins of the distal part of the ventral surface are parallel (see Delfino, 2002). Until very recently, these fossil remains were classified as *Anguis fragilis* Linnaeus (cf. Bona et al., 2009; Delfino, 2002, 2004; Delfino and Sala, 2007). Four years ago, Gvoždík et al. (2013) established based on biomolecular analyses that the populations of slow worms of the Italian peninsula and southeastern France are clearly different from *A. fragilis* of northern Europe at a species level. They proposed the use of the specific name *Anguis veronensis* Pollini for these populations. The same authors described morphological differences but unfortunately only with respect to external characters (Gvoždík et al., 2013). Nevertheless, all the Plio-Pleistocene anguids collected in Italy belonging to the genus *Anguis* can reasonably be ascribed to *A. veronensis*. The species inhabits a wide variety of environments, usually mesophilous or even damp (Luiselli et al., 2011–as *A. fragilis*).

#### *Natrix natrix* (Linnaeus, 1758)

Snakes are represented in Area 3 of CM by two species of the family Colubridae. Five preloacal vertebrae belong to the grass snake, *Natrix natrix*. They are characterized by a high neural arch, a strong, distally obtuse hypapophysis and by a robust parapophyseal process (see Szyndlar, 1984). The species is known from several Italian fossiliferous sites of Pleistocene age (Delfino, 2002; Delfino, 2002, with references; Delfino and Atzori, 2013; Holman, 1998) and it prefers areas with fresh water (Scali et al., 2011).

#### *Hierophis viridiflavus* (Lacépède, 1789)

Two preloacal vertebrae (robust, with a rather flattened haemal keel, straight zygosphenes and long prezygapophysis processes; see Delfino, 2002; Szyndlar, 1984) belong to the green whip snake *Hierophis viridiflavus*. Fossil specimens from various fossiliferous Pleistocene sites of Italy have been assigned to this species (Curcio et al., 2007; Delfino, 2002, 2004; Holman, 1998). *Hierophis viridiflavus* is found in every type of natural habitat (Vanni and Zuffi, 2011).

#### Aves indet.

Two fragments of vertebrae belong to birds.

#### *Arvicola italicus* (Savi, 1838)

The largest number of finds belong to the family Arvicolidae (now considered by most zoologists as Arvicolinae, a subfamily of the family Cricetidae) and in particular to the Italian water vole, *Arvicola italicus*, the only species of small mammal present in both layers SU11 and SU12. In

SU11, three diagnostic elements of *Arvicola* were found (a mandibular ramus with three molars and two fragments of mandibular rami bearing m1 and m2) and six non-diagnostic teeth but certainly belonging to the same species given their consistent size ( $L$  of m1 = min. 3.78 mm, mean 3.90 mm, max 3.96 mm). Five mandibular rami with m1 (Fig. 4D), eight m1 and twenty-six other teeth belonging to the same species were collected in the SU12 layer ( $L$  of m1 = min. 3.76 mm, mean 3.98 mm, max. 4.24 mm). The morphology of the specimens collected in the two layers is identical.

*Arvicola italicus* appears in Italy at the beginning of the late Pleistocene (Kotsakis et al., 2003 with references; Sala and Masini, 2007) and is present in almost all Late Pleistocene and Holocene fossiliferous sites of mainland Italy (Berto and Rubinato, 2013; Berto et al., 2016; Bona, 2011; Bona et al., 2009; Di Canzio and Petronio, 2001; Kotsakis et al., 2003, 2011; López-García et al., 2004, 2015; Salari, 2014; Tang and Kotsakis, 2008; among others), reported as *Arvicola amphibius* Linnaeus or *Arvicola terrestris* Linnaeus (the latter taxon is now considered a subspecies of *A. amphibius* (see Musser and Carleton, 2005)).

The SDQ ratio (=Schmelzbanddifferenzierungsquotient= enamel differentiation ratio, after Heinrich, 1978) of the studied specimens was measured according to the scheme indicated by Heinrich (1982) and Maul et al. (1998, Fig. 1a) on the labial anticlines Al4, Al3, Al2, and on the buccal anticlines Ab2 and Ab2. It was possible to carry out measurements on two m1 of the SU11 layer and on seven m1 of the SU12 layer, as on the other specimens the enamel was damaged for the digestion by the birds of prey. The SDQ ratio is equal to an average of 104.42 (min. 93.33–max 128.57) and does not show any difference between the two layers. It perfectly matches the SDQ ratio indicated by Maul et al. (1998) for Italy's southern populations of the latest Pleistocene.

Maul et al. (1998) consider it impossible for the populations of peninsular Italy to belong to a “northern” evolutionary lineage and classify the late Pleistocene populations of southern Italy as *Arvicola* sp. (see also Masini et al., 2003) a position accepted by Piras et al. (2012). Recently, Castiglia et al. (2016) demonstrated the existence of a divergent mtDNA lineage for the populations of *Arvicola amphibius* (s.l.) in Italy and proposed a resurrection of the specific name *Arvicola italicus* (Savi, 1838) for this species. We follow this attribution and, taking into account the observations of Maul et al. (1998) on the extinct populations of southern Italy, we classify our specimens as *A. italicus*.

The Italian semi-aquatic members of *Arvicola* are typical of humid plains or valleys and banks of rivers, ditches, ponds, swamps and lakes with rich vegetation (Cagnin, 2008 as *A. amphibius*).

*Microtus (Terricola) savii* (de Selys Longchamps, 1838)

A mandibular ramus with m1, a second fragment of mandibular ramus bearing m1–m2, 2 m1 ( $L=2.26$  mm and 2.54 mm), and a fragment of a maxillary with M3 of simplex type (Fig. 4B) characterized by the pitymyan rhombus belong to the second species of arvicolid

collected in SU11. The morphology of the anterior cap and of the pitymyan rhombus corresponds perfectly to the m1 of the Savi's pine vole, *Microtus (Terricola) savii* (see Petruso et al., 2011; Piras et al., 2009, 2010), at present the most common arvicolid in peninsular Italy and in particular in its central and southern areas. It is notably abundant during the warmer periods of the late middle and late Pleistocene in many fossiliferous sites of central-southern Italy (Berto et al., 2017; Kotsakis, 2008; Kotsakis et al., 2003, 2011; Petruso et al., 2011; Sala and Masini, 2007). *Microtus (T.) savii* prefers rather open areas and is limited primarily by edaphic factors (Contoli et al., 2008).

*Microtus (Microtus) arvalis* (Pallas, 1778)

The third arvicolid is the common vole *Microtus (Microtus) arvalis*; 5 m1 (Fig. 4C) of this species have been found in SU12 ( $L$ =min 2.60 mm, mean 2.72 mm, max 2.81 mm). The morphology of m1 is characterized by five closed, rather symmetrical triangles and a rounded anterior cap typical of this species (Nappi, 2001). It has been present in central and southern Italy since the late middle Pleistocene (Berto et al., 2017; Kotsakis et al., 2003, 2011; López-García et al., 2015; Tang and Kotsakis, 2008), only being absent during MIS 5 and the late Holocene (Kotsakis et al., 2003 with references; Salari, 2014) and is currently found only in northern Italy where it is abundant in the fossil record (Berto and Rubinato, 2013; Berto et al., 2016; Bona, 2011; Bona et al., 2008; López-García et al., 2015; among others). This species is typical of open environments and cool climate (Paolucci and Amori, 2008).

*Myodes glareolus* (Schreber, 1780)

Two M3 both of complex type (Fig. 4G) and a M2 belong to a fourth species of arvicolid, a rhizodont form, the bank vole *Myodes glareolus*. For a long time the generic name used for the species *glareolus* and for numerous other species both extant and fossil was *Clethrionomys*. According to Musser and Carleton (2005 with references), following the law of priority, the generic name *Myodes* must be used. This position was challenged by Tesakov et al. (2010) and defended by Carleton et al. (2014). Until a final decision of the International Commission for the Zoological Nomenclature is made, we decided to adopt the term *Myodes* without going into the details of the discussion. This small rodent is present in Italian assemblages since the beginning of the middle Pleistocene (Berto et al., 2016; Curcio et al., 2007; Kotsakis, 2008; Kotsakis et al., 2003, 2011; López-García et al., 2017). The species lives mostly in woods (Amori, 2008).

*Apodemus* gr. *A. sylvaticus* (Linnaeus, 1758) – *A. flavicollis* (Melchior, 1834)

Scarce remains of the murid belonging to the genus *Apodemus* (two teeth, one m1 and one m2, and a fragment of a second m1) (Fig. 4E) are present. The dimensions of m1 ( $L=1.60$ ) and m2 ( $L=1.12$ ) fall within the variability values of *A. sylvaticus* (Linnaeus), but in the lowest limit of the metric range of *A. flavicollis* (Melchior) (see Argenti, 1999; Pasquier, 1974). However, since there are no





**Fig. 5.** Cava Muracci (Cisterna di Latina, central Italy), late Pleistocene, SU 11: macromammal long-bones in dorsal view: metatarsus II of *Lepus* sp. (A); metacarpus III of *Equus ferus* (B); metatarsus III of *Equus ferus* (C); metacarpus of *Bos primigenius* (D). Scale bar = 3 cm.

**Fig. 5.** Cava Muracci (Cisterna di Latina, Italie centrale), Pléistocène supérieur, US 11 : os longs de macromammifères en vue dorsale : métatarse II de *Lepus* sp. (A) ; métacarpe III d'*Equus ferus* (B) ; métatarse III de *Equus ferus* (C) ; métacarpe de *Bos primigenius* (D). Barre d'échelle = 3 cm.

morphological characters on the two specimens that can allow a distinction between the two species, it is preferable to assign such remains to *Apodemus* sp. Wood mouse and yellow-necked mouse make their first appearance in Italy during the last phases of the early Pleistocene (Kotsakis et al., 2003 with references; Marcolini et al., 2013; Siori et al., 2014). *Apodemus sylvaticus* is very common in the fossil assemblages of middle and late Pleistocene whilst *A. flavicollis* is less common; however, in most cases the remains of *Apodemus* are classified as *A. gr. sylvaticus-flavicollis* (see Berto et al., 2016; Bona, 2011; Kotsakis, 2008; Kotsakis et al., 2003 with references; López-García et al., 2015). *Apodemus sylvaticus* is an opportunistic species living in various environments but with greater preference for forested areas whilst *A. flavicollis* lives in a forest environment of both coniferous and hardwood (Capizzi and Filippucci, 2008a, 2008b).

#### *Glis glis* (Linnaeus, 1766)

The glirid *Glis glis* is also very uncommon and represented by only one m3 ( $L = 2.53$  mm) (Fig. 4F). Fat dormouse appears in Italy at the beginning of the middle Pleistocene and is very common in various assemblages, especially in the late Pleistocene (Kotsakis et al., 2003 with references; Curcio et al., 2007; Kotsakis, 2008; Bona et al., 2009; López-García et al., 2014, 2017). *Glis glis* is an arboreal species that lives in deciduous or mixed forests (Capizzi and Filippucci, 2008c).

#### *Lepus* sp.

Lagomorphs are represented by hare, *Lepus* sp. (Table 2). The following remains belong to this genus: a fragment of an incisor, a humerus, the distal part of a second humerus, the proximal part of an ulna, two fragments of coxal, a femur, a tibia, two calcanei, two astragali, a second (Fig. 5A), a third and a fourth metatarsal, and three other metatarsals (Table 3). The tibia, a calcaneum, an astragalus and three metatarsals (2nd, 3rd and 4th) most likely belong to the same individual. These remains are quite robust and allow to exclude an attribution to the genus *Oryctolagus*, but are insufficient for a classification at species level within the genus *Lepus*. The genus *Lepus* appears in Italy in the later part of early Pleistocene (Van der Meulen, 1973) and is rather common in middle and late Pleistocene mammalian assemblages (Kotsakis et al., 2003 with references). Without an attribution at a specific level, any ecological inference is impossible.

#### *Mustela nivalis* Linnaeus, 1766

*Mustela nivalis* is represented by a single M1 ( $L = 2.19$  mm) collected in layer SU12 (Table 2). *Mustela nivalis* is known from the middle Pleistocene onwards (Bona et al., 2009; Petronio et al., 2011; Salari et al., 2011) and is an opportunistic species (Angelici, 2003).

#### *Meles meles* (Linnaeus, 1758)

The presence of badger is indicated by a proximal fragment of a tibia (Table 3). This species has been present

**Table 3**

Cava Muracci (Cisterna di Latina, central Italy), late Pleistocene. Macromammals from SU11 and SU12: distribution of anatomical elements.

**Tableau 3**

Cava Muracci (Cisterna di Latina, Italie centrale), Pléistocène supérieur. Macromammifères des US11 et US12 : distribution des éléments anatomiques.

Body part	<i>Lepus</i> sp.	<i>M. nivalis</i>	<i>C. lupus</i>	<i>M. meles</i>	<i>C. crocuta</i>	<i>E. ferus</i>	<i>S. hemitoechus</i>	<i>S. scrofa</i>	Cervidae	<i>C. capreolus</i>	<i>C. elaphus</i>	<i>D. dama</i>	<i>B. primigenius</i>	
Horn/Antler									5		40	4	2	
Skull					1						1		2	
Maxillary					1	7					3			
Upper teeth		1			5	57					16	6	35	
Mandible					3	5		1		1	13	1	7	
Lower teeth					2	42	1	1			9	4	23	
Indeterminate teeth	1				2	11			1				6	
Atlas									1				1	
Epistropheus													1	
Vertebrae													8	
Rib														
Scapula														3
Humerus	2				1	2					3	1	22	
Radius						2					6	1	5	
Ulna	1				1								2	
Radius + Ulna						2							7	
Carpal bones						1					1			
Metacarpus			1			5					3	2	20	
Pelvis	2					12							11	
Femur	1					2					1		13	
Tibia	1			1		6					5	1	26	
Astragalus	2					6							18	
Calcaneus	2					6							17	
Tarsal bones													5	
Metatarsus	6		1			14			1		10	3	31	
Metapodial bones					1	10			1		2		7	
Phalanx I						1					1		1	
Phalanx II						2								
Phalanx III						1								
Total	18	1	2	1	17	194	1	2	9	1	114	23	273	656

**Table 4**

Cava Muracci (Cisterna di Latina, central Italy), late Pleistocene. Small and large mammals from SU 11 and SU12: minimum number of individuals (MNI) by age at death.

**Tableau 4**

Cava Muracci (Cisterna di Latina, Italie centrale), Pléistocène supérieur. Petits et grands mammifères des US11 et US12 : nombre minimum d'individus (MNI) selon l'âge au décès.

Taxon	Young	Adult	Old	Indet	Total
<i>A. italicus</i>	2	5	2		9
<i>M. (Terricola) savii</i>		2			2
<i>M. (Microtus) arvalis</i>		2	1		3
<i>M. glareolus</i>		1			1
<i>A. gr. sylvaticus-flavicollis</i>		2			2
<i>G. glis</i>		1			1
<i>Lepus</i> sp.	1	1			2
<i>C. lupus</i>		1			1
<i>Mustela nivalis</i>		1			1
<i>M. meles</i>	1				1
<i>C. crocuta</i>	3	1			4
<i>E. ferus</i>	3	5	2		10
<i>S. hemitoechus</i>	1				1
<i>S. scrofa</i>	1		1		2
<i>C. capreolus</i>		1			1
<i>C. elaphus</i>	2	3	3		8
<i>D. dama</i>	1	1	1		3
<i>B. primigenius</i>	3	4	5	2	14
Total	18	31	15	2	66

in Italy since the late early Pleistocene (Petronio and Marcolini, 2013) and it is present in several environments (Pigozzi and De Marinis, 2003).

#### *Crocota crocuta* (Erxleben, 1777)

Seventeen remains can be referred to *Crocota crocuta* (Table 2). The postcranial skeleton is only represented by a metapodial bone and a fragmented humerus whilst the cranial remains are represented by a fragment of skull, a few teeth and fragmented mandibles and maxillae (Table 3 and Figs. 6A–C). The remains can be referred to at least four individuals of different ages, which include a neonatal individual and two cubs (Table 4). The presence of the spotted hyena is also supported by the discovery of abundant coprolites in SU 11 of Area 3 (= 66) and in a few other caves of the CM quarry (i.e. Area 4 (= 10) and Area 7 (= 31)) (Gatta and Rolfo, 2017).

*Crocota crocuta* first occurred in Italy during the Ponte Galeria Faunal Unit (middle Pleistocene; see Marra et al., 2014; Sardella and Petrucci, 2012) and became extinct in the Peninsula during late MIS 3 (around 31 ka cal. BP: see Stuart and Lister, 2014). The species is widely distributed, in particular during the late Pleistocene (Petronio et al., 2007), surviving in a wide range of climates and landscapes (Churchill, 2014; Conti et al., 2012).

#### *Canis lupus* Linnaeus, 1758

Two remains are referred to the wolf: a metapodial bone and a second metatarsal (Table 3). The morphology of the bone is typical of a large-sized canid and the morphometry of the specimen falls within the size range of *C. lupus* from the Pleistocene of Italy and Hungary (Salari et al., 2017 and references therein; LP unpublished data from Hungarian Natural History Museum). In Italy, *C. lupus*

occurs for the first time in the late middle Pleistocene (Marra et al., 2014; Salari et al., 2017 and references therein). Records of *C. lupus* are relatively abundant in the late Pleistocene of Italy, under both temperate-warm and cold climate conditions, and the wolf persists into the Holocene (Bertè and Pandolfi, 2014; Petronio et al., 2007, 2011; Sansalone et al., 2015).

#### *Equus ferus* Boddaert, 1785

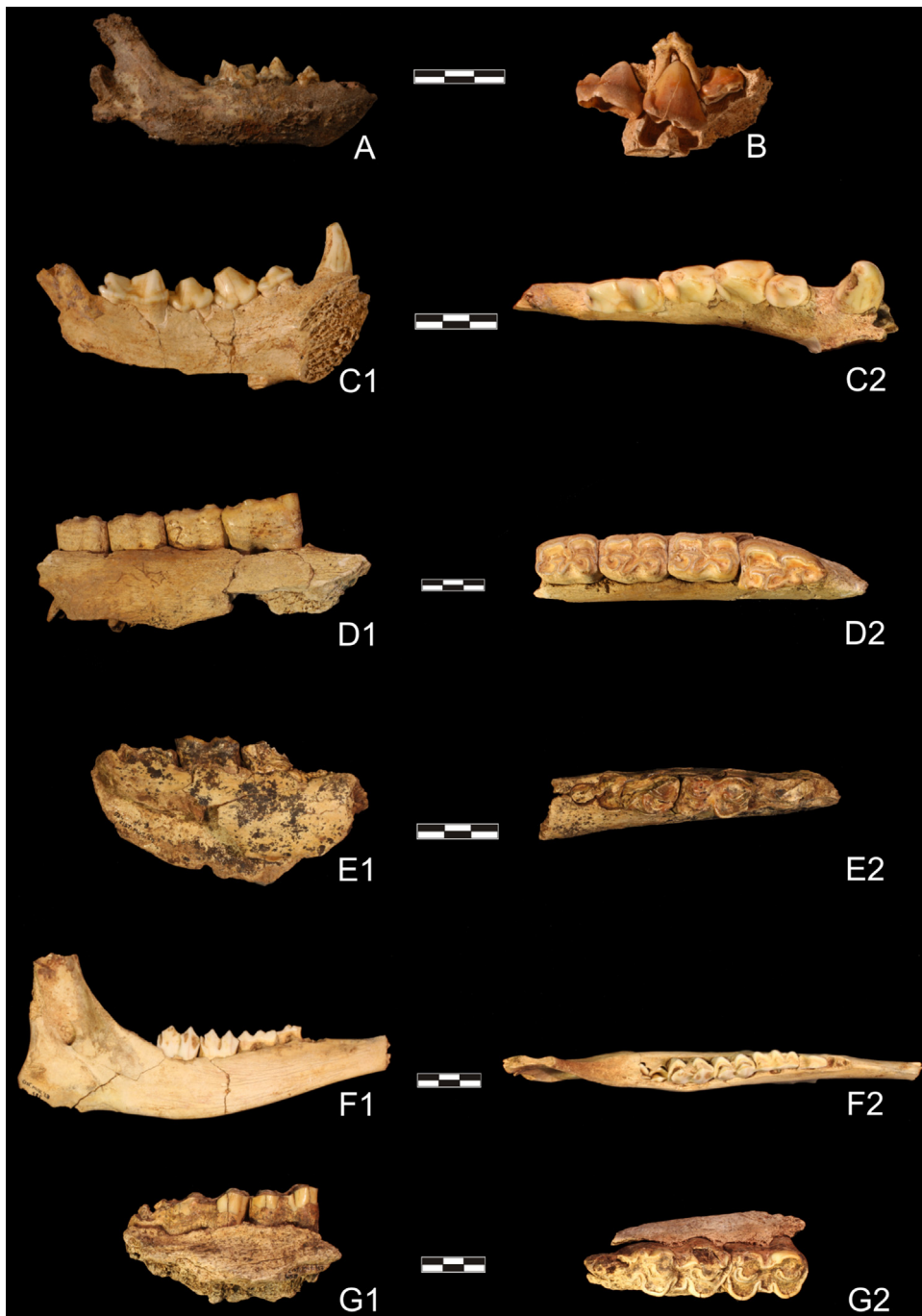
The Equidae are represented at CM exclusively by the horse species *Equus ferus*. The fossil remains attributed to this species are 194 in total and represent about one-third of the entire assemblage (Table 2). Therefore, *E. ferus* is the second most abundant species, following *Bos primigenius*. The best represented skeletal portion is the cranium, with ca. 63% of the remains, among which are 110 teeth; with regard to the postcranial skeleton, the hindlimb elements account for 24% of the total and are four times more numerous than the forelimb (Table 3 and Figs. 5 and B). The juvenile remains are very scarce (Table 4), and the majority of the teeth are permanent and the long bones have fused epiphyses. Upper molars and premolars show usually an asymmetric and lengthened protocone. In the lower cheek teeth, the lingual flexid is mainly of caballine type and, as for the upper teeth, the plis caballin was observed in most of the cases where the occlusal surface is clearly visible (see Conti et al., 2010; Eisenmann, 1980, 1981).

*Equus ferus* seems to have reached Europe during the middle Pleistocene (Galerian), probably deriving from earlier forms of *Equus* from central Asia and Mongolia (Conti et al., 2010 with references). From this point onwards, the species split into numerous chronological and geographical varieties, which some authors consider to be different species or subspecies (e.g., *E. ferus germanicus* Nehring, *E. ferus gallicus* Prat, *E. ferus gmelini* Boddaert, etc.), distinguished essentially by their size and skeletal proportions (Conti et al., 2010; Eisenmann, 1992).

The first representatives of these wild horses (*E. ferus*) appear in Italy in the middle Galerian (Isernia FU) and they are distinguished from the preceding Villafranchian equids by the structures of the enamel in the upper teeth, with a more elongated protocone that tends to progressively assume an asymmetrical conformation, by the metacarpus that is more compressed anterior-posteriorly and by the proportions of the post-cranial skeleton that generally takes on a more slender aspect (Conti et al., 2010; Petronio et al., 2011). *Equus ferus* was quite common in the late Pleistocene, preferring open environments like steppes, and its last occurrence in Italy is in the early Holocene (Conti et al., 2010; Petronio et al., 2007, 2011).

#### *Stephanorhinus hemitoechus* (Falconer, 1859)

Three lower teeth and a fragment of a juvenile femur attributable to *S. hemitoechus* have been collected from CM (Gatta and Rolfo, 2015; Gatta et al., 2016; Pandolfi et al., 2017). A molar tooth of *S. hemitoechus* has been found in SU11 of Area 3 (Table 3) and yielded an age of  $36,885 \pm 350$  (LTL15760A), 42,054–40,804 cal. BP (Gatta et al., 2016; Table 3). The specimens have been identified and described by Pandolfi et al. (2017).



**Fig. 6.** Cava Muracci (Cisterna di Latina, central Italy), late Pleistocene, SU 11: macromammal teeth and mandibles. A. Juvenile hemimandible of *Crocota crocuta* in labial view with d2–d4. B. Fragmentary juvenile mandible of *Crocota crocuta* in labial view with d3 and erupting p2–p4. C. Hemimandible of adult *Crocota crocuta* with c and p2–m1: (1) lingual view, (2) occlusal view. D. Fragmentary hemimandible of *Equus ferus* with p2–m1: (1) labial view, (2) occlusal view. E. Fragmentary mandible of an old individual of *Cervus elaphus* with m2 and m3: (1) labial view, (2) occlusal view. F. Juvenile hemimandible of *Dama dama* with d3, d4, m1, m2 and erupting m3: (1) lingual view, (2) occlusal view. G. Fragmentary mandible of *Bos primigenius* with m2 and m3: (1) lingual view; (2) occlusal view. Scale bars = 3 cm.

**Fig. 6.** Cava Muracci (Cisterna di Latina, Italie centrale), Pléistocène supérieur US 11 : dents et mandibules de macromammifères. A. Hémimandibule juvénile de *Crocota crocuta* en vue labiale avec d2–d4. B. Mandibule juvénile fragmentaire de *Crocota crocuta* en vue labiale avec d3 et p2–p4 en train de percer. C. Hémimandibule de *Crocota crocuta* adulte avec c et p2–m1 : (1) vue linguale, (2) vue occlusale. D. Hémimandibule fragmentaire de *Equus ferus* avec p2–m1 : (1) vue labiale, (2) vue occlusale. E. Mandibule fragmentaire d'un individu âgé de *Cervus elaphus* avec m2 et m3 : (1) vue labiale, (2) vue occlusale. F. Hémimandibule juvénile de *Dama dama* avec d3, d4, m1, m2 et m3 en train de percer : (1) vue linguale, (2) vue occlusale. G. Mandibule fragmentaire de *Bos primigenius* avec m2 et m3 : (1) vue linguale ; (2) vue occlusale. Barres d'échelle = 3 cm.

**Table 5**

Cava Muracci (Cisterna di Latina, central Italy), Late Pleistocene. Body parts from SU11 with evident gnaw marks.

**Tableau 5**

Cava Muracci (Cisterna di Latina, Italie centrale), Pléistocène supérieur. Parties du corps de l'US11, avec des marques évidentes de rongeurs.

Gnaw marks	<i>C. crocuta</i>	<i>E. ferus</i>	Cervidae	<i>C. capreolus</i>	<i>C. elaphus</i>	<i>D. dama</i>	<i>B. primigenius</i>	
Horn/Antler			3		33	4	1	
Skull	1							
Mandible				1	1		1	
Atlas							1	
Scapula							1	
Humerus		2			1	1	16	
Radius		1			5		3	
Ulna								
Radius + Ulna		2					4	
Metacarpus		5			2	1	14	
Pelvis		6					7	
Femur		1			1		11	
Tibia		5			2	1	18	
Astragalus		1					11	
Calcaneus		5					15	
Tarsal bones							1	
Metatarsus		9			5		24	
Metapodial bones		9			1		6	
Phalanx I							1	
Phalanx II		2						
Total	1	48	3	1	51	7	135	246

In Italy, the steppe rhinoceros was present at least until 41 ka cal. BP (Pandolfi and Marra, 2015; Pandolfi and Tagliacozzo, 2015; Pandolfi et al., 2017). *Stephanorhinus hemitoechus* probably inhabited temperate open habitats rich in low growing vegetation (Fortelius, 1982; Guérin, 1980 and reference therein). According to Fortelius et al. (1993), *S. hemitoechus* displays remarkable convergence in many details with *Coelodonta antiquitatis*, although it was not a true grazer but an intermediate feeder on low growing vegetation in open habitats.

#### *Sus scrofa* Linnaeus, 1758

A large size canine and a fragmented mandible of a young individual are assigned to *Sus scrofa* (Table 3). The species is recorded in Italy from the early–middle Pleistocene transition (Marra et al., 2014; Petronio et al., 2011) and it prefers humid woods and swampy areas (Apollonio, 2003a).

#### *Capreolus capreolus* (Linnaeus, 1758)

A fragmented small mandible with hypsodont teeth and with gnaw marks is assigned to the roe deer (Tables 3 and 5). *Capreolus capreolus* is well documented during the late Pleistocene (Petronio et al., 2007) but it is also recorded during the middle Pleistocene (Marra et al., 2014). The species lives in forested environments (Perco, 2003).

#### *Cervus elaphus* Linnaeus, 1758

*Cervus elaphus* is well documented in Area 3 at CM (Table 2). This species is mainly represented by fragmentary antlers, fragmentary mandibles (Fig. 6E), teeth and several postcranial bones (Table 3). The morphology of the collected specimens is similar to that of the extant *C. elaphus* (see Di Stefano et al., 2015; Petronio et al., 2007), and

so are the morphometric values. The fragmentary antlers, most of which are naturally shed, are relatively large in size and lack the bez tine, therefore they probably belonged to subadult individuals or to specimens dead in autumn, when the bez tine is not yet present.

The species occurred for the first time in Italy during the early Galerian (Slivia Faunal Unit) at the early–middle Pleistocene transition, with the subspecies *C. elaphus acoronatus* Beninde, which was replaced by *C. elaphus eostephanoceros* Di Stefano and Petronio during the late Galerian (Fontana Ranuccio Faunal Unit). During MIS 11, the endemic form *C. elaphus rianensis* Leonardi and Petronio is present in central Italy. *C. elaphus rianensis* and *C. elaphus aretinus* Azzaroli are replaced by a subspecies of *C. elaphus* ssp. with antler morphology similar to that of the extant populations at the beginning of the late Pleistocene (Di Stefano and Petronio, 1993, 2002; Di Stefano et al., 2015; Petronio et al., 2007, 2011). The red deer is particularly common in open woodland with large grassy clearings (Mattioli, 2003).

#### *Dama dama dama* (Linnaeus, 1758)

The remains of fallow deer are 3.5% only of the identified specimens (Table 2). The fragmentary antlers, however, display the typical morphological characters of the extant *D. dama dama* (Di Stefano and Petronio, 1997).

The occurrence of the genus *Dama* in Italy has been recently referred to ca. 650 ka by Marra et al. (2014) (Vitinia lower gravels). Remains of an archaic fallow deer, *D. dama tiberina* Di Stefano and Petronio, were reported from fluvial-lacustrine deposits in the area of Rome chronologically related to MIS 8.5–7 (Marra et al., 2014, 2015), whereas the extant subspecies, *D. dama dama*, occurred for the first time at the beginning of the late Pleistocene. The latter subspecies gradually became rare during the Last Glacial, and became extinct in Italy before

the Last Glacial Maximum (Di Stefano and Petronio, 1997; Marra et al., 2014; Petronio et al., 2007, 2011). The fallow deer is a cervid typical of temperate and warm climates and it prefers Mediterranean environments with maquis and open woodlands (Apollonio, 2003b).

#### *Bos primigenius* Bojanus, 1827

The aurochs is mainly represented by long bones and teeth (Table 3 and Figs. 5A and 6G), which can be referred to at least 14 individuals (Table 4). It is the most abundant taxon collected in Area 3 with 41.6% of the total NISP (Table 2); 49% of the remains show traces of gnawing (Table 5).

*Bos primigenius* occurred early in Italy at Venosa–Notarchirico and the Cretone Basin, ca. 600 ka (Cassoli et al., 1999; Lefèvre et al., 2010; Marra et al., 2016) and it has been recorded in several localities geochronologically dated at ca 500 ka (MIS 13, Marra et al., 2014; Petronio et al., 2011). The parallelism in the diffusion of *Bos* and the Acheulean culture (Mode II tools) has been hypothesized by Martínez-Navarro et al. (2007, 2010) and also recently discussed by Ceruleo et al. (2015) and Marra et al. (2016). The early aurochs appear smaller and slenderer than those from the late middle Pleistocene (Pandolfi et al., 2011, 2013). Large-sized aurochs are documented during the late middle and early late Pleistocene, but a decrease in the postcranial bone dimensions seems to take place during the climatic deterioration at the end of the late Pleistocene (Pandolfi et al., 2011, 2013). The dimensions of the metapodial bones of our sample are close to the values of several *B. primigenius* from latest Pleistocene and Holocene localities from Italy and Hungary and are slightly smaller on average than those from Avetrana (early late Pleistocene) (see Pandolfi et al., 2011,

2013; Pandolfi unpublished data from the Hungarian Natural History Museum) (MC Cisterna:  $L=240\text{--}250.49\text{ mm}$ ,  $n=4$ ; MC Avetrana:  $L=251\text{--}275\text{ mm}$ ,  $n=11$ ; MT Cisterna:  $L=270.51\text{--}302\text{ mm}$ ,  $n=3$ ; MT Avetrana:  $L=288\text{--}302\text{ mm}$ ,  $n=5$ ).

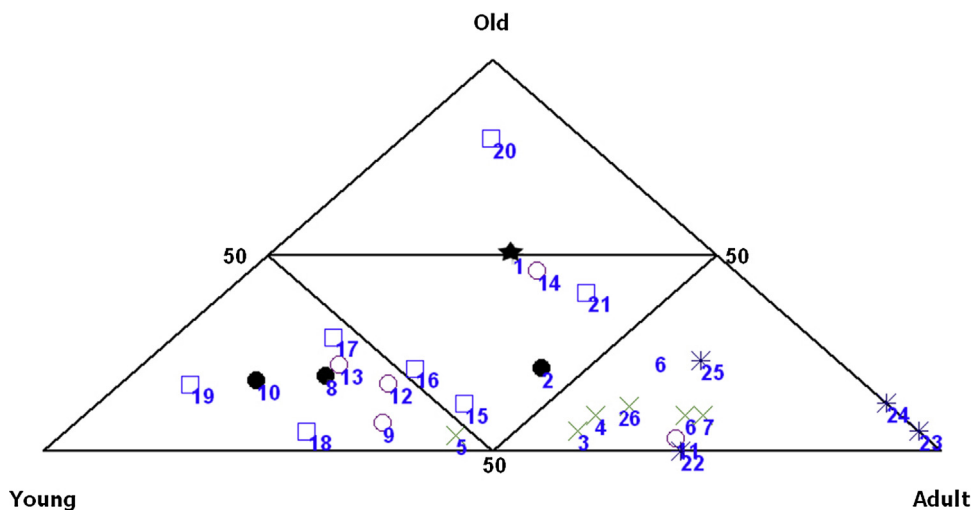
*Bos primigenius* inhabited hilly areas with open woodland in a temperate climate (Pandolfi et al., 2011, 2013; Van Vuure, 2002).

## 5. Results

### 5.1. Taphonomic observations

A process of fossilisation by mineralisation has been triggered by the closed context of the cave and the calcium carbonate-rich travertine, and characterises coprolites and fossils, which are in a very good state of preservation (Gatta and Rolfo, 2015). The fragmentation is extremely variable. Short and long bones are found both intact and fragmented ranging from 1 cm to a few decimetres in size. The textures and patinas are also variable, especially between the finds recovered deep in the archaeological layers and those found on the surface, exposed at the time to severe local climate factors such as warm summer sun and prolonged winter rains. The indeterminate material includes bone fragments, with size ranges between 1–10 cm, which could not be attributed to any faunal element or anatomical part.

The widespread presence of hyena coprolites and the large number of gnaw-marks (Table 5) suggests that layer SU11 of Area 3 was probably a hyena den, in which the selective impact of carnivore activity has determined the nature of the remains found (Gatta et al., 2016). A total of 245 bones (Table 5), which encompass ca. 37% of the total macromammals (656 specimens), show traces of gnawing



**Fig. 7.** Ternary diagram showing the mortality profile of the aurochs population from Cava Muracci and catastrophic and predation structures. 1 = Cava Muracci; 2 = population model; 3–7 = catastrophic structures; 8 = predation model; 9–14 = predation structures (wolf); 15–21 = predation structures (hyena); 22–25 = aurochs population structures from prehistoric sites; 26 = catastrophic aurochs assemblage from Avetrana (data from Stiner, 1990; Pandolfi et al., 2013, and references therein).

**Fig. 7.** Diagramme ternaire montrant le profil de mortalité de la population des aurochs de Cava Muracci et les structures catastrophiques et de prédation. 1 = Cava Muracci; 2 = modèle de population; 3–7 = structures catastrophiques; 8 = modèle de prédation; 9–14 = structure de prédation (loup); 15–21 = structures de prédation (hyène); 22–25 = structures de la population des aurochs des sites préhistoriques; 26 = assemblage catastrophique d'auroch d'Avetrana (données de Stiner, 1990; Pandolfi et al., 2013, et références incluses).

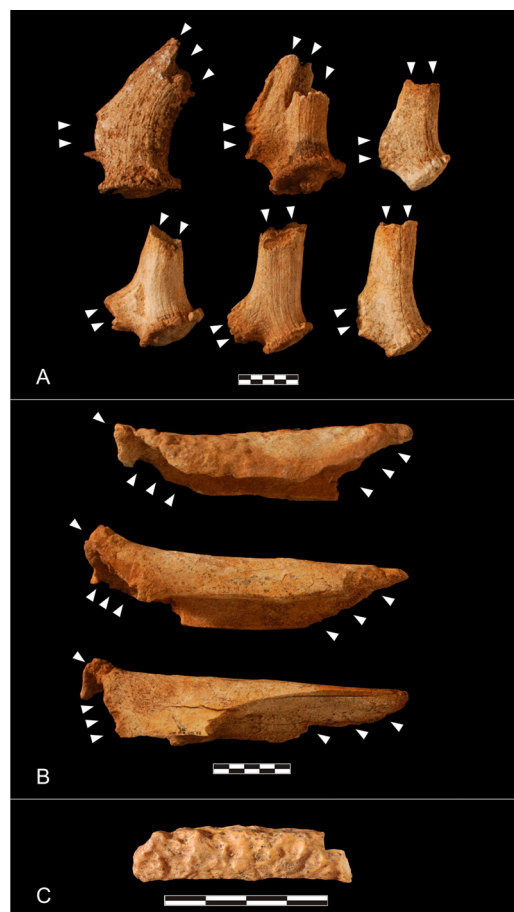
and/or bite marks. Considering only the bone remains (i.e. excluding individual teeth), the gnawed specimens represent ca. 56% of the total macromammal remains (434 specimens; Table 3).

Following the tooth-wear classification reported by Stiner (1990), the population of aurochs of CM is represented by at least twelve individuals, three calves (mainly represented by deciduous teeth) and 9 adults. Among the adults, at least five old individuals (each represented by very worn lower M3) are present. In Fig. 7, the aurochs population from CM falls into the old-dominated field and would indicate either a bone accumulation formed by scavengers, or an attritional accumulation of skeletal remains of animals that died from natural causes. However, the percentage of young individuals (denoted by deciduous teeth), adults (denoted by unworn or slight worn lower M3) and old individuals (very worn lower M3) is close to that reported for the wolf-killed white-tail deer (*Odocoileus virginianus* (Zimmermann)) population from Ontario (Canada) and for hyena-killed and scavenged mountain zebra (*Equus zebra* Linnaeus) from Namibia (Stiner, 1990; Table 4).

The percentages differ significantly from those reported for assemblages accumulated by humans or by catastrophic death assemblages (data from Pandolfi et al., 2013 and references therein; Stiner, 1990) (Fig. 7). The mortality profile of CM differs also from the carnivore accumulations that show a U-shaped mortality pattern with dominance of very young and old individuals. This is the result of a predation strategy that focusses on the most vulnerable prey. In archaeological sites, bones accumulated by human activity show a mortality pattern dominated by prime adults; this pattern is uncommon in nature and is the result of selective ambush hunting (Stiner, 1990). Finally, the death pattern of living-structure is the result of non-selective actions (Stiner, 1990). In these cases, all animals in a population have an equal probability of dying and the mortality is age-independent (Stiner, 1990).

Considering the presence in the site of coprolites and neonatal and juvenile individuals of hyena, but very few specimens of wolf, the age profile of the aurochs population supports the hypothesis that the CM site is predominantly a hyena accumulation (Gatta and Rolfo, 2017; Gatta et al., 2016). Further confirmation of such an interpretation is the taphonomic condition of certain body parts, which show similar damage marks typical of systematic bone exploitation (Fig. 8B); the collection and chewing of deer antlers by the cave hyena during the late Pleistocene is well attested (Diedrich, 2014) and gnaw marks on antlers recovered at CM show similarities with those from other hyena dens (Fig. 8A). Finally, a partially digested long bone fragment has been recovered at CM (Fig. 8C); the regurgitation of long bone fragments is typical of a few medium-large carnivores (i.e. dogs, cave hyenas, cave lions) during the late Pleistocene (Kolska Horwitz, 1990) but cave hyena is the only one attested at CM.

About 32% of arviculids (including all molars and not only m1) show very light or light traces of digestion (Andrews, 1990; Fernández-Jalvo and Andrews, 2016; Fernández-Jalvo et al., 2016), probably from a raptor (strigiform?). An additional 2% exhibit moderate traces of



**Fig. 8.** Cava Muracci (Cisterna di Latina, central Italy), late Pleistocene. A. Shed antlers of *Cervus elaphus* from SU11 with conspicuous gnaw marks. B. radius fragments of *Bos primigenius* from SU11 displaying systematic bone exploitation. C. Long bone fragment from SU11 partially digested.  
**Fig. 8.** Cava Muracci (Cisterna di Latina, Italie centrale), Pléistocène Supérieur. A. Bois perdus de *Cervus elaphus* de l'US11 avec des marques visibles de rongeurs. B. Fragments de radius de *Bos primigenius* de l'US11 montrant une exploitation osseuse systématique. C. Fragment d'os long, partiellement digéré, de l'US11.

digestion (Fernández-Jalvo and Andrews, 2016). The totality of small mammal remains with these traces comes from the layer SU11, while no specimen collected in SU12 has traces of digestion.

The sporadic presence of lithic industries from both SU11 and SU12 is perhaps attributable to some flooding events in the area, which most likely transported the artefacts into the cave, as well as sediments, clasts and some small vertebrates. This circumstance is supported by the absence of cut marks on the bone remains and particularly by the use-wear assessment of the assemblage, which shows a heavy abrasion of the flint surface compatible with water transport. Although some macromammal remains could have been transported within the cave by abiotic agents, the interpretation of SU11 as a hyena den is demonstrated. The preservation of coprolites composed of several connected pellets and the identification of specific areas with a higher concentration of bones in sub-horizontal

deposition suggest that these were in primary deposition and small or absent post-depositional processes occurred before they were covered.

## 6. Discussion

### 6.1. Reconstruction of past landscape

The environmental indications provided by faunal remains, combined with previously published pollen data (Gatta et al., 2016), enabled us to reconstruct the local environmental conditions of the Pontine Plain between 34–44 ka BP. The local scale of this reconstruction, which also applies to pollen data (Gatta et al., 2016), is determined by the hunting behaviour of *Crocota crocuta*, which is known to hunt within a radius of up to 50 km from the den (Mills, 1989), although they usually remain within 15 km (Argant, 2004; Argant and Dimitrijevic, 2007; Scott, 1987).

Micro- and macro-remains are consistent, indicating the presence of mixed environments within a short distance. Carnivores from CM are extremely adaptable to several climates and vegetational environments and, therefore, cannot provide detailed information towards the palaeoenvironmental reconstruction, although badgers prefer woodlands and hyenas open environments. The herbivores, on the other hand, provide useful climatic and vegetational information. Cervids and *Bos primigenius* indicate the presence of more or less open wooded areas. *Equus ferus* and *Stephanorhinus hemitoechus* instead suggest the presence of extensive steppe with low vegetation. *Sus scrofa* confirms the presence of marshlands since prehistoric times, which persisted until vast reclamations began in 1926. This assemblage suggests a temperate climate, even if *Equus ferus* and *Bos primigenius* can resist to colder environments.

Temperate conditions are also supported by microvertebrates. *Bufo* sp. and *Microtus (Terricola) savii* indicate the presence of open environments while *Apodemus gr. sylvaticus-flavicollis*, *Myodes glareolus* and *Glis glis* prefer forested habitats. The other species are widely distributed in various types of environments but the presence of water/humid demanding fauna (i.e. *Bufo bufo*; *Rana* (s.l.); *Anguis veronensis*; *Natrix natrix*; *Arvicola amphibius*) and fish remains indicate the presence of water bodies. Finally, it is worth mentioning the presence of *M. arvalis* in SU12 as opposed to *M. (T.) savii* in SU11, which suggests a cooler phase during SU12. This observation, which is plausible due to the several cold/warm oscillations of the Last Glacial, should nonetheless be considered with caution due to the small sample of fossil finds upon which this thesis is based.

The reconstruction based on fauna suggests, therefore, the presence of at least three coexisting habitats: (i) temperate open woodlands, perhaps in the hilly areas beneath the Lepino–Ausoni ridge; (ii) the centre of the Pontine Plain was possibly characterised by wide open spaces such as steppe; (iii) humid areas such as ponds, lakes and swamps were probably widespread along the coastline and the major rivers. This ecological picture is compatible with and corroborated by pollen data (Fig. 3), which also indicate the presence of mixed environments with woodland, steppe and wetland habitats. Moreover, such a complex

framework is supported by the particular morphology of the region, which, within a distance of 30 km, varies abruptly west to east from a coastal environment to hilly areas and mountains over 1500 m high.

On a broader view, Europe was characterised by extreme climate instability during the 34–44 ka interval considered in this paper. Palaeoclimatic and palaeoenvironmental archives worldwide recorded rapid and abrupt climate changes which severely affected vegetation and fauna at decade-to-century time-scale (Moreno et al., 2014). Pollen data from lakes sediment in southern Italy (Allen et al., 1999) and marine cores (Sanchez-Goñi et al., 2002; Fletcher and Sánchez-Goñi, 2008) indicate that a dry climate characterised the Mediterranean, causing a substantial decrease of arboreal taxa and an increase of steppe environments. A progressive cooling trend and dry conditions are also documented from speleothem records in south-western Europe during the MIS 3 (Moreno et al., 2014). Additionally, these environmental changes are indicated as a main cause of the megafauna extinction that occurred during the late Pleistocene (Lister and Stuart, 2008; Wroe et al., 2006).

A remarkable vegetational dynamism characterised by forest and non-forest successions has been detected in central Italy (Follieri et al., 1998) and suggests that the Latium region was extremely sensitive to global climate oscillations during MIS 3. However, this study did not prove a similar situation in the Pontine Plain between 34–44 ka BP. Since it was impossible to obtain a better temporal resolution of SU11, pollen analysis of CM coprolites could equally reflect one or more climatic oscillations of this MIS 3 interval or the proposed coexistence of different arid and humid habitats (Gatta et al., 2016). On the other hand, the diverse faunal taxa identified within the hyena occupational layer (SU11) and their palaeoecological inferences, if considered to be coeval, are better indicators of the contemporary presence of distinct environments and related climate stability. The discovery at CM of one of the latest narrow-nosed rhinoceros of Italy (Pandolfi et al., 2017) seems to support the interpretation that the Pontine Plain did not go across abrupt and severe climatic changes; detailed enamel analyses on selected mammal taxa will be performed to investigate this issue. Moreover, remains of *Microtus arvalis* in SU12 suggest that the Pontine Plain was cooler at some point during the time-span between 69–45 ka BP rather than between the entire 44–34 ka BP interval. Further environmental reconstructions, possibly combining different reconstruction techniques on material from a small time-scale setting, are needed to clarify this aspect and to provide reliable information on possible minor climate oscillations in the Pontine Plain.

## 7. Conclusions

The faunal assemblage recovered from Area 3 of CM is fully described in this paper. Despite the taxa identified being relatively common in Italy during the late Pleistocene, novel environmental information was obtained through their analysis. These are consistent with the previous palaeoecological analyses and provide a reliable environmental reconstruction.



A total of 1466 macro-remains have been examined in this study, 44.7% of which have been taxonomically classified into a total of twelve different taxa (i.e. *Lepus* sp., *Mustela nivalis*, *Canis lupus*, *Meles meles*, *Crocuta crocuta*, *Equus ferus*, *Stephanorhinus hemitoechus*, *Sus scrofa*, *Capreolus capreolus*, *Cervus elaphus*, *Dama dama* and *Bos primigenius*), together with less abundant small mammal fauna, avi-, herpeto-, and ichthyofauna.

Data collected indicate the feeding and probably scavenging activity of *Crocuta crocuta* as the main agent of bone accumulation and the SU11 of Area 3 as a probable hyena den. Taphonomic analysis highlighted that 37% of the total macrofaunal NISP (56% if teeth are excluded) shows gnawing marks compatible with those of a large carnivore. The large number of coprolites attributed to cave hyena, the presence of at least four individuals of different ages of this species, among which are two cubs and a newborn, and the mortality pattern of the large prey animals with a dominance of old individuals followed by adult and very young individuals support these hypotheses. There is no certain evidence of human presence in the site. However, the presence of lithic artefacts transported by water into layers SU11 and SU12 suggests the presence of people in the lowlands surrounding CM.

The landscape of the Pontine Plain was characterised during MIS 3 by the proximity of at least three different ecosystems: (i) humid and swampy areas along the coast and the rivers, rich in vegetation, inhabited by wild boar and small mammals, amphibians and reptiles; (ii) extensive steppes and grasslands with occasional small patches of woodland, primarily occupied by large mammals such as wild horse, rhinoceros and cave hyena; (iii) hilly areas covered by Mediterranean and mesophilous woods/forests, populated by cervids, aurochs, wolf, and other small animals.

A multidisciplinary approach has permitted a reliable environmental reconstruction through the combination of pollen and faunal data, therefore improving our understanding of the Pontine Plain landscape between 34–44 ka BP. In addition, this research provides a local environmental framework useful for the interpretation of the many archaeological sites of the region during the highly debated Middle-to-Upper Palaeolithic transition. This is particularly relevant referring to the Middle Palaeolithic site of Grotta Breuil, which represents one of the latest Neanderthal occupations in Italy at present (Grimaldi and Spinapolice, 2010).

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