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Marked regionalism during the Last Glacial across the Italian Peninsula: Evidence from the large mammal assemblage of Santa Maria di Agnano (Apulia, southern Italy)

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ABSTRACT

In this study, we present the mammal sample collected from Stratigraphic Unit 8 of the external excavation area of Grotta di Santa Maria di Agnano (Apulia, southern Italy). The material was collected during the 2011, 2015, and 2016 excavation seasons and it is described here for the first time. In this level, lithic tools consistent with the Gravettian techno-complex have been identified. Grotta di Santa Maria di Agnano is renowned for the Upper Palaeolithic burials, Ostuni 1 and Ostuni 2, found inside the cave and dated between 29,495–28,766 years cal BP and 27,809–27375 years cal BP. Thousands of lithic tools, shells, and vertebrate remains have also been found during more than twenty years of excavations. These data provide valuable information about the terrestrial ecosystems of Mediterranean Europe at the end of the Pleistocene and human-animal interactions in the course of the period of dramatic climatic changes that occurred over the last 40,000 years. Finally, we compare this assemblage with other faunal assemblages recovered in Gravettian contexts across the Italian Peninsula, offering an overview of marked regional differences in climatic and environmental conditions reflected in the diversity of mammalian palaeocommunities.

1. Introduction

During the last 80,000 years, European terrestrial ecosystems were significantly affected by the global climatic cooling trend that began in the late Middle to Late Pleistocene, resulting in dramatic environmental changes (Ramstein et al., 1997; Kahlke, 2014). The climatic deterioration culminated in the Last Glacial Maximum (LGM, MIS 2), profoundly impacting mammal palaeocommunities and terrestrial ecosystems. During the severe glacial episodes, forests retreated to refugia in southern Europe, replaced by open, steppe-like landscapes dominated by grasses, sedges, and hardy shrubs (Combourieu-Nebout et al., 2015; Sadori, 2018; Di Pasquale et al., 2020). These climatic and environmental changes recognized at the end of Pleistocene led to substantial changes in faunal composition, with the extinction of some large mammals, leading to an important loss in biodiversity of European mammalian palaeocommunities (Sommer, 2020). Some mammalian species adapted to new environments or shifted in their geographic ranges toward southern regions where temperate climates and wooded landscapes characterized fragmented refugia (Gliozzi et al., 1997; Palombo, 2009; Masini and Sala, 2011; Sommer, 2020; Leonardi et al., 2022). The spread of open environments, combined with the general cooling climatic trend, supported cold-adapted mammals such as woolly mammoths, woolly rhinoceroses, reindeer, and steppe bison at southern latitudes of the northern hemisphere (Kahlke, 2014 and reference therein). These cold adapted mammalian species of the Eurasian Late Pleistocene are commonly known as "*Mammuthus-Coelodonta* faunal complex" (Chow et al., 1959; Kahlke, 1994, 1999, 2014).

In the Italian Peninsula, which primarily extends along the latitudinal axis, the climatic instability of the Late Pleistocene was reflected in the pronounced regional differences creating heterogeneous climatic and environmental conditions (Sala, 1983; Gliozzi et al., 1997; Masini and Sala, 2011; Manzi et al., 2011).

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These regional climatic differences, especially at the end of the Late Pleistocene, resulted in asynchronous mammal dispersal events (Gliozzi et al., 1997; Masini and Sala, 2011). The Italian fossil record of the Last Glacial (MIS 5d-2) is mainly represented by fossils collected at archaeological sites, where the human presence is documented through artefacts of Middle and Upper Palaeolithic provenance. Examples are Arene Candide (Cassoli and Tagliacozzo, 1994a), Grotta della Cala (Boscato et al., 1997), Grotta Paglicci (Sala, 1983; Boschin et al., 2018,2019) Grotta della Serratura (Boscato et al., 2005), Riparo Fumane (Cassoli and Tagliacozzo, 1994b), and Riparo Mochi (Tagliacozzo et al., 2012). The paleontological record from these deposits is primarily examined from a zooarchaeological perspective, as the remains are often highly fragmented due to human exploitation of animal carcasses. This aspect significantly limits the study of the "*Mammuthus-Coelodonta* faunal complex" in the Italian Peninsula. However, some genera representatives within this cold-adapted assemblage were not found in this territory (e.g., *Saiga, Ovibos*) (Sala et al., 1992; Gliozzi et al., 1997), whereas others were poorly documented and frequently only in the northern areas of the peninsula (e.g, *Alces alces*; Sala et al., 1992; Gliozzi et al., 1997; Sala, 2005), or only in western side of the southern areas of the peninsula (e.g., *Bison priscus;* Spagnolo et al., 2020).

Of considerable interest is the faunal assemblage found at the site of Cardamone (Lecce, Apulia) biochronologically attributed to the climax of the Last Glacial Maximum (22–18 ka), mainly based on the presence of the woolly mammoth and the woolly rhinoceros (Rustioni et al., 2003). The mammalian record of Cardamone documents one of the southernmost occurrences of the "*Mammuthus-Coelodonta* faunal complex" in Europe, demonstrating the significant impact of climatic

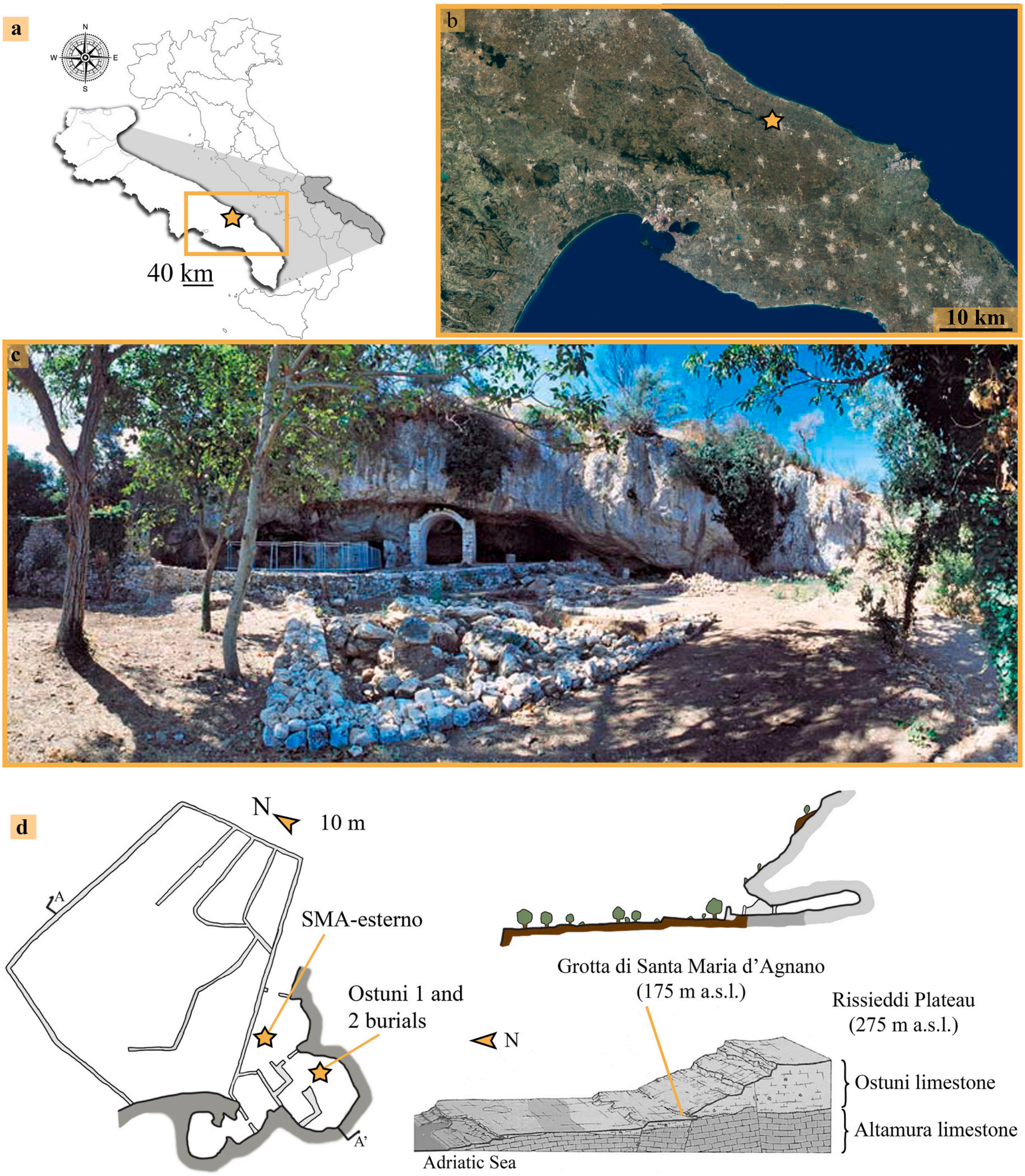

Fig. 1. Geographical position of Grotta di Santa Maria di Agnano-Esterno (Brindisi, Apulia) (a–b), its panoramic view (c), and the position of the outside area (d).

changes during the Last Glacial. In addition to typical elements of the "*Mammuthus-Coelodonta* faunal complex", the Cardamone mammals included species indicating more temperate climatic conditions, such as *Bos primigenius, Equus ferus*, and *Cervus elaphus.* This is not surprising given that the Italian Peninsula is considered one of the glacial refugia of Europe, where species adapted to temperate climate could persisted during cooler periods (Sommer and Nadachowski, 2006; Bhagwat and Willis, 2008; Provan and Bennett, 2008; Stewart and Cooper, 2008; Stewart et al., 2010).

Grotta di Santa Maria di Agnano (Ostuni, Apulia) was discovered during the 1960s by the ASER (Studies and Research Association; Associazione Studi e Ricerche in Italian). Systematic excavations of the site began in 1991 and lasted until 2019. In the long and well-preserved sedimentary succession, several funerary complexes have been discovered, notably the Upper Palaeolithic burials Ostuni 1 and Ostuni 2 (Coppola, 1992, 2012; Vacca et al., 1992; Vacca and Coppola, 1993; Nava et al., 2017). These relevant findings immediately made Grotta di Santa Maria di Agnano a key-site for understanding human activity and their adaptation in Europe during the Late Pleistocene. The deposit shows evidence of human presence from the Middle Palaeolithic to recent times (Coppola, 2012; Coppola et al., 2017). Since 2007, excavations also took place outside the cave, where fossil remains and artefacts dating to the Upper Palaeolithic have been recovered (Baills, 2015; Coppola et al., 2017). To date, the stratigraphic succession of Santa Maria di Agnano – Esterno (SMA-esterno) consists of thirteen levels, pointing to human frequentation from the Gravettian to the final Epigravettian.

The aim of this research is to describe the mammalian faunal assemblage from the Gravettian level (Stratigraphic Unit 8, SU8) of the SMA-Esterno for the first time. The studied assemblage is then compared to other published faunal assemblages associated with Gravettian tools found in Italy in order to identify regional differences among mammalian palaeocommunities.

2. Stratigraphic, archaeological and palaeontological setting

Grotta di Santa Maria di Agnano is located on the north-western edge of the Risieddi promontory, at the altitude of about 175 m (Fig. 1). The Murge cliffs are composed of two Cretaceous formations: the Ostuni limestone formation and the Altamura Formation. Grotta di Santa Maria di Agnano opens at the contact of these different Cretaceous Formations (Coppola, 2012; Parise, 2012; Parise and Pepe, 2016). The Santa Maria di Agnano – Esterno (SMA-Esterno) excavation zone is situated outside the cave, near the current entrance, and covers an area of 21 square metres. However, the Gravettian occupation was only excavated over a small area of 3 square metres, corresponding to grid squares b3, c3, and d3 (Fig. 2).

2.1. *Stratigraphic sequence*

The complete stratigraphic sequence currently includes at least thirteen levels (SU, Stratigraphic Unit; Fig. 2). The bottom of the cultural deposits corresponds to SU13, a clay formation containing no limestone blocks. SU12 lays directly on top of SU13, containing a few heavily eroded blocks with rounded fractures encased in clay identical to that of SU13. The faunal remains exhibit very dark surfaces, a coloration probably linked to the presence of manganese in the sediment. SU11 is a sub-angular limestone gravel. The size of the clasts varies between 5 and 10 cm, embedded in a brown-orange clay matrix. SU10 is a brownish clay, about 30 cm thick, containing numerous faunal remains associated with lithic artefacts. SU9 is a disorganized deposit of medium-sized blocks between 70 cm and 150 cm, encased in a brownish clay matrix (40 cm thick). This level was dated to 27,135–26,446 cal BP (Fig. 3; Table 1). SU9 is covered by a brownish clay-sandy sediment, 10 cm thick (SU8), dated to 28,463–27,787 cal BP (Fig. 3; Table 1). Numerous faunal remains and tools culturally attributable to the broad sense of the Gravettian were unearthed in SU8.

SU7, with a thickness of 10 cm, is a brownish clay with a few thin intercalated layers of possible tephra. This layer is covered by SU6, a reddish-brown clay containing small clasts between 2 and 8 cm in size and a thickness of 15 cm. SU6A is a reddish clay deposit containing numerous medium-sized clasts between 2 and 8 cm. This level was dated to 19,881–19,560 cal BP (Fig. 3; Table 1). This filling layer is covered by SU5, a chaotic deposit of large blocks between 100 cm and 150 cm in size, corresponding to the collapse of the original porch. SU4C is a grayish-reddish clay formation (50 cm thick), dated to 18,725–18,288 cal BP (Fig. 3; Table 1). This level is overlain by SU4B, a lenticular reddish clay of variable thickness (averaging 10 cm thick). SU4A, a reddish-gray clay deposit, caps the filling (50 cm thick). The top of SU4A was dated to 11,698–11,248 cal BP, placing it at the onset of the

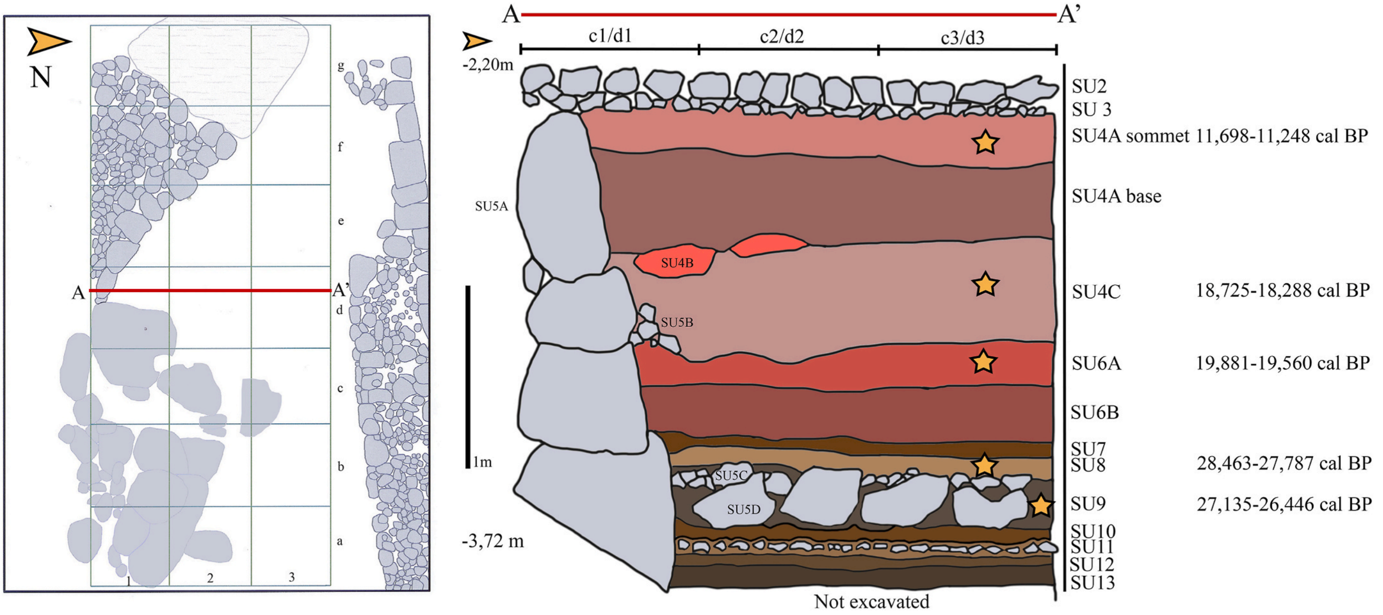

Fig. 2. Planimetry and stratigraphic sequence of the Grotta di Santa Maria di Agnano-Esterno. Orange stars indicate the position of the sample dated with radiocarbon method. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

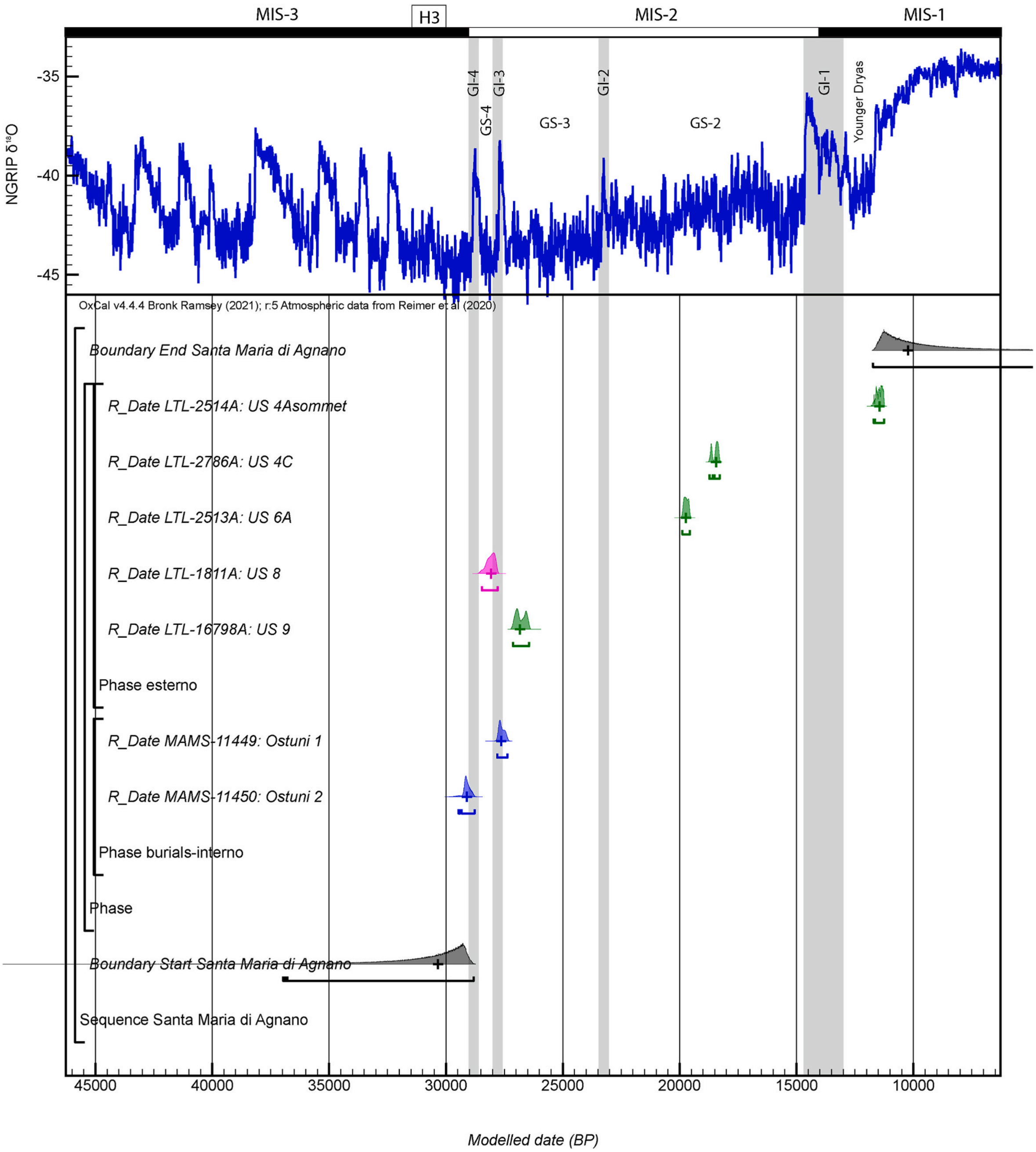

Fig. 3. Bayesian modeling of all available dates from Santa Maria di Agnano plotted against the North Greenland (NGRIP) δ18Oice record and event stratigraphy; Greenland Stadial/Interstadial (GS/GI) cycles for the last 48 kyr BP (before 2000 AD). The large square brackets and OxCal v. 4.4 CQL2 keywords define the overall model exactly. Blue: human; magenta: faunal bone; green: charcoal.

Holocene. (Fig. 3; Table 1).

2.2. Archaeological context

In the lower part of the filling, SU13-12, lithic tools have been found, but their study is still in progress. From SU11 to SU6, the lithic industry consists of 526 tools attributed to the Gravettian (Baills et al., 2021). This is particularly the case for the corpus from SU8 to SU6B, attributed to a late or evolved phase of the Gravettian, while the industry collected in SU11 to SU10 has been linked to an earlier phase of the Gravettian (Baills et al., 2021). The tools are mainly made from laminar or lamellar blanks. Among these, backed points and backed pieces dominate the assemblage. In the vast majority of cases, backed points, or Gravette points, are shaped by deep straight retouching. They can also exist as Vachons points with characteristic flat inverse retouch at their ends. These prototypes can be double pointed. A significant number of backed points were made from blanks morphologically resembling burin spalls. These prototypes are quite easily distinguishable from their straight counterparts made from lamellae with a central ridge produced by debitage. Those made from spalls are distinguished by their strong equilateral section. Their thick section may have made them more robust than their lamellar counterparts. In general, burins are the most represented tool in all Gravettian levels of SMA-Esterno. The two most frequent types are the burin on a break and the burin on a truncation. They can sometimes be multiple or mixed. Dihedral burins exist but are numerically less significant. A few rare burins resemble the Raysse type with debitage developing on the ventral face of the core. Endscrapers are half as numerous as burins. The carinated or atypical carinated type

Table 1
Radiocarbon measurements from inside and outside contexts of Grotta di Santa Maria di Agnano.

Santa Maria di Agnano – Esterno (outside

Code	Stratigraphic unit	Material	Specie and anatomic identification	Radiocarbon age	Cal yr BP (2σ) OxCal v. 4.4.4	δ13C (‰)	Laboratory	References
LTL 2514A	4Asommet	Charcoal		9973 ± 55	11,698–11,248	−19.6 ± 0.2	Centre for Applied Physics, Dating and Diagnostics (CEDAD)	Baills (2015)
LTL 2786A	4C	Charcoal		15255 ± 55	18,725–18,288	−20.7 ± 0.1	Centre for Applied Physics, Dating and Diagnostics (CEDAD)	Baills (2015)
LTL 2513A	6A	Charcoal		16347 ± 55	19,881–19,560	−20.2 ± 0.3	Centre for Applied Physics, Dating and Diagnostics (CEDAD)	Baills (2015)
LTL 1811A	8	Bone	Undetermined	23945 ± 110	28,463–27,787	−15.4 ± 0.5	Centre for Applied Physics, Dating and Diagnostics (CEDAD)	Baills (2015)
LTL 16798A	9	Charcoal		22515 ± 100	27,135–26,446	−25.5 ± 0.3	Centre for Applied Physics, Dating and Diagnostics (CEDAD)	Baills (2021)

Grotta di Santa Maria di Agnano (inside)

Code	Stratigraphic unit	Species	Sample	Radiocarbon age	Cal yr BP (2σ) IntCal20	d13C	Laboratory	References
MAMS-11449	Burial	Bone	*Rib of Homo sapiens*	23446 ± 107	27,809–27,375	NA	Max Planck Institute for Evolutionary Anthropology	Fu et al. (2016)
MAMS-11450	Burial	Bone	*Rib of Homo sapiens*	24910 ± 125	29495–28786	NA	Max Planck Institute for Evolutionary Anthropology	Fu et al. (2016)

dominates the stock, but there are also flat endscrapers of good quality on retouched blades. Endscrapers can also be part of composite tools, such as the endscraper-point. Truncations, notches, backs with truncations, and denticulates are present in the tool corpus but are rare. Points are also rare. Thick retouched blades reminiscent of Aurignacian prototypes are also found. This same retouching is used to shape distal scrapers on flakes. Finally, a few notched tools complete this lithic series. Despite its relatively small size, this Gravettian lithic assemblage is quite easily distinguishable from the one found in the overlying Epigravettian levels, which comprise US6A to US4A. These upper levels, which have yielded an important lithic series of 3985 tools, are not the focus of this brief presentation and have been reported in previous publications (Baills, 2015, 2021, 2022).

A micromorphological analysis carried out on sediments dating to the Epigravettian levels revealed the presence of bone and shall fragments as well as charcoals, providing further evidence of anthropic activity in this deposit (Chakroun et al., 2018; Baills and Coppola, 2023).

2.3. Zooarchaeological data

A preliminary zooarchaeological study has been published for the SU8 uncovered during the excavation campaigns directed by one of the authors (HB) between 2007 and 2019 (Baills et al., 2021). The anthropogenic accumulation is the result of several seasonal occupations, at least one of which took place in autumn, according to the presence of the long bone of a horse foetus. The faunal spectrum is represented by 10 species of meso/macrofauna. The horse (*E. ferus*)/aurochs (*B. primigenius*) pair clearly dominates the bone assemblage in terms of the number of remains and individuals, with 13 and 9 specimens respectively. Adults are more common in these two species than juveniles, which are under-represented. Among the ungulates, the secondary taxa are red deer (*Cervus elaphus*, MNI = 3), wild boar (*Sus* scrofa, MNI = 2), and ibex (*Capra ibex*, MNI = 1).

The Gravettian humans practised hunting focused on adult horses and aurochs in the vast plain bordering the Adriatic Sea to acquire various meat resources. The presence of numerous butchering marks on the skeletal elements bears witness to filleting, and carcass disarticulation in order to consume the meat. In addition, bone fracturing, particularly of long bones, is consistent with a systematic marrow exploitation. The Gravettian humans probably first processed the carcasses at the killing site and then transported large sections to the site. However, the selection of elements transported was more restrictive in the aurochs than in the horse, according to the frequencies recorded for elements of the axial skeleton and the basipodial bones. Other ungulates present near the site, such as deer, wild boar, and ibex, were occasionally preyed upon by human populations, perhaps on the Risieddi promontory surrounding the site. It should be noted that the systematic fracturing of bones (axial skeleton, epiphyses of long bones, diaphysis, short bones, and phalanges) expressed in the study of bone survival and the proportions of unidentified material could mean that bone fat was exploited, perhaps by boiling or destruction, rather than being used as fuel (Baills et al., 2021).

3. Materials and methods

The fossil material described here, currently housed in the "Museo di Civiltà Preclassiche della Murgia meridionale" (Ostuni, Apulia), was found during the 2011, 2015, and 2016 excavation campaigns. The studied assemblage was recovered in SU8 and was marked by a different acronym: SMA-E\2011- for the material excavated during the 2011 field season; field labels/numbers (b2\-, c1\-,c2\-, c3\-, d2\-,d3\-) correspond to the material excavated during the 2015 and 2016 field seasons.

Skeletal elements were identified to the closest taxonomic unit and remains, whether identifiable or not, were assigned to size-classes. Each postcranial element is assigned to an anatomical portion in order to evaluate the minimum number of elements (MNE). Minimum Number of

Individuals is estimated for dental and postcranial material to determine species abundance and the age structure of the main species are estimated on the basis of cheek teeth eruption sequences and dental wear stages.

The cortical bone surfaces were observed with the naked eye, a magnifying glass (x20) and a digital microscope in order to determine the impact of weathering or biological damage on the assemblage, such as that caused by climatic factors or human and carnivorous activities. The identification criteria follow those established in the scientific literature (e.g. Behrensmeyer, 1978; Binford, 1981; Lyman, 1994). Bone fracturing was analysed following the recommendations of Bunn (1983), Villa and Mahieu (1991), and Reitz and Wing (1999) concerning the morphology of fracture edges and the intensity of diaphysis fracture. The thermal modifications visible on the bones were documented by classifying them according to the degree of combustion and colour (Shipman et al., 1984).

For investigating possible chronological variability in fossil series from late Middle Pleistocene to Early Holocene sites of Apulia, biometric comparisons of selected taxa (*Bos primigenius*, *Cervus elaphus* and *Canis lupus*) have been carried out. We used boxplots of lower third molar length (M_3L) for *B. primigenius* and lower fourth premolar length (P_4L) for *C. elaphus,* and *C. lupus*.

For *B. primigenius*, the maximum meso-distal length above the root-crown junction of the lower third molar (M_3L) was measured. In addition to the best documented teeth in our sample, the M_3 is easily distinguishable from the other lower molars, which makes it more reliable when using the literature data for comparison. As comparative material, we used the literature data from the following sites: Cava Spagnulo (Mecozzi et al., 2018), Fondo Cattìe (Corridi, 1987), Grotta del Cavallo level F (Sarti et al., 1998), Grotta Paglicci (Boscato, 1994), and Grotta delle Mura (Bon and Boscato, 1993). Biometric data for *B. primigenius* remains stored in the following institutions have also been collected: State Institute of Higher Education “Galilei-Costa-Scarambone” (GCS, Lecce, Cardamone), PaleoFactory laboratory, Department of Earth Sciences, Sapienza, University of Rome (PL, Rome, Avetrana 2–7, Avetrana 8, Grotta Romanelli and Melpignano – Cava Bianco), Italian Institute of Human Paleontology (IsIPU, Frosinone, Grotta delle Tre Porte and Grotta dei Giganti). We also considered subfossil samples of *Bos taurus* from Elvas-Kreuzwiese (Boschin, 2018) and Silves-lix (Davis et al., 2008).

For *C. elaphus*, we considered the material housed in the following institutions: PL (Grotta Romanelli, Ingarano, Melpignano – Cava Bianco, San Sidero 3, and Vieste) and IsIPU (Fondo Focone, Grotta dei Giganti, Grotta dei Ladroni and Grotta delle Tre Porte). For comparative purposes, literature data have also been included from the following: Fondo Cattìe (Corridi, 1987) and Grotta del Cavallo level F (Sarti et al., 1998). The extant material considered here is preserved at PL and Museo delle Civiltà (Rome).

For *C. lupus*, we used the P_4 length since it is the most significative tooth for size comparison in the available sample. Fossil specimens from the following sites have been considered: Grotta Romanelli level G (Bertè, 2014; Sardella et al., 2014), Avetrana bed 8 (Mecozzi and Bartolini Lucenti, 2018), Cava Spagnulo (Mecozzi et al., 2018), and Grotta Paglicci (Boscato, 1994; Bertè, 2014). Biometric data on canid remains stored in the following institutions have also been collected: GCS (Cardamone), PL (Avetrana, Grotta Romanelli, Ingarano, Melpignano, San Sidero), and IsIPU (Grotta dei Giganti, Grotta delle Tre Porte).

The measurements of the studied materials have been taken with digital callipers to the nearest 0.01 mm, following von den Driesch (1976). The faunal assemblage coming from the SU8 of the SMA-esterno was compared with assemblages of other Gravettian sites of the Italian Peninsula, such as Arene Candide (Cassoli and Tagliacozzo, 1994a), Grotta del Rio Secco (Peresani et al., 2014), Grotta del Romito (Bertini Vacca, 2021), Grotta della Cala (Boscato et al., 1997), Grotta della Serratura (Boscato et al., 2005), Grotta di Roccia San Sebastiano (Belluomini et al., 2007), Grotta Paglicci (Sala, 1983; Boscato, 2004), Riparo Fumane (Cassoli and Tagliacozzo, 1994b), and Riparo Mochi (Tagliacozzo et al., 2012).

4. Results

4.1. General remarks

From 2334 fossils from SMA-esterno, 960 fossils have been taxonomically identified (Figs. 4 and 5; Table 2). The faunal assemblage from SMA-esterno is dominated by *Equus ferus* (62 % of the NISP). The aurochs is well represented, whereas the pachyderms are absent. The carnivores are very poorly represented in the analysed sample (ca.1 % of the NISP). In particular, *Panthera pardus* is represented only by two juvenile specimens (Table 2). The taxonomic determination rate is high at 41%. The largest part of the collection is highly fragmented, and only a few specimens were found in anatomical connection.

The sample is in good state of preservation, showing a slight brownish thin limestone crust on 5.6% of the material. Many unidentifiable specimens come from long bone shaft fragments of large size (bovids and equids) and medium size (cervids) ungulates. Traces of butchery have been found on the bones of the main ungulate species, particularly horses and aurochs. The striations mainly concern oblique and longitudinal incisions found on long bone shafts and rib fragments, testifying to the removal of soft tissue from the bone (Fig. 6; Table 2). Green bone fractures related to the extraction of marrow are widespread in the two main prey species (horse and aurochs), with helical fracture morphologies, oblique angles, and smooth edges. Sometimes, percussion impacts are clearly identifiable on the diaphysis. The frequency of this indicator is particularly high in aurochs (16.2%, Fig. 6; Table 3) due to the preferential anthropogenic transport of the most nutritious skeletal elements (stylopodials and zeugopodials). Damage caused by carnivores is scarce. A few bones show perforations, evidence of gnawing, or even gastric erosion, which may be compatible with the activity of small to medium-sized carnivores, such as wolves and foxes (Fig. 6; Table 3). Traces of rodents are even more exceptional, as only one horse sesamoid exhibits small parallel marks left by rodent incisors. Linear marks with smoothly rounded edges due to the development of plant roots on the cortical surface can be seen on ca.15% of the material, but they remain very limited and superficial (Table 3).

A small proportion of faunal material shows evidence of surface abrasions or weathering, such as exfoliation (visible on 6% of the material) or micro-fractures (on 17,5% of the material), excluding the long transport prior to the final deposition or a long-time exposure on the surface before burial. We can state that when this type of damage is present it is usually limited and not very invasive (Fig. 6; Table 3). Around 10% of the material shows slight deposit areas or coating of black oxide, probably manganese (Fig. 6; Table 3).

4.2. Systematic paleontology

Order Artiodactyla, Owen,1848

Family Bovidae, Gray, 1821

Subfamily Bovinae, Gray, 1821

Genus *Bos*, Linnaeus, 1758

Bos primigenius, Bojanus, 1827

The aurochs is well represented species in the assemblage (MNE = 81; Fig. 4; Table 2). The MNI calculated on postcranial elements (humerus) revealed the presence of nine individuals including at least one young. The largest part of the sample consists of portions of postcranial skeleton (particularly humerus, femur, and tibia shafts) but several upper and lower teeth are diagnostic (Table S1). The teeth display slight wear of the cusps, hence can be assigned to adult specimens.

The following morphological features can be identified: a well-

Fig. 4. Mammal remains from Grotta di Santa Maria di Agnano-Esterno: c2/20b-77, right hemimandible of *Equus ferus*; c2/20b-80 (a1-3), left hemimandible of *Equus ferus* (b1-3); SMA-E\2011–54, left hemimandible of *Bos primigenius* (c1-3); SMA-E\2011-C2-2, right hemimandible of *Cervus elaphus* (d1-3); b2/18-19-38, right lower second molar of *Capra ibex* (e1-3); SMA-E/2011–41, upper right second molar of *Sus scrofa* (f1-3); c2/20b-67, left hemimandible of *Lepus corsicanus* (g1-3). Fossils in labial (1), lingual (2) and occlusal (3) views. Scale bars 3 cm.

developed entostyle and a columnar and hypsodont appearance (swelling absent) of the upper molars in mesial and distal views; V-shaped enamel around the central cavity of both the upper and the lower molars in buccal view; two main lobes are more developed mesiodistally in the lower molars in occlusal view; in the lower third molar, presence of a small accessory stylid between hypoconid and hypoconulid in labial view, and obtuse angle between the hypoconid and hypoconulid in occlusal view. In mesial or distal view, the labial and buccal margins of the molars are sub-parallel. These features of teeth morphology are generally observed in *Bos primigenius* (Sala, 1986; Slott-Moller, 1990).

The fossil specimens from SMA-Esterno are large-sized, comparable with other aurochs remains from Late Pleistocene sites of Apulia, especially with Cardamone, Fondo Cattìe, level F of Grotta del Cavallo, and Grotta Paglicci (Fig. 7). All samples of *B. primigenius* are larger than subfossil specimens of *B. taurus.*

Subfamily caprinae, Gray, 1821

Genus *Capra*, Linnaeus, 1758

Capra ibex, Linnaeus, 1758

Only four remains were found (MNE = 4; MNI = 1), representing one of the taxa less frequently found among the ungulates. The right teeth (M$_2$ and M$_3$) show a slight wear of cusps allowing their designation to a young adult individual. The crown of the second molar is sub-complete (the apical part of the mesostylid is missing), but the third molar is fragmented, leading to the loss of the basal part of the tooth and the hypoconulid (Table S2). The two lower molars show the buccal margins of hypoconid and protoconid pointed (appearing triangular in shape), a feature commonly observed in *Capra ibex* (Halstead et al., 2002). The lingual wall of the M$_2$ has discrete stylids, whereas those of the M$_3$ are narrow and more prominent, notably the metastylid. The metaconids and entoconids of the M$_2$ are slightly dilated, separated by a wide, flattened valley and those of the M$_3$ are thin and faded. In labial view, the protoconids and hypoconids form an asymmetrical relief that is offset distally. The conids are separated by a deep, narrow groove. The caprine fold is clearly visible in the upper mesio-labial part of the first lobe in the M$_3$.

Family cervidae, Goldfuss, 1820

Subfamily Cervinae, Goldfuss, 1820

Genus *Cervus*, Linnaeus, 1758

Cervus elaphus, Linnaeus, 1758

This species is represented by a few remains in a good state of

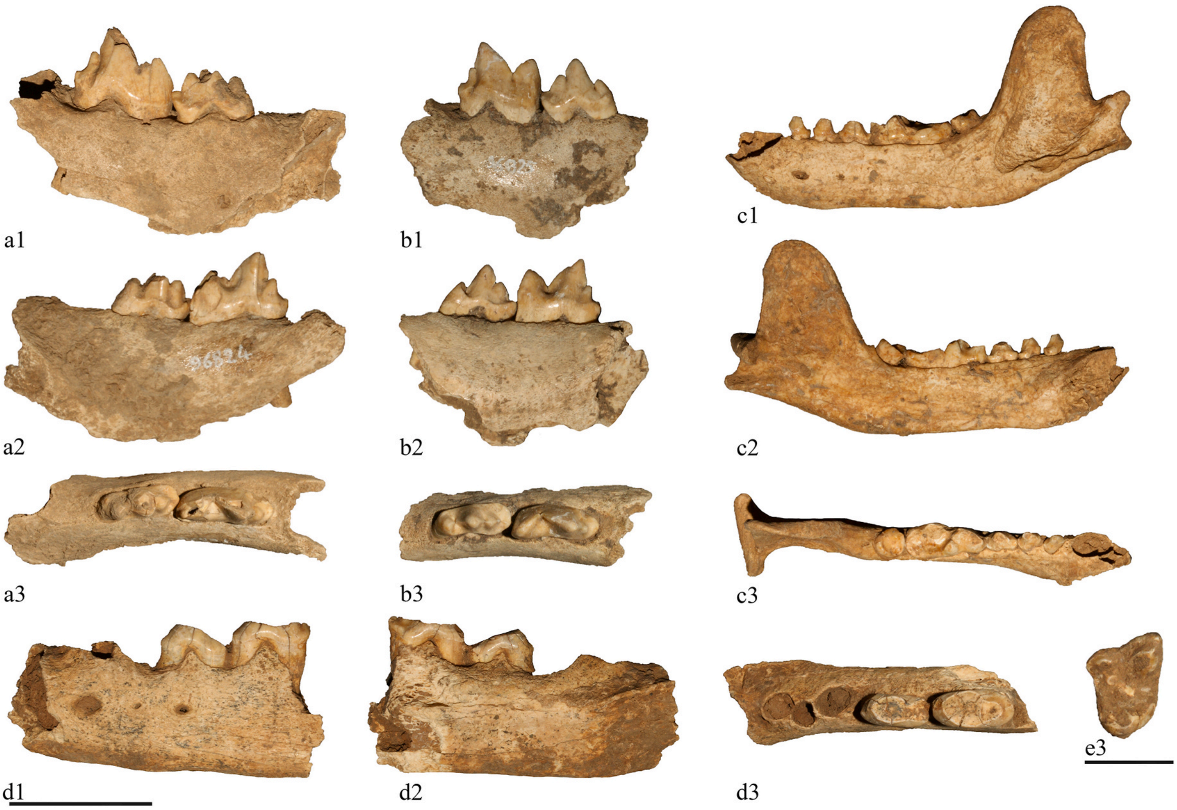

Fig. 5. Mammal remains from Grotta di Santa Maria di Agnano-Esterno: SMA-E\2011–72, right hemimandible of *Panthera pardus* (a1-3); SMA-E\2011–73, right hemimandible of *Panthera pardus* (b1-3); SMA-E\2011–69, left hemimandible of *Meles meles* (c1-3); SMA-E\2011–70, left hemimandible of *Canis lupus* (d1-3); SMA-E \2011–47, right upper first molar of *Vulpes vulpes* (e3). Fossils in (labial (1), lingual (2) and occlusal (3) views. Scale bars 3 cm.

Table 2
Mammal remains from Grotta di Santa Maria di Agnano – Esterno. Abbrevations: NISP – number of identified specimens; MNE – minimum number of elements; MNI – minimum of the number individuals.

Species	NISP	%NISP	MNE	MNI
Equus ferus	599	62.4	228	13
Bos primigenius	261	27.2	81	9
Capra ibex	4	0.4	4	1
Cervus elaphus	69	7.2	27	3
Sus scrofa	15	1.6	12	2
Panthera pardus	2	0.2	2	2
Canis lupus	4	0.4	4	1
Vulpes vulpes	2	0.2	2	1
Meles meles	1	0.1	1	1
Lepus corsicanus	3	0.3	3	1
Total	**960**			**34**
Unidentified	**1374**			
NRT	**2334**			

preservation (MNE = 27; MNI = 3) (Fig. 4; Table 2). The postcranial material can be ascribed to adult individuals based on the complete fusion of the epiphyses. No (sub-)complete antler remains were discovered in the Gravettian level of SMA-Esterno. Only a point, a distal part of tine, can be attributed to *Cervus* (SMA-E\2011-C1-4). The P_3 and P_4 of the right mandibular fragment SMA-E\2011-C2-2, well preserved but very worn, are characteristic of the genus *Cervus*. In occlusal view of the P_3, the parastylid is thin and not very prominent. The paraconid is poorly individualised and forms a wall which tends to flatten out with the parastylid. The metaconid is highly developed and extends strongly on the lingual side, outside a virtual parastylid/entostylid line. The valley between the paraconid and the metaconid is marked, forming a slightly asymmetrical V-shape. The entoconid is poorly individualised and develops obliquely to the long axis of the mandible. The valley between the metaconid and entoconid appears closed, forming an enamel island, due to the pronounced distal development of the metaconid and the tooth wear. The entostylid rises perpendicular to the sagittal axis and joins the metaconid at the base of the crown. On the vestibular side, the protoconid is regularly curved in occlusal view. The boundary with the hypoconid is faintly marked by a very discreet groove. In occlusal view, the parastylid and paraconid of the P_4 are unified. The presence of a small mesio-buccal enamel island shows that the parastylid was slightly detached from the paraconid at the apex of the crown when the animal was younger. The metaconid is broad, well individualised and lies within the virtual parastylid/entostylid line. The anterior wing of the metaconid is not very well developed, which leaves valley 2 wide open (P_4 not molarised, unlike the pattern generally observed in red deer populations). The posterior wing of the metaconid is poorly developed but unites with the entoconid on this worn tooth, which closes valley 3 to form an enamel island. The entoconid initially develops perpendicular to the sagittal axis of the mandible in the buccal direction, then clearly obliquely in the distal direction. The entostylid is perpendicular to the long axis of the mandible. It tends to merge with the entoconid at the base of the crown on this worn tooth. On the labial side, the anterior wing of the protoconid is regularly curved. However, there is a very slight inflection on the anterior wall, and even a thin vertical groove, a remnant of the mesial cingulum. The hypoconid is separated from the protoconid by a well-defined groove. On postcranial elements, several morphological features of the metacarpal (split separating the lateral and medial epicondyles is well developed in posterior view and the posterior epicondyle crests are well elongated proximally in anterior and posterior views) and the first phalanx (the posterior border of the proximal articular surface is grooved) can be observed. According to Lister (1996), these features are clearly referable to the red deer. The biometric comparison of fossil and extant red deer shows that the length of the P_4 of SMA-E\2011-C2-2 hemimandible from SMA-Esterno is the longest among the remains from late Middle Pleistocene and Early Holocene sites of Apulia, and extant specimens (Fig. 8). The dimensions of the tooth (length and breadth) reach the highest values found in several European Middle and Upper Pleistocene sites, as for example the Lazaret cave (Liouville, 2007), Arma delle Manie (Psathi, 2003), Combe-Grenal (Guadelli, 1987) and La Ferrrasie (Delpech, 1984).

Family Suidae, Gray, 1821

Subfamily Suinae, Gray, 1821

Genus *sus*, Linnaeus, 1758

Sus scrofa, Linnaeus, 1758

Few remains in a good state of preservation attested the presence of suids (MNE = 12; MNI = 2) (Fig. 4; Table 2). Among the sample, composed mainly of postcranial bone fragments, an upper right M^2 was identified. The tooth is robust, bunodont, and brachydont, with a rectangular shape in occlusal view. The four main cusps have a similar development, an accessory cusp is present between the mesial and distal cusps and a pentacone is distinguishable in the distal end of the tooth. The mesial and distal cingulum are present. These are clearly indicative of *Sus scrofa* (Iannucci et al., 2020). One distal end of tibia has a trapezoidal outline, with two marked but asymmetrical sub-parallel grooves. The lateral groove is wide, open, and quadrangular-shaped when viewed distally, while the medial groove is narrower, closed, and ellipsoid. This characteristic is typical of the distal tibia of suids. The fossils from SMA-Esterno were included in a large biometric comparison of suids from Apulia (Iannucci et al., 2020). The results of this work revealed that the size of *Sus scrofa* fluctuated during the Late Pleistocene, with the smallest specimens found during the glacial periods (MIS 4 and MIS 2).

Order Perissodactyla, Owen1848

Family Equidae, Gray, 1821

Subfamily Equinae, Steinmann and Döderlein, 1890

Genus *equus*, Linnaeus, 1758

Equus ferus, Pallas, 1775

The wild horse is the better represented species in the studied sample (MNE = 228) (Fig. 4; Table S3). The MNI calculated on right M^1 and left P_2 is 8 individuals (Table 2). The studied material is in a good state of preservation and is especially composed of mainly of long bones fragments (basipodial bones are under-represented) but isolated upper and lower teeth, complete or fragmented, are frequent contrary to the patterns observed in previous ungulates. The premaxillary and maxillary bones are fragmented and often constituted by the alveolar portions of the teeth. Based on the analysis of the dental wear and the fusion of the epiphyseal suture, the large part of studied specimens is assigned to

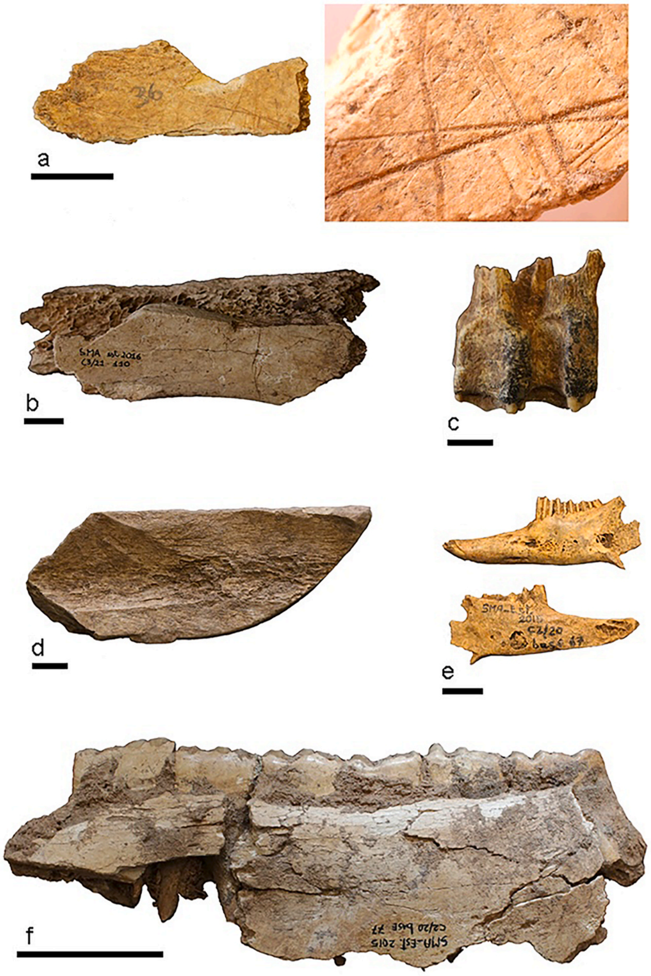

Fig. 6. Taphonomic examples from Grotta di Santa Maria di Agnano-Esterno: a – cutmarks on a rib fragment (SMA-E/C2_21_36); b – Linear marks of plant roots and cracks on a right scapula of Bos, SMA-E/C3_21_110); c – oxide deposit area on a right upper fourth deciduous of *Equus* (SMA-E/C3_21_112); d – green bone fracture and percussion notches on a metapodial shaft of *Equus* (SMA-E/B2_grav2806); e – carnivore modifications on a left mandible of *Lepus corsicanus* (SMA-E/C2_20b_67); f – cracks on a right mandible of *Equus ferus* (SMA-E/C2_20b_77). All scale bars of 1 cm (except f.: 5 cm). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 3

Number of remains with anthropogenic and taphonomic damages from Grotta di Santa Maria di Agnano-Esterno. * remark: for anthropogenic, carnivore, and rodent modifications, percentages establish function of the number of remains without isolated teeth.

Species	*Biologic modifications*										*Weathering, physical and chemical damages*							
	Cut-maks *		*Bone breakage* *		*Carnivore* *		*Rodent* *		*Roots*		*Cracks*		*Abrasion*		*Exfoliation*		*Oxide deposit*	
	n	*%*	*n*	*%*	*n*	*%*	*n*	*%*	*n*	*%*	*n*	*%*	*n*	*%*	*n*	*%*	*n*	*%*
Equus ferus	66	14.2	23	5	2	0.4	1	0.2	120	20	158	26.4	37	6.2	51	8.5	113	18.9
Bos primigenius	40	16.6	39	16.2	1	0.4			69	26.4	88	33.7	14	5.4	23	8.8	32	12.3
Capra ibex											3	75	1	25	1	25		
Cervus elaphus	2	3	2	3	1	1.5			9	13	8	11.6	2	2.9	4	5.8	5	7.2
Sus scrofa	1	7.7			1	7.7			2	13.3	1	6.7	1	6.7				
Panthera pardus											1	50	1	50	2	100		
Canis lupus											1	25			1	25	3	75
Vulpes vulpes																		
Meles meles									1	100			1	100				
Lepus corsicanus					1	33.3					1	33.3					1	33.3
Undeterminated	60	4.4	9	0.7	6	0.4			141	10.3	148	10.8	40	2.9	58	4.2	76	5.5
Total	169	7.8	73	3.4	12	0.6	1	0.05	342	14.7	409	17.5	97	4.2	140	6	230	9.9

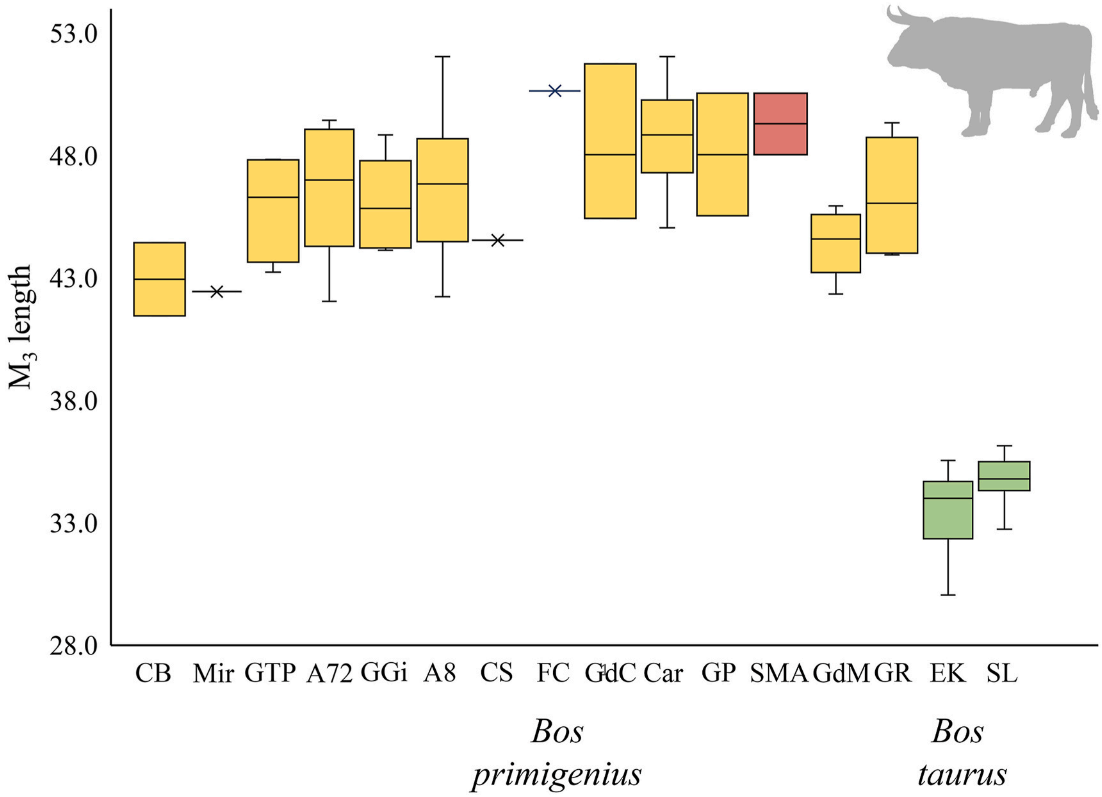

Fig. 7. Box plot of the length of the lower third molar (M_3 in mm) of *Bos primigenius* (in orange) from late Middle to Late Pleistocene Apulian sites, *Bos primigenius* (red) from Grotta di Santa Maria di Agnano, and Holocene samples of *Bos taurus* (in green). Abbreviations: CB – Cava Bianco - Melpignano; Mir – Mirigliano Collection Melpignano; GTP – Grotta delle Tre Porte; A72 – Avetrana beds 7-2; GGi – Grotta dei Giganti; A8 – Avetrana bed 8; CS – Cava Spagnulo; FC – Fondo Cattìe; GdC – Grotta del Cavallo; Car. Cardamone; GP – Grotta Paglicci; SMA – Grotta di Santa Maria di Agnano - Esterno; GdM – Grotta delle Mura; GR – Grotta Romanelli; EK – Elvas-Kreuzwiese; SL – Silves-lix. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

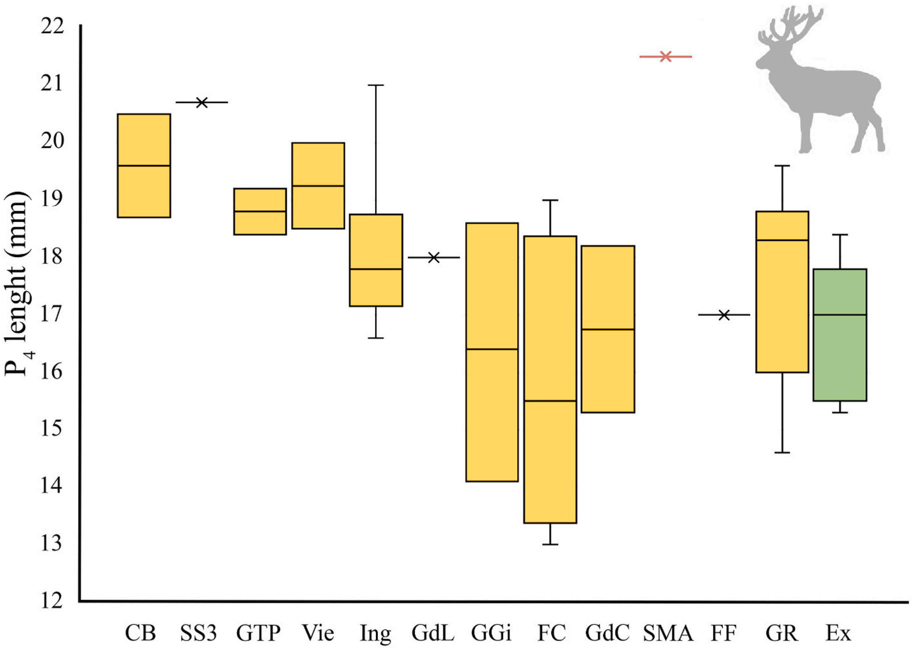

Fig. 8. Box plot of the length of the lower forth premolar (P_4 in mm) of *Cervus elaphus* from late Middle to Late Pleistocene Apulian sites (in orange), *Cervus elaphus* (red) from Grotta di Santa Maria di Agnano, and extant specimens (in green). Abbreviations: CB – Cava Bianco - Melpignano; SS3 – San Sidero 3; GTP – Grotta delle Tre Porte; Vie – Vieste; Ing – Ingarano; GdL – Grotta dei Ladroni; GGi – Grotta dei Giganti; FC – Fondo Cattìe; GdC – Grotta del Cavallo; SMA – Gortta di Santa Maria di Agnano - Esterno; FF – Fondo Focone; GR – Grotta Romanelli; Ex – Extant *Cervus elaphus*. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

adult individuals. Morphologically, several characters can be detected in the upper premolars (P^3-P^4) and molars (M^1-M^2): a long and asymmetric protocone in mesostyle and parstyle of similar size, the pli caballin simplified and short; and a distally open post-protoconal on M^3. On lower premolars (P_3-P_4) and molars (M_1-M_2), the lingual sulcus is U-shaped, the preflexide and the postflexide are well separated, the labial profile of the protoconid and the hypoconid is quite straight and the plie caballine (caballine fold) is present, but short. These features are generally observed in *Equus ferus* (Boulbes, 2009; van Asperen et al., 2012; Boulbes and Gardeisen, 2018).

The wild horse sample from SMA-Esterno was studied by Mecozzi and Strani (2022), providing a large comparative analysis of fossil specimens from late Middle to Late Pleistocene sites of Apulia. The results of this work revealed no statistically significative differences among the latest Middle Pleistocene to Early Holocene samples of *E. ferus*.

Order carnivora, Bowditch, 1821

Family Mustelidae, Fischer von Waldheim, 1817.

Subfamily Melinae Bonaparte, 1838

Genus *Meles*, Brisson, 1962

Meles meles, Linnaeus, 1758

This species is mainly represented by a well preserved hemimandible (SMA-E\2011–71) (Fig. 5; Table 2). It is in a very good state of preservation, even though the incisors and the canine are not preserved, and the P_1 is broken at the level of the root-crown junction (Table S4). In lateral view, the mandibular corpus has a slightly convex ventral profile with an inflexion point at the distal end of M_2. It displays a large mental foramen at the level of the M_2. The mesial border of the masseteric fossa does not reach the distal border of M_2. The angular process is small and slender, whereas the angular ramus is low. The P_1 is monocupsed, and smaller in size than the other premolars. The P_2 and the P_3 display an asymmetrical and mesially directed protoconid and a weakly marked distal cingulum. The P_2 roots are unfused. The P_4 shows a symmetric and stouter protoconid, with mesial and distal cingula weakly marked. The M_1 has the talonid relatively longer than trigonid. The procotonid is mesiodistally elongated, whereas the paraconid is larger than the metaconid. Even if the talonid shows an advanced wear of cusp, the hypoconid and the entoconid seem to be larger than both the entoconulid and hypoconulid. The distal cingulum is quite marked, and it connected the entoconulid to the hypoconulid. The M_2 shows a rounded occlusal outline, with a deep talonid basin and a marked and continuum cingulum along the margin of the teeth. These features are generally observed in *Meles meles* (Baryshnikov et al., 2003; Mecozzi, 2022). The SMA-E\2011-71 was also studied by Mecozzi (2022), which carried out a large morphological and biometric comparison of the *M. meles* record from the Italian Peninsula.

Family Canidae, Fischer von Waldheim, 1817

Subfamily caninae, Fischer von Waldheim, 1817

Genus *canis*, Linnaeus, 1758

Canis lupus, Linnaeus, 1758

This species is the best representative carnivoran of this fossiliferous deposit (MNE = 4) (Fig. 5; Table 2). The SMA-E\2011-69 specimen shows a highly advanced wear of the cusp, whereas the sutures of the postcranial remains are completely fused. Based on this observation, the canid sample can be assigned to an adult individual. The most diagnostic is partial hemimandible SMA-E\2011–69 (Table S5). The mandibular profile is quite straight in lateral view, with three foramina: the first at the level of the P_2; the second between the P_2-P_3; the third at the level of the P_3. The P_3 is elongated mesiodistally, with an asymmetric protocone mesially directed. No accessory cusps or distal cingulum are detected. The P_4 is mesiodistally elongated, with a symmetric protocone, a marked distal accessory cusp and distal cingulum cusp-shaped. The morphologies fall in those generally observed in extant and fossil *Canis lupus* (e.g., Sardella et al., 2014; Mecozzi and Bartolini Lucenti, 2018). Biometrically speaking, the length of P_4 of the SMA-E\2011-69 falls in the variability of the sample from Avetrana bed 8, and is similar to the largest specimens from Cardamone (Fig. 9).

Genus *Vulpes,* Linnaeus, 1758

Vulpes vulpes, (Linnaeus, 1758)

The red fox is rare in the deposit (MNE = 2) (Fig. 5; Table 2). In the sample, a right M^1 SMA-E\2011-47 was identified (Table S6). The occlusal surface of M^1 is partially encrusted by brownish patina. The tooth is elongated buccolingually, and relatively mesiodistally short. The metacone and the paracone have a similar size, and the buccal cingulum is quite marked. The lingual cingulum is also quite marked and the hypocone is well developed. These features are clearly indicative of *V. vulpes* (e.g., Szuma, 2003, 2004, 2007, 2011; Madurell-Malapeira et al., 2021).

Family Felidae, Fischer von Waldheim, 1817

Subfamily Pantherinae, Fischer von Waldheim, 1817

Genus *panthera*, Oken, 1816

Panthera pardus, Linnaeus, 1758

The leopard is documented by two hemimandibles, SMA-E\2011-71 and SMA-E\2011–72, belonging to young individuals (MNI = 2) (Fig. 5; Table 2). Both specimens possess deciduous teeth, the Dp2 and Dp3 (Table S7). The Dp2 displays a symmetric protoconid with marked mesial and distal accessory cusps and a marked distal cingulum. The Dp3 has an asymmetric protoconid distally directed, with a large mesial cusp and a marked distal accessory cusp. Size and morphology of these remains resembles that of the extant specimens of *Panthera pardus* (e.g., Diedrich, 2013; Sauqué and Cuenca-Besćos, 2013).

Order lagomorpha, Brandt, 1855

Family leporidae, Gray,1821

Subfamily Leporinae, Trouessart, 1880

Genus *Lepus,* Linnaeus, 1758

Lepus corsicanus, De Winton, 1898

Only three remains can be ascribed to this species (MNE = 3) (Fig. 4; Table 2). The left hemimandible has a long diastema, with a mental foramen located at the level of the mesial border of the P_3. In the P_3, the crenulations in the hypoconid are absent and the paraflexid in the antero-lingual edge of the tooth is absent. These features are generally observed in *Lepus corsicanus,* differing from those observed in *Lepus timidus* and *Lepus europaeus* (Callou, 1997; Vismara, 2012).

5. Discussion

5.1. Paleoenvironmental implications

Pollen analyses conducted at Santa Maria di Agnano (inside and outside the cave) indicated the existence of open lowlands, characterised by the prevalence of steppe and grasslands, interspersed with occasional mesophilous and thermophilous trees during the Late Glacial (Renault-Miskovsky et al., 2011, 2015). In particular, palaeobotanical analyses were carried out on sediments collected from the Ostuni 1 burial, which was dated at 27,809–27,375 years cal BP (Table 1). This chronological bracketing is quite similar to SU8 of SMA-Esterno, (28,463–27,787 years cal BP). Pollen data from the Ostuni 1 burial revealed cold and dry climate and steppe environment (Renault-Miskovsky et al., 2011, 2015). Another environmental information from Santa Maria

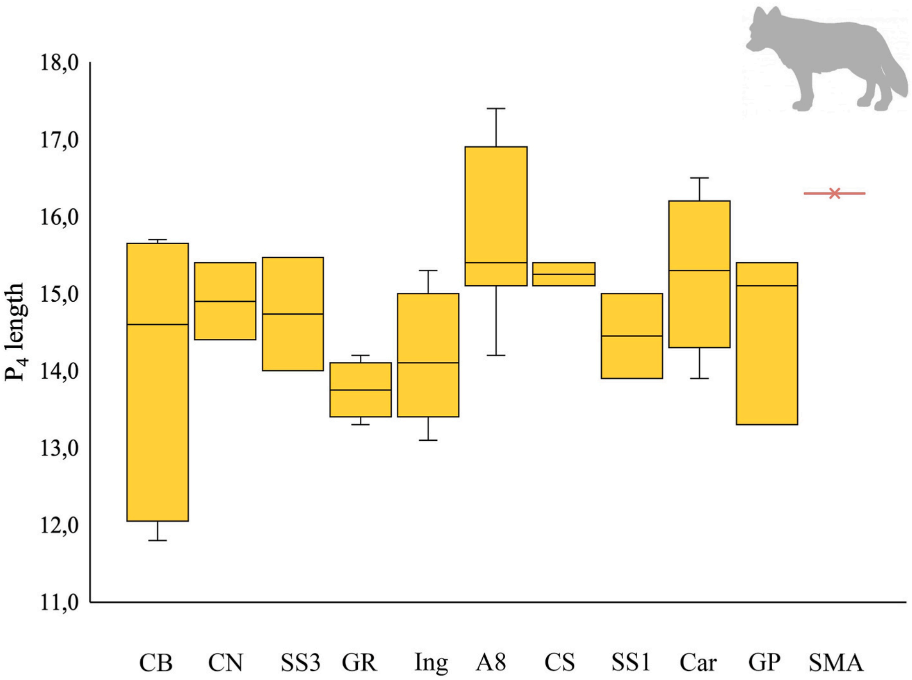

Fig. 9. Box plot of the length of the lower fourth premolar (P_4 in mm) of *Canis lupus* from late Middle to Late Pleistocene Apulian sites (in orange) and from Grotta di Santa Maria di Agnano (red). Abbrevations: CB – Cava Bianco - Melpignano; CN – Cava Nuzzo - Melpignano; SS3 – San Sidero 3; GR – Grotta Romanelli; Ing – Ingarano; A8 – Avetrana bed 8; CS – Cava Spagnulo; SS1 – San Sidero-fissure 1; FC – Fondo Cattìe; Car. Cardamone; GP – Grotta Paglicci; SMA – Grotta di Santa Maria di Agnano – Esterno. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

d'Agnano is provided by δ^{13}C values obtained from radiocarbon measurements. Generally speaking, carbon isotope values higher than −22.5 ‰ indicate open environments or lack of woodland covers (Stevens et al., 2008; Drucker et al., 2011). Four of five measurements at SMA-Esterno were carried out on charcoals, whose δ^{13}C could be altered during the burning activity (Philippsen et al., 2019). The δ^{13}C value of the undetermined bone from SU 8 is −15.4 ± 0.5 ‰ (LTL, 1811A), and, although limited in scope, it indicates the presence of open environments.

Similar results were obtained in the study of the palaeoenvironmental and palaeoclimatic context of Grotta Paglicci (northern part of the Apulia), which added significant data on the Late Glacial of Mediterranean Europe (Berto et al., 2017). Based on the study of micromammals, the authors stated that in the lower part of the succession (levels 24-17, dated from 34,925 to 32,007 years cal BP and 22,384–20,932 years cal BP, Huertas et al., 1997; calibrated with the online software OxCal v. 4.4.4), the landscape was mainly open with dry meadows and scarce forest areas. The analysis of the large mammals from Grotta Paglicci also confirmed this interpretation, supporting a long persistence of open environment (steppes and forest steppes) from the Aurignacian up to the final Epigravettian (Boschin et al., 2018). The climatic impact on terrestrial ecosystems at the end of the Late Pleistocene in Apulia is therefore quite evident, with the dominance of open environments.

The zooarchaeological analyses carried out here suggest that nearly the complete faunal sample of SMA-Esterno is the result of human exploitation of animal carcasses, commonly documented in the European Upper Palaeolithic anthropogenic contexts. As is well-documented in the literature, Palaeolithic humans were skilled hunters capable of capturing fish, birds, and mammals, which also implies that the faunal spectrum found in these deposits reflects the prevailing palaeoenvironmental and palaeoclimatic condition. The basic assumption is that the animals hunted by humans and identified in these Palaeolithic contexts represent the species present in that territory at that time, especially for land mammals and birds. The faunal assemblage from the Gravettian level of SMA-Esterno (SU8) included *Bos primigenius, Capra ibex, Cervus elaphus, Sus scrofa, Equus ferus, Meles meles, Canis lupus, Vulpes vulpes, Panthera pardus*, and *Lepus corsicanus*.

The mammalian fauna is largely dominated by *E. ferus,* which supports the presence of open shrublands and grasslands alongside fairly cold climatic conditions. In Apulia, fossils of the wild horse are frequently associated with the remains of European ass *Equus hydruntinus* (e.g., Boschin and Boscato, 2016; Mecozzi et al., 2021; Conti et al., 2010, 2012). Horse material from Apulia, as is the case with other mammals, is usually not formally described, probably because these remains are generally highly fragmented due to the exploitation of carcasses by humans (Sarti et al., 1998; Boscato et al., 2006). Recently, Mecozzi and Strani (2022) carried out a substantial revision of the date that also included the material from SMA-Esterno, suggesting a morphological and biometric homogeneity of the wild horse record from Apulia throughout the Late Pleistocene, with the exception of a proportion of muzzle. The two nearly complete crania from Cardamone have wide and short muzzle, pattern observed in specimens found in deposits attributed to a glacial stage (Mecozzi and Strani, 2022). However, the absence of body-size variation implies that wild horses in Apulia faced low competition for resources within a stable landscape, predominantly characterized by open-environments (i.e, steppe-like and/or grasslands) over the last 300 ka.

The second well represented taxon in the studied sample is the aurochs (*B. primigenius*). A number of studies focused on its size variability, characterized by a decrease of the dimension from the large-sized specimens of the Middle Pleistocene to small-sized ones of the Holocene (Grigson, 1969; Degerbøl and Fredskil, 1970; Brugal, 1983; Cerilli and Petronio, 1992). The comparison of the fossil sample from Apulia shows a reduced variability, with a slight increase trend across time. For instance, the mean value of the samples from glacial sites (Grotta Paglicci, Cardamone, SMA-Esterno) is generally larger than that of the latest Pleistocene to Early Holocene deposits of Grotta delle Mura and Grotta Romanelli. The Bovinae are included in the ecological categories of grazers (75 % of diet is represented by grasses), browsers (reduced amount of grasses), or mixed-feeders (25 %–75 % of grass) (see Masini et al., 2013 for discussion). The increase of the lower third molar length during the Late Pleistocene took place during the global climatic cooling trend culminating in the Last Glacial stage at the end of Late Pleistocene (MIS 2). As previously mentioned, the areas covered by forests decreased in favour of open landscapes during the MIS 2, with the landscapes mainly represented by grass-dominated meadows (Petrucci et al., 2005; Renault-Miskovsky et al., 2011, 2015; Gatta et al., 2016; Berto et al., 2017; Giustini et al., 2024). The observed trend of increasing teeth size in *Bos primigenius* could be a response to cold climatic conditions, which likely contributed to the transformation of the typical Mediterranean environments documented in southern Europe into more open environments (likely documented at Grotta di Santa Maria di Agnano, and Grotta Paglicci). This change would have enhanced the availability of trophic resources for *Bos primigenius*, the diet of which is mostly based on grasses (Schulz and Kaiser, 2007 and reference therein).

The presence of the wild boar in the Gravettian and Epigravettian levels of SMA-Esterno was previously reported by Iannucci et al. (2020). The authors carried out a large revision of the fossil sample of this species from Apulian deposits chronologically encompassing the period from the late Middle Pleistocene to the Early Holocene. The results of the biometric comparison and the body mass estimation revealed the presence of size fluctuations, giving no support to the hypothesis of a progressive trend toward small dimension generally supposed in palaeontological literature. Two distinct groups of *S. scrofa* were identified: large-sized from interglacial stages and small-sized from glacial ones (including the SMA-Esterno fossils). The authors interpreted the size reductions as an effect of the decrease of available trophic resources and the increase in the competition due to the deterioration and fragmentation of forests during the glacial times.

At SMA-Esterno, the ibex (*C. ibex*) is poorly represented. This species is typically associated with rocky or steep mountain walls and foothill environments, occupying open rocky habitats or open and sunny woodlands interspersed with rocky surfaces (Villaret et al., 1997; Grignolio et al., 2003). The studied sample also includes the red deer (*C. elaphus*) and the Sardinian hare (*L. corsicanus*), which inhabit open deciduous woodlands, Mediterranean scrubs, and coniferous woodlands. These species have been reported in faunal assemblages referred to as both glacial and periglacial stages in the Apulian Late Pleistocene (e.g., Rustioni et al., 2003; Boscato, 1994; Conti et al., 2012).

The carnivores are quite scarce in SU8 of SMA-Esterno. The Eurasian badger is typical of the forest, such as deciduous woodlands, mixed and coniferous woodlands and scrub (Boitani et al., 2003). The leopard has a wide habitat tolerance, ranging from rainforests to deserts, from mountainous habitats to coastal scrubs or swampy areas (Nowell and Jackson, 1996). Likewise, the canids (*C. lupus* and *V. vulpes*) show a wide geographical distribution and ecological tolerance, which allows them to occupy a number of different habitats (Ungar, 2010). In Upper Palaeolithic contexts, carnivores were generally captured for their fur, as supported by the prevalence of skinning traces recovered on distal limb elements and on cranial bones (e.g., Tagliacozzo et al., 2003).

Santa Maria di Agnano is located at the north-western margin of the Risieddi promontory, at about 175 m a.s.l., between the coastal plain and the hill of the Murge plateau, offering a wide visibility on the surrounding areas (Fig. 10). The Gravettian occupation of SMA-Esterno is dated to the onset of the Last Glacial period, shortly after the MIS 3-MIS 2 transition (attested at ca. 29 ka; Clark et al., 2009; Hughes et al., 2013). Sea levels were affected by an extent drawdown at around 40 ka ago, reaching the lowest level during the LGM (c. 22 ka). This significant sea-level drop exposed landscapes, positioning the coastline approximately 20 km from the current one far below present-day levels (Fig. 10). This created a large flat plain that facilitated the movement of Palaeolithic humans and the hunting of large mammals. At a regional scale, lower sea levels reduced the distance between territories separated by sea, providing new opportunities for mammal and human populations to disperse via short crossings (Benjamin et al., 2017 and the references therein). The submerged plain of the Adriatic Sea is as an example of a new land bridge between the Balkans and the Italian Peninsula (Fig. 10). Subsistence strategies were quite constant at SMA-Esterno, with Gravettian hunting focused mainly on the wild horse and aurochs, probably captured in the extended coastal plain bordering the Adriatic Sea during the MIS 2 and dominated by open environments. The sporadic fossils of other species indicate that they were also able to exploit relatively diverse habitats of the rugged terrain and plateau close to the site. The presence of *Capra ibex* suggests open and rocky landscapes in the Risieddi plateau, while the limited forest cover around the site (in the top of Risieddi plateau and its slopes) is inferred by the presence of *C. elaphus*, *L. corsicanus*, and *S. scrofa*.

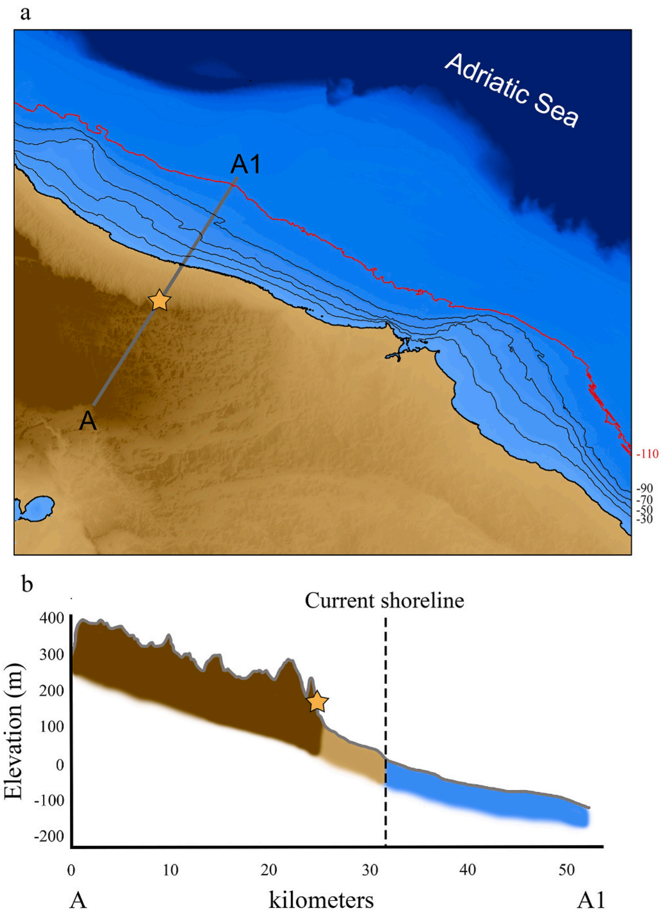

Fig. 10. Topography of the study area and the shoreline at the Last Glacial Maximum (red line) (a). Topographic profile along the A-A1 transept (location in Fig. 9a) (b). Orange stars indicate the position of Grotta di Santa Maria di Agnano – Esterno. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

5.2. Regional differences in mammal paleocommunities

The Italian Peninsula, alongside the Iberian and Balkan Peninsulas, played the role of a glacial refugium during the Late Glacial (MIS 5d-2), where species adapted to temperate climatic conditions could survive during the glacial stages (Sommer and Nadachowski, 2006; Bhagwat and Willis, 2008; Provan and Bennett, 2008; Stewart et al.,2010). This territory was characterised, as it is today, by marked regional climatic differences, mainly due to its peculiar latitudinal extension and the presence of the Alpine and Apennine chains (see Manzi et al., 2011 for discussion). The pattern of regionalism, especially at the end of the Pleistocene, resulted in an asynchrony in mammalian dispersal events and extinctions in the Italian Peninsula (Gliozzi et al., 1997; Masini and

Sala, 2011). Mammalian taxa that had been adapted to warm and wet climate disappeared after the Last Interglacial (MIS 5; e.g., *Palaeoloxodon antiquus* and *Hippopotamus*; Mecozzi et al., 2021; Pieruccini et al., 2022; Mecozzi et al., 2024), whereas others became less frequent until their complete disappearance during MIS 3 (e.g., *Stephanorhinus hemitoechus* and *Dama dama*; Gliozzi et al., 1997; Pandolfi et al., 2017; Mecozzi et al., 2021). The ongoing climate cooling during the Late Pleistocene favoured the diffusion of species well adapted to cold and arid conditions and open environments. An example of an asynchronic dispersal event is documented for *Mammuthus primigenius*: its earliest dispersal in northern and central Italy, albeit sporadic, was attested at the end of the Middle Pleistocene (MIS 6), becoming relatively frequent during the Late Glacial (Braun and Palombo, 2012). In southern Italy, *M. primigenius* was found only at Cardamone (probably MIS 2) (Rustioni et al., 2003).

One of the factors limiting the study of the impact of climatic changes of the Late Pleistocene on terrestrial ecosystems relates to the human exploitation of animal carcasses, the remains of which are often found in association with Middle and Upper Palaeolithic tools, creating generally highly fragmented assemblages. Such fossil assemblages have rarely been studied from a palaeontological perspective, and often not formally described or documented. By analysing the remains found in association with Gravettian tools in the Italian Peninsula, several differences in mammal palaeocommunities can be observed for the period of approximately 30–20 ka, allowing us to investigate the effect of climate on terrestrial ecosystems (Table 3; Fig. 11). Indeed, the mammal remains found in these Gravettian contexts represent animals hunted by humans, likely consisting of species that were the most common in that specific territory at that time. As aforementioned, humans were skilled hunters capable of capturing land and water animals, and therefore the fossil sample associated with lithic tools provided a wide spectrum of hunting strategies, but also reflects the palaeoenvironmental and palaeoclimatic contexts. Thus, comparing these mammalian assemblages allows us to identify differences in the environments and climates of various Italian contexts.

At the northern sites, level D of Riparo Mochi, levels P13-P9 of Arene Candide, and levels D1d-D1e of Riparo Fumane, the cold adapted species were reported, such as *Marmota marmota, Alces alces, Megaloceros giganteus, Mustela nivalis*, and *Mustela erminea* (Table 4). The wild horse (*E. ferus*) and the European ass (*E. hydruntinus*) seem to have been completely absent. In the south, these two equids are well represented in Grotta di Roccia San Sebastiano and Grotta Paglicci (Table 4). In addition, the species adapted to cold climatic conditions were not reported in the Gravettian deposits of southern Italy, excepted for *M. marmota* recorded at Grotta del Romito and Grotta Paglicci (Table 4). This species, however, was also recorded in the final Upper Palaeolithic levels (generally known as *terre brune,* levels E-A, ISU5) of Grotta Romanelli (Apulia, southern Italy; Tagliacozzo, 2003) and of Grotta Paglicci (Boschin, 2019). The Alpine marmot is found in alpine meadows and high-altitude pastures, typically on south-facing slopes from 1200 to 3000 m a.s.l. Its presence in southernmost part of the Apulia, the territory that is flat and without hills, points to harsh climatic conditions during the latest Pleistocene.

Other taxa well adapted to cold climatic conditions were documented generally in northern and central Italy. The remains of *M. primigenius* are relatively diffused in northern and central Italy, but never found associated with Gravettian tools, as documented in the faunal assemblages from Buca della Iena, Canale delle Acque Alte (= Canale Mussolini, central Italy), Montecatini Terme, Pagano d'Asolo, Riparo Tagliente, San Giovanni di Valdobbiadine, Settepolesini di Bondeno, and Torrente Conca (Braun and Palmbo, 2012 and reference therein). The woolly mammoth was also recorded at Arene Candide but associated with Epigravettian tools (level P9 dated to 20,470 ± 320 years BP and level P1 dated to 18,560 ± 210 years BP; Cassoli and Tagliacozzo, 1994a). Another iconic species of the Late Glacial is *Coelodonta antiquitatis*. This taxon was found at Riparo Fumane (but not in the Gravettian levels; Billia and Graovac, 1999), Monte Circeo (Palmarelli and Palombo, 1981), Fadalto nel Veneto, Opcina, Polesine (Leonardi, 1947, 1948), and Ingarano (Billia, 2001). Unfortunately, the majority of these specimens lacks clear stratigraphic and chronological data, which prevents the reconstruction of the specie' comprehensive biochronological framework in the Italian Peninsula. The woolly rhinoceros was found associated with *M. primigenius* at Settepolesini di Bondeno (Gallini and Sala, 2001) and Cardamone (Rustioni et al., 2003), representing the Italian records of "*Mammuthus-Coelodonta* faunal complex." Cardamone, in particular, is of considerable interest because this site represents one the southernmost occurrences of this cold-adapted faunal assemblage in Europe (Rustioni et al., 2003; Kahlke, 2014). Unfortunately, the deposit was discovered at the end of the 1800s, and it is completely destroyed today. The mammalian assemblage from Cardamone, in addition to the woolly mammoth and the woolly rhinoceros, includes *Equus ferus, Bos primigenius*, *Cervus elaphus*, *Canis lupus, Vulpes vulpes, Crocuta crocuta, Lepus europaeus, Oryctolagus cuniculus*, and *Erinaceus europaeus* (Rustioni et al., 2003).

Other two taxa representative of the Late Glacial are *Bison priscus* and *Alces alces*. The moose was mainly found in the Po' Valley (including Settepolesini del Bondeno), with only three records found at other sites in the northern Italian Peninsula: Arene Candide, Diamantina, and Balzi Rossi (Breda, 2001 and reference therein). This species inhabits a wide range of woodland habitats in boreal to temperate zones, with a marked preference for second growth boreal forest, opening, swamps, lake and wetlands (Bauer and Nygrén, 1999; Janík et al., 2021). The specific identification of bovinae fossils of late Middle to Late Pleistocene faced considerable difficulties, especially for isolated and/or fragment fossils, due to the strong morphological similarities between *Bos primigenius* and *Bison priscus*. The specimens from archaeological deposits are highly fragmented, which further complicates their specific identification. Often, these samples are classified as *Bos vel Bison*, Bovidae indet or Bovinae indet. However, the geographical distribution of these two species in the Late Pleistocene is quite different: the presence of *B. primigenius* is quite abundant, with fossils found across all the Italian Peninsula (Minieri et al., 1995) while *B. priscus* was generally recognized only in the northern regions of the peninsula, with sporadic specimens (Paronuzzi et al., 2018; Terlato et al., 2019). However, the cranial remains found at Riparo del Molare, attributed to MIS 5d-a, extend its palaeoareal into the western areas of southern Italy during the early Late Pleistocene (Spagnolo et al., 2020).

To sum up, mammalian palaeocommunities during the Last Glacial of the Italian Peninsula show strong regionalism differences, which were linked to climatic conditions that, in turn, largely affected terrestrial ecosystems. Between 30 and 20 ka ago, as fossil remains associated with Gravettian tools show, the species adapted to cold climates occupied the northern and central part of Italian Peninsula, while in the southern regions of the peninsula only mammalian species adapted to temperate conditions survived. Only during the LGM the woolly mammoth and the woolly rhinoceros reached the southern areas, with the unique date documented at Cardamone (even though no radiometric measurements have been carried out to confirm this). These results, therefore, reinforce the idea that the Italian Peninsula played the role of a glacial refugium during the Late Glacial, especially in its southern parts.

6. Conclusions

The study of the fossil remains from the Gravettian level (SU8) of the SMA-Esterno is reported here for the first time. The faunal assemblage includes *Bos primigenius, Capra ibex, Cervus elaphus, Sus scrofa, Equus ferus, Meles meles, Canis lupus, Vulpes vulpes, Panthera pardus*, and *Lepus corsicanus.* These fossils were found associated with Gravettian tools, which testify to human frequentations of the site. The bones are highly fragmented, and several of these also show cutmarks, documenting a human exploitation of carcasses.

The faunal assemblage from SU8 is dominated by *Equus ferus* and *Bos*

Fig. 11. Maps of the selected Italian localities of with mammalian remains associated with Gravettian tools and sites with the presence of *Coelodonta antiquitatis* and/or *Mammuthus primigenius*. Legend: 1 – Riparo Mochi; 2 – Arene Candide; 3 – Riparo Fumane; 4 – Grotta del Rio Secco; 5 – Grotta di Roccia San Sebastiano; 6 – Grotta Paglicci; 7 – Grotta di Santa Maria di Agnano; 8 – Grotta della Cala, Grotta della Serratura; 9 - Grotta del Romito; 10 – Buca della Iena; 11 – Torrente Conca; 12 - Settepolesini di Bondeno; 13 – Polesine; 14 – Riparo Tagliente; 15 – Pagano d'Asolo, San Giovanni di Valdobbiadine; 16 – Fadalto nel Veneto; 17 – Opcina; 18 – Montecatini Terme; 19 – Sant'Anna; 20 – Canale delle Acque Alte (= Canale Mussolini); 21 – Monte Circeo; 22 – Ingarano; 23 – Cardamone (see the text for references).

Table 4
The mammalian faunas from the Gravettian occupations in the Italian Peninsula.

Site	Riparo Mochi (Tagliacozzo et al., 2012)	Arene Candide (Cassoli and Tagliacozzo, 1994a)	Riparo Fumane. (Cassoli and Tagliacozzo, 1994b)	Grotta del Rio Secco (Peresani et al., 2004)	Grotta di Roccia San Sebastiano (Belluomini et al., 2007)	Grotta della Cala (Boscato et al., 1997)	Grotta della Serratura (Boscato et al., 2003)	Grotta del Romito (Bertini Vacca, 2012)	Grotta Paglicci (Sala, 1983; Boscato, 2004)	SMA-esterno
Levels - Dating	D	P13 25.620 ± 220 P9 20.470 ± 320	D1d - D1e	6 - 27080 ± 230–28300 ± 260	c2 - 23.600	3 dm - 26.880 ± 320–26.380 ± 260	F E 25.970 ± 140 D - 20.670 ± 520	G - 19351 ± 180–19373 ± 90 BP H - 20210 ± 245 BP I - 23475 ± 190 BP	23A - 28.100 ± 400 18b2 - 20.200 ± 305	SU8
Species										
Bos primigenius	•	•			•	•	•	•	•	•
Capra ibex	•	•	•	•		•	•	•	•	•
Rupicapra rupicapra	•		•	•		•				
Rupicapra sp							•	•	•	
Cervus elaphus	•	•	•		•	•	•		•	•
Capreolus capreolus	•	•	•			•	•	•	•	
Alces alces	•									
Megaloceros giganteus		•	•							
Sus scrofa	•					•	•	•	•	•
Equus ferus					•				•	•
Equus hydruntinus					•				•	
Canis lupus		•	•		•			•	•	•
Vulpes vulpes	•	•	•		•	•	•	•	•	•
Crocuta spelaea	•	•							•	
Ursus arctos			•				•	•	•	
Ursus spelaeus		•								
Ursus sp.	•									
Panthera pardus	•	•	•			•				•
Lynx lynx	•	•	•				•	•		
Felis sylvestris	•	•	•			•	•	•		
Meles meles		•								
Martes martes		•								
Mustela putorius			•							
Mustela nivalis		•	•							
Mustela erminea		•								
Marmota marmota	•	•	•					•	•	
Castor fiber				•						
Lepus corsicanus										•
Lepus europaeus						•			•	
Lepus sp.	•	•					•	•		
Oryctolagus cuniculus	•	•								
Erinaceus europaeus	•	•						•		

primigenius, which strongly hint at the widespread presence of open environments, probably in the large coastal plains. This conclusion is also backed by palaeobotanical analyses. Sporadic finds of *Cervus elaphus* and *Sus scrofa* are also indicative of limited wooded areas, probably developed along the top of the Risieddi plateau and its slopes.

The comparison of mammalian assemblages from the Last Glacial of the Italian Peninsula revealed a remarkable regionalism of the terrestrial ecosystems affected by a strong climatic gradient due to the latitudinal extension of the Italian Peninsula and the presence of the Alps and the Apennines. These geographical constraints are reflected in significant differences among mammalian palaeocommunities, with species well adapted to glacial conditions recorded in the northern and central parts of the Italian Peninsula. The cold adapted species in the southern regions of the Italian Peninsula were recognized only at Cardamone, supporting their diffusion over these territories only during the peak of the Last Glacial Maximum.

CRediT authorship contribution statement

B. Mecozzi: Writing – review & editing, Writing – original draft, Visualization, Funding acquisition, Formal analysis, Conceptualization. **P. Magniez:** Writing – review & editing, Writing – original draft, Visualization, Formal analysis. **D. Coppola:** Writing – review & editing, Supervision, Project administration, Investigation, Funding acquisition, Conceptualization. **D. Borić:** Writing – review & editing, Visualization. **H. Baills:** Writing – review & editing, Writing – original draft, Supervision, Project administration, Investigation.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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References

Baills, H., 2015. Les industries lithiques des occupations Epigravettiens des SMA-esterno (Fouilles 2007-2010) (Santa Maria di Agnano, Ostuni, Italie). Bulletin du Musée Anthropologie préhistorique de Monaco 55, 105–122.

Baills, H., 2021. The Shouldered Pieces from the Santa Maria di Agnano Cave (SMA-Extern). Their Chrono-cultural Positioning During the Upper Paleolithic in Southern Italy. Lithic Technol. 46 (3), 192–203. https://doi.org/10.1080/01977261.2021.1887611.

Baills, H., 2022. Stratégies et objectifs de débitage entre 25.000 et 10.000 BP. Le cas de la zone SMA-Externe de la grotte Santa Maria di Agnano (Ostuni, Italie). Preistoria Alp. 52, 23–38.

Baills, H., Coppola, D., 2023. Les parures de la zone externe de la grotte Santa Maria di Agnano (Ostuni, Italie): premiers résultats. PALEO. Revue d'archéologie préhistorique (33), 26–37.

Baills, H., Magniez, P., Coppola, D., 2021. Les occupations gravettiennes de la Grotte Santa Maria di Agnano (Pouilles, Italie) – Zone SMA-Esterno : typo-technologie lithique et archéozoologie. L'anthropologie 125, 102853.

Baryshnikov, G.F., Puzachenko, A.Y., Abramov, A.V., 2003. New analysis of variability of cheek teeth in Eurasian badgers (Carnivora, Mustelidae, Meles). Russ. J. Theriol. 1 (2), 133–149.

Bauer, K., Nygrén, K., 1999. Alces alces. In: Mitchell-Jones, A.J., Amori, G., Bogdanowicz, W., Kryštufek, B., Reijnders, P.J.H., Spitzenberger, F., Stubbe, M., Thissen, J.B.M., Vohralík, V., Zima, J. (Eds.), The Atlas of European Mammals. Academic Press, London, UK, pp. 394–395.

Behrensmeyer, A.K., 1978. Taphonomic & ecological information from bone weathering. Paleobiology 4, 150–162.

Belluomini, G., Calderoni, G., Collina, C., Fedi, M., Fiore, I., Gallotti, R., Garofalo, B., Pennacchioni, M., Piperno, M., Salvadei, L., Santangelo, N., Santo, A., Tagliacozzo, A., 2007. La grotta di Roccia san Sebastiano (Mondragone, CE). In: Atti XL Riunione Scientifica "Strategie Di Insediamento Tra Lazio e Campania in Età Preistorica e Protostorica. Istituto Italiano di Preistoria e Protostoria, Firenze, pp. 319–333.

Benjamin, J., Rovere, A., Fontana, A., Furlani, S., Vacchi, M., Inglis, R.H., Galili, E., Antonioli, F., Sivan, D., Miko, S., Mourtzas, N., Felja, I., Meredith-Williams, M., Goodman-Tchernov, B., Kolaiti, E., Anzidei, M., Gehrels, R., 2017. Late Quaternary sea-level changes and early human societies in the central and eastern Mediterranean Basin: an interdisciplinary review. Quat. Int. 449, 29–57.

Bertè, D.F., 2014. L'evoluzione del genere *Canis* (Carnivora, Canidae, Caninae) in Italia dal wolf-event a oggi: implicazioni biocronologiche, paleoecologiche e paleoambientali. PhD Dissertation 390. Sapienza, Università di Roma, Roma.

Bertini Vacca, B., 2021. The hunting of large mammals in the upper palaeolithic of southern Italy: A diachronic case study from Grotta del Romito. Quat. Int. 252, 155–164.

Berto, C., Boscato, P., Boschin, F., Luzi, E., Ronchitelli, A., 2017. Paleoenvironmental and paleoclimatic context during the upper palaeolithic (late upper pleistocene) in the Italian peninsula. The small mammal record from grotta Paglicci (Rignano Garganico, Foggia, southern Italy). Quat. Sci. Rev. 168, 30–41.

Bhagwat, S.A., Willis, K.J., 2008. Species persistence in northerly glacial refugia of Europe: a matter of chance or biogeographical traits? J. Biogeogr. 35 (3), 464–482.

Billia, E., 2001. First finding of wolly rhino *Coelodonta antiquitatis* (Blumenbach, 1799) (Mammalia, Rhinocerotidae) in Gargano (Apulia, southern Italy). Evolution of life on the Earth. Proceedings of the II International Symposium, pp. 471–476.

Billia, E.M.E., Graovac, S.M., 1999. Amelogenesis Imperfecta on a Deciduous Molar of *Coelodonta antiquitatis* (Blumenbach, 1799) (Mammalia, Perissodactyla, Rhinocerotidae) from Grotta Fumane (Verona, Northern Italy): a Rare Case Report. XI International Symposium of Dental Morphology, pp. 179–186. Oulu, Finland. 1998.

Binford, L.R., 1981. Bones: Ancient Men and Modern Myths. Academic Press, New York.

Boitani, L., Lovari, S., Vigna Taglianti, A., 2003. Fauna d'Italia. Mammalia III. Carnivora – Artidactyla, Calderini ed., p. 434 Bologna.

Bon, M., Boscato, P., 1993. Analisi paleontologica e paleoecologica di macro e micromammiferi dei livelli romanelliani e mesolitici della Grotta delle Mura (Monopoli, Bari). Quat. Nova 3, 53–104.

Boscato, P., 1994. Grotta Paglicci: la fauna a grandi mammiferi degli strati 22-24 (Gravettiano antico-Aurignaziano). Riv. Sci. Preist. 46, 145–176.

Boscato, P., Ronchitelli, A., Wierer, U., 1997. Il Gravettiano antico della Grotta della Cala a Marina di Camerota: paletnologia e ambiente. Riv. Sci. Preist. 48, 97–186.

Boscato, P., Di Giuseppe, Z., Martini, F., 2005. Grotta della Serratura (Marina di Camerota-SA). Primi dati sulle faune a macromammiferi della sequenza gravettiana. Atti 4 Convegno Nazionale di Archeozoologia, Quaderni Museo Archeologico del Friuli occidentale 6, 75–85.

Boscato, P., Crezzini, J., Pellegrini, A., 2006. Le parti mancanti: faune del Paleolitico Medio nel deposito esterno della Grotta di Santa Croce, Bisceglie (BA). In:

Tecchiati, U., Sala, B. (Eds.), Studi di Archeozoologia in onore di Alfredo Riedel. Ripartizione Beni Culturali, Ufficio Beni Archeologici, Bolzano, pp. 39–50.

Boschin, F., 2018. Animal remains from the multilayered site of Elvas-Kreuzwiese pf 574 (South Tyrol, Italy). Annalen des Naturhistorischen Museums in Wien. Serie A für Mineralogie und Petrographie, Geologie und Paläontologie. Anthropologie und Prähistorie 120, 195–210.

Boschin, F., 2019. Exploitation of carnivores, lagomorphs and rodents at Grotta Paglicci during the Epigravettian: the dawn of a new subsistence strategy? J. Archaeol. Sci. Rep 26, 101871.

Boschin, F., Boscato, P., 2016. *Equus ferus* and *Equus hydruntinus* in the Epigravettian series of grotta Paglicci (Rignano Garganico – Foggia). Annali dell'Università degli Studi di Ferrara Museologia Scientifica e Naturalistica 12 (1), 307–312.

Boschin, F., Boscato, P., Berto, C., Crezzini, J., Ronchitelli, A., 2018. The palaeoecological meaning of macromammal remains from archaeological sites exemplified by the case study of Grotta Paglicci (Upper Palaeolithic, southern Italy). Quat. Res. 90 (3), 470–482.

Boulbes, N., 2009. Étude comparée de la denture d'*Equus hydruntinus* (Mammalia, Perissodactyla) dans le Sud-Est de la France. Implications biogéographiques et biostratigraphiques. Quaternaire 20 (4), 449–465.

Boulbes, N., Gardeisen, A., 2018. *Equus asinus* remains (Mammalia, Perissodactyla) from the protohistoric site of Pech Maho (Sigean, south of France) and variation in donkey size during the Iron age. Int. J. Osteoarchaeol. 28 (4), 428–438.

Braun, I.M., Palombo, M.R., 2012. *Mammuthus primigenius* in the cave and portable art: an overview with a short account on the elephant fossil record in Southern Europe during the last glacial. Quat. Int. 276, 61–76.

Breda, M., 2001. *Alces alces* (Linnaeus, 1758) del Pleistocene superiore e dell'Olocene antico in Italia Nord-Orientale. Boll. Mus. Civ. St. Nat. Verona 25, 27–39.

Brugal, J.-P., 1983. Applications des Analyses Multidimensionnelles a l'Étude du Squelette des Membres des Grands Bovides Pléistocènes (Grotte de Lunel-Viel, Hérault); perspectives évolutives. Thèse de doctorat, Université d'Aix-Marseille II. Faculté des Sciences de Marseille-Luminy 449.

Bunn, H.T., 1983. Evidence on the diet & subsistence patterns of Plio-pleistocene hominids at Koobi Fora, Kenya, & Olduvai Gorge, Tanzania. In: Clutton-Brock, J., Grigson, C. (Eds.), Animals & Archaeology: 1. Hunters & Their Prey. British Archaeological Report, Oxford, pp. 21–30.

Callou, C., 1997. Diagnose différentielle des principaux éléments squelettiques du lapin (genre *Oryctolagus*) et du lièvre (genre *Lepus*), en Europe occidentale. Fiches d'Ostéologie Animale pour l'Archéologie, Série B, Mammifères 8, 1–21.

Cassoli, P.F., Tagliacozzo, A., 1994a. I macromammiferi dei livelli tardopleistocenici delle Arene Candide (Savona, Italia): Considerazioni paleontologiche e archeozoologiche. Quat. Nova 4, 101–262.

Cassoli, P.F., Tagliacozzo, A., 1994b. Considerazioni paleontologiche, paleoecologiche e archeozoologiche sui macromammiferi e gli uccelli dei livelli del Pleistocene superiore del Riparo di Fumane (VR) scavi 1988–91. Boll. Mus. Civ. St. Nat. Verona 23, 85–117.

Cerilli, E., Petronio, C., 1992. Biometrical variations of *Bos primigenius*, Bojanus, 1827 from middle pleistocene to Holocene. In: Spitz, F., Janeau, G., Gonzalez, G., Aulagnier, S. (Eds.), Proceedings of the International Symposium on 'Ongulés/ Ungulates. S.F.E.P.M. -I.R.G.M., Paris and Tolouse, pp. 37–42.

Chakroun, A., Baills, H., Coppola, D., 2018. The Site of Santa Maria di Agnano (Brindissi, Italy). Global Journal of Archaeology Anthropology 4 (2), 1–3.

Chow, M., Chang, Y.P., Hu, C.K., Liu, H.I., Hsu, Y.H., Chou, P.H., Lee, Y.C., Hsien, H.H., 1959. Pleistocene mammalian fossils from the northeastern provinces. Institute of Vertebrate Paleontology, Academia Sinica, Beijing (in Chinese, with English summary).

Clark, P.U., Dyke, A.S., Shakun, J.D., Carlson, A.E., Clark, J., Wohlfarth, B., Mitrovica, J. X., Hostetler, S.W., McCabe, A.M., 2009. The last glacial maximum. Science 324, 720–714.

Combourieu-Nebout, N., Bertini, A., Russo-Ermolli, E., Peyron, O., Klotz, S., Montade, V., Fauquette, S., Allen, J., Fusco, F., Goring, S., Huntley, B., Joannin, S., Lebreton, V., Magri, D., Martinetto, E., Orain, R., Sadori, L., 2015. Climate changes in the central Mediterranean and Italian vegetation dynamics since the Pliocene. Rev. Palaeobot. Palynol. 218, 127–147.

Conti, N., Petronio, C., Salari, L., 2010. The late pleistocene equids from "Tana delle Iene" (Ceglie Messapica, Brindisi, southern Italy). Boll. Soc. Paleontol. It. 49 (2), 227–236.

Conti, N., Coppola, D., Petronio, C., Petrucci, M., Sardella, R., Salari, L., 2012. La fauna del Pleistocene superiore di Tana delle Iene (Ceglie Messapica, Brindisi, Italia meridionale). Boll. Mus. Civ. Stor. Nat. Verona 36, 63–76.

Coppola, D., 1992. Nota preliminare sui rinvenimenti nella grotta di S. Maria di Agnano (Ostuni, Brindisi): i seppellimenti paleolitici ed il luogo di culto. Riv. Sci. Preist. 44, 211–227.

Coppola, D., 2012. Il riparo di Agnano nel paleolitico superiore: la sepoltura di Ostuni 1 ed i suoi simboli. Terra. Università di Roma Tor Vergata 368. Roma.

Coppola, D., Pinto, N.D., Pellegrino, M., Baills, H., Stasolla, V., Dewailly, M., Russo, J., Bartolomeo, J., 2017. Santa Maria di Agnano (Ostuni, Puglia). Chronique des activités archéologiques de l. 'École française de Rome, pp. 1–18.

Corridi, C., 1987. Faune pleistoceniche del Salento 2. La fauna di fondo Cattie, Maglie, Lecce. I Quaderni del Museo Comunale di Paleontologia di Maglie 3, 5–65.

Davis, S.J., Gonçalves, M.J., Gabriel, S., 2008. Animal remains from a Moslem period (12th/13th century AD) lixeira (garbage dump) in Silves, Algarve, Portugal. Revista portuguesa de Arqueologia 11 (1), 183–258.

Degerbøl, M., Fredskild, B., 1970. The urus (*Bos primigenius* Bojanus) and Neolithic domesticated cattle (*Bos taurus domesticus* Linné) in Denmark. Denmark. Det Kongel. Dansk. Videnskab. Selskab Biol. Skr 17, 5–178.

Delpech, F., 1984. La Ferrassie : Carnivores, Artiodactyles et Périssodactyles. In: Delporte, H. (Ed.), Le grand abri de la Ferrassie. Fouilles 1968-1973. Etudes Quaternaires, mémoire n°7, Editions du Laboratoire de Paléontologie Humaine et de Préhistoire. Institut de Paléontologie Humaine, Paris, pp. 66–70.

Di Pasquale, G., Saracino, A., Bosso, L., Russo, D., Moroni, A., Bonanomi, G., Allevato, E., 2020. Coastal Pine-Oak glacial refugia in the Mediterranean basin: a Biogeographic approach based on charcoal analysis and Spatial Modelling. Forests 11 (6), 673.

Diedrich, C.G., 2013. Late Pleistocene leopards across Europe e northernmost European German population, highest elevated records in the Swiss Alps, complete skeletons in the Bosnia Herzegowina Dinarids and comparison to the Ice Age cave art. Quat. Sci. Rev. 76, 167–193.

Driesch, A., von, den, 1976. A guide to the measurement of animal bones from archaeological sites. Peabody Museum Bulletin 1 (3–4), 1–137.

Drucker, D.G., Bridault, A., Cupillard, C., Hujic, A., Bocherens, H., 2011. Evolution of habitat and environment of red deer (*Cervus elaphus*) during the Late-glacial and early Holocene in eastern France (French Jura and the western Alps) using multi-isotope analysis (δ13C, δ15N, δ18O, δ34S) of archaeological remains. Quat. Int. 245, 268–278.

Gallini, B., Sala, B., 2001. Settepolesini di Bondeno (Ferrara – Eastern Po Valley): the first example of mammoth steppe in Italy. In: Cavarretta, G., Gioia, P., Mussi, M., Palombo, M.R. (Eds.), Proceedings of the 1st International Congress "The World of Elephants''. CNR (Consiglio Nazionale Delle Ricerche. Publishing House, Roma, pp. 247–254.

Gatta, M., Sinopoli, G., Giardini, M., Giaccio, B., Hajdas, I., Pandolfi, L., Bailey, G., Spikins, P., Rolfo, M., Sadori, L., 2016. Pollen from Late Pleistocene hyena (*Crocuta crocuta spelaea*) coprolites: an interdisciplinary approach from two Italian sites. Rev. Palaeob. Palynol. 233, 56–66.

Giustini, F., Iannucci, A., Porcelli, G., Micarelli, I., Brilli, M., Sardella, R., Mecozzi, B., 2024. Taxonomic and stable isotope analyses of mammal remains from the Lateglacial site of Grotta Polesini (central Italy): Paleoenviromental implications. J. Quat. Sci. 39 (7), 1098–1115.

Gliozzi, E., Abbazzi, L., Argenti, A., Azzaroli, A., Caloi, L., Capasso Barbato, L., Di Stefano, G., Esu, D., Ficcarelli, G., Girotti, O., Kotsakis, T., Masini, F., Mazza, P., Mezzabotta, C., Palombo, M.R., Petronio, C., Rook, L., Sala, B., Sardella, R., Zanalda, E., Torre, D., 1997. Biochronology of selected mammals. Molluscs and Ostracodes from the middle Pliocene to the late pleistocene in Italy. The state of the art. Riv. It. Paleont. Strat. 103, 369–388.

Grignolio, S., Parrini, F., Bassano, B., Luccarini, S., Apollonio, M., 2003. Habitat selection in adult males of Alpine ibex, *Capra ibex ibex*. Folia Zoologica Praha 52 (2), 113–120.

Grigson, C., 1969. The uses and limitations of differences in absolute size in the distinction between the bones of aurochs (*Bos primigenius*) and domestic cattle (*Bos taurus*). In: Ucko, P.J., Dimbleby, G.W. (Eds.), The Domestication and Exploitation of Plants and Animals. Duckworth, London, UK, pp. 277–294.

Guadelli, J.-L., 1987. Contribution à l'étude des zoocénoses préhistoriques en Aquitaine (Würm ancien et interstade würmien). Thèse de doctorat de l'Université de Bordeaux I, p. 568.

Halstead, P., Collins, P., Isaakidou, V., 2002. Sorting the sheep from the goats: morphological distinctions between the mandibles and mandibular teeth of adult *Ovis* and *Capra*. J. Archaeol. Sci. 29 (5), 545–553.

Huertas, A.D., Iacumin, P., Longinelli, A., 1997. A stable isotope study of fossil mammal remains from the Paglicci cave, southern Italy, 13 to 33 ka BP: palaeoclimatological considerations. Chem. Geol. 141 (3–4), 211–223.

Hughes, P.D., Gibbard, P.L., Ehlers, J., 2013. Timing of glaciation during the last glacial cycle: evaluating the meaning and significance of the 'Last Glacial Maximum' (LGM). Earth Sci. Rev. 125, 171–198.

Iannucci, A., Sardella, R., Strani, F., Mecozzi, B., 2020. Size shifts in late middle pleistocene to early Holocene *Sus scrofa* (Suidae, Mammalia) from Apulia (southern Italy): ecomorphological adaptations? Hystrix 31, 10–20.

Janík, T., Peters, W., Šálek, M., Romportl, D., Jirků, M., Engleder, T., Ernst, M., Neudert, J., Heurich, M., 2021. The declining occurrence of moose (*Alces alces*) at the southernmost edge of its range raise conservation concerns. Ecol. Evol. 11 (10), 5468–5483.

Kahlke, R.D., 1994. Die Entstehungs-, Entwicklungs- und Verbreitungsgeschichte des oberpleistozänen Mammuthus-Coelodonta-Faunenkomplexes in Eurasien (Großsäuger). Abh. Senckenb. Natforsch. Ges. 546, 1–164.

Kahlke, R.D., 1999. The history of the origin, evolution and dispersal of the Late Pleistocene *Mammuthus-Coelodonta* faunal complex in Eurasia (large mammals). Mammoth Site of Hot Springs, South Dakota.

Kahlke, R.D., 2014. The origin of eurasian mammoth faunas *Mammuthus–Coelodonta* faunal complex). Quat. Sci. Rev. 96, 32–49.

Leonardi, P., 1948. Resti fossili inediti di rinoceronti conservati nelle collezioni dell'Istituto Geologico dell'Universita' di Padova. Memorie dell'Istituto di Geologia dell'Universita' di Padova 15, 1–30.

Leonardi, P., 1947. Resti fossili di rinoceronti del Museo di Storia Naturale di Trieste. Atti Mus. Civico Storia Nat. Trieste 16, 145–164.

Leonardi, M., Boschin, F., Boscato, P., Manica, A., 2022. Following the niche: the differential impact of the last glacial maximum on four European ungulates. Commun. Biol. 5, 1038.

Liouville, M., 2007. Variabilité du cerf élaphe (*Cervus elaphus* Linné 1758) au cours du Pléistocène moyen et supérieur en Europe occidentale : approches morphométrique, paleoécologique et cynégétique. Thèse de doctorat du MNHN, Paris, p. 408.

Lister, A.M., 1996. The morphological distinction between bones and teeth of fallow deer (*Dama dama*) and red deer (*Cervus elaphus*). Int. J. Osteoarchaeol. 6 (2), 119–143.

Lyman, R.L., 1994. Vertebrate Taphonomy. Cambridge University Press, Cambridge.

Madurell-Malapeira, J., Lucenti, S.B., Alba, D.M., 2021. Middle pleistocene fox from the Vallparadís section (Vallès-Penedès basin, NE Iberian Peninsula) and the earliest records of the extant red fox. Riv. Ital. Paleontol. Stratigr. 127 (1), 179–187.

Manzi, G., Magri, D., Palombo, M.R., 2011. Early–Middle Pleistocene environmental changes and human evolution in the Italian peninsula. Quat. Sci. Rev. 30 (11–12), 1420–1438.

Masini, F., Sala, B., 2011. Considertions on an integrated biochronological scale of Italian quaternary continental mammals. Il Quaternario, Italian. J. Quat. Sci. 24 (2), 193–198.

Masini, F., Palombo, M.R., Rozzi, R., 2013. A reappraisal of the early to middle pleistocene Italian Bovidae. Quat. Int. 288, 45–62.

Mecozzi, B., 2022. *Meles meles* from middle pleistocene to early Holocene of the Italian peninsula within the evolution of European badgers in the quaternary of Eurasia. Palaeontogr. Abt. A: Palaozool. Stratigr. 319 (1–6), 133–159.

Mecozzi, B., Bartolini Lucenti, S., 2018. The late pleistocene *Canis lupus* (Canidae, Mammalia) from Avetrana (Apulia, Italy): reappraisal and new insights on the European glacial wolves. It. J. Geosci. 137, 138–150.

Mecozzi, B., Strani, F., 2022. Equids from the late middle pleistocene to early Holocene of the Apulia peninsula (southern Italy): reassessment of their taxonomy and biochronology. Geodiversitas 44 (2), 17–45.

Mecozzi, B., Chakroun, A., Baills, H., Iurino, D.A., Sardella, R., Coppola, D., 2018. Late pleistocene mammal faunal assemblage from Cava Spagnulo (Grottaglie, Apulia, SE Italy). Alp. Mediterr. Quat. 31 (1), 5–19.

Mecozzi, B., Bellucci, L., Giustini, F., Iannucci, A., Iurino, D.A., Mazzini, I., Strani, F., Sardella, R., 2021. A reappraisal of the Pleistocene mammals from the karst infilling deposits of the Maglie area (Lecce, Apulia, southern Italy). Riv. Ital. Paleontol. Stratigr. 127 (2), 355–382.

Mecozzi, B., Bona, F., Conti, J., Lembo, G., Mariani, G.S., Mazzini, I., Muttillo, B., Pieruccini, P., Sardella, R., 2024. Large mammal faunas and ecosystem dynamics during the late Middle to early Late Pleistocene at Grotta Romanelli (southern Italy). Quat. Sci. Adv. 16, 100237.

Minieri, F., Petronio, C., Sardella, R., Scarano, M.R., 1995. Le faune a mammiferi del Pleistocene Superiore dell'Italia peninsulare. In: Bonomi, S., Dall'Aglio, P.L., De Guio, A., Peretto, R., Salzani, L., Zarbinatti, E. (Eds.), Atti del 1° Convegno di Archeozoologia. Grafiche Dielle, pp. 75–87. Stanghella (Padova).

Nava, A., Coppa, A., Coppola, D., Mancini, L., Dreossi, D., Zanini, F., Bernardini, F., Tuniz, C., Bondioli, L., 2017. Virtual histological assessment of the prenatal life history and age at death of the Upper Paleolithic fetus from Ostuni (Italy). Sci. Rep. 7 (1), 1–10.

Nowell, K., Jackson, P., 1996. Wild Cats. Status Survey and conservation action plan. IUCN/SSC Cat Specialist Group. Gland, Switzerland and Cambridge, UK.

Palmarelli, A., Palombo, M.R., 1981. Un cranio di *Coelodonta antiquitatis* (Bluemenbach) (Rhinocerotidae) del Pleistocene superiore del Monte Circeo (Lazio meridionale). Boll. Serv. Geo. Ital. 102, 281–312.

Palombo, M.R., 2009. Biochronology of terrestrial mammals and Quaternary subdivisions: a case stydy of large mammals from the Italian peninsula. Il Quaternario 22(2). Italian Journal of Quaternary Sciences 291–306.

Pandolfi, L., Boscato, P., Crezzini, J., Gatta, M., Moroni, A., Rolfo, M., Tagliacozzo, A., 2017. Late Pleistocene last occurrence of the narrow-nosed rhinoceros *Stephanorhinus hemitoechus* (Mammalia, Perissodactyla) in Italy. Riv. Ital. Paleontol. Stratig. 123 (2), 177–191.

Parise, M., 2012. Caratteri geologici e speleogenesi della Grotta di Santa Maria di Agnano (Ostuni, Provincia di Brindisi). In: Coppola, D. (Ed.), Il riparo di Agnano nel Paleolitico superiore: la sepoltura di Ostuni 1 ed i suoi simboli. Università di Tor Vergata, Roma, pp. 75–91.

Parise, M., Pepe, M., 2016. Esempi di cartografia geomorfologico-carsica in Puglia. In: Gili, R., Lana, E., Peano, G. (Eds.), Atti del Convegno Nazionale "La ricerca carsologica in Italia". Cuneo, pp. 49–56.

Paronuzzi, P., Berto, C., Ghezzo, E., Thun Hohenstein, U., Massarenti, A., Reggiani, P., 2018. Nota preliminare sulla sequenza UMG di ex Cava a Filo (Croara, BO): gli aspetti stratigrafico-sedimentari, paleontologici e antropici alla luce delle ultime indagini (2006-2016). Memorie dell'Istituto di Speleologia, II serie 32, 131–144.

Peresani, M., Romandini, M., Duches, R., Jéquier, C., Nannini, N., Pastoors, A., Picin, A., Schmidt, I., Vaquero, M., Weniger, G.-C., 2014. New evidence for the Mousterian and Gravettian at Rio Secco cave, Italy. J. Field Archaeol. 39 (4), 401–416.

Petrucci, M., Giardini, M., Sadori, L., 2005. Analisi pollinica di coproliti di iena macchiata (Crocuta crocuta Erxleben) dell'ultimo glaciale della Puglia. Inf. Bot. Ital. 37 (1), 932–933.

Philippsen, B., Olsen, J., Sørensen, S.A., Måge, B., 2019. δ13C values of wood and charcoal reveal broad isotopic ranges at the base of the food web. Radiocarbon 61 (6), 2003–2017.

Pieruccini, P., Forti, L., Mecozzi, B., Iannucci, A., Yu, T.L., Shen, C.-C., Bona, F., Lembo, G., Muttillo, B., Sardella, R., Mazzini, I., 2022. Stratigraphic reassessment of Grotta Romanelli sheds light on Middle-Late Pleistocene palaeoenvironments and human settling in the Mediterranean. Sci. Rep. 12, 13530.

Provan, J., Bennett, K.D., 2008. Phylogeographic insights into cryptic glacial refugia. Trends Ecol. Evol. 23 (10), 564–571.

Psathi, E., 2003. Les sites de l'Arma delle Mani et de la Caverna delle Fate (Ligurie, Italie). Etude paléontologique, archéozoologique et biostratigraphique de la grande faune. Thèse de doctorat du MNHN, Paris, p. 612.

Ramstein, G., Fluteau, F., Besse, J., Joussaume, S., 1997. Effect of orogeny, plate motion and land-sea distribution on Eurasian climate change over the past 30 million years. Nature 386, 788–795.

Reitz, E.J., , et al.Wing, E.S., 1999. Zooarchaeology. Cambridge University Press, Cambridge.

Renault-Miskovsky, J., Baills, H., Marquer, L., Coppola, D., 2011. — Environnement vegetal et paléoclimatologies des Pouilles au Paléolithique Supérieur. Palynologie du Gravettian et de l'Épigravettien de la grotte de Santa Maria d'Agnano (Ostuni, Brindisi, Italie). Bull. Musee Anthropol. Prehist. Monaco 51, 75–86.

Renault-Miskovsky, J., Baills, H., Marquer, L., Coppola, D., 2015. Santa Maria di Agnano (Ostuni, Brindisi, Italie). Préhistoire et Palynologie, Paléoclimatologie et Paléoenvironnement, vol. 65. Rivista di Scienze Preistoriche, pp. 5–27.

Rustioni, M., Ferretti, M.P., Mazza, P., Pavia, M., Varola, A., 2003. The vertebrate fauna from Cardamone (Apulia, southern Italy): an example of Mediterranean mammoth fauna. Deinsea 9 (1), 395–404.

Sadori, L., 2018. The Lateglacial and Holocene vegetation and climate history of Lago di Mezzano (central Italy). Quat. Sci. Rev. 202, 30–44.

Sala, B., 1983. Variation climatiques et séquences chronologiques sur la base des variations des associations fauniques à grands mammifères. Riv. Sci. Preist. 38, 161–180.

Sala, B., 1986. *Bison schoetensacki* Freud. from Isernia la Pineta (early Mid-Pleistocene, Italy) and revision of the European species of bison. Palaeontogr. Ital. 74, 113–170.

Sala, B., 2005. Mammalian faunas and environment from the Würmian Glacial Maximum of the Italian peninsula (approx. 22 ± 2 ka cal BP). In: Fugagnoli, A., Bassi, D. (Eds.), Giornata di Studi Paleontologici "Prof. C. Loriga Broglio." Annali dell'Università degli Studi di Ferrara Museologia Scientifica e Naturalistica, Ferrara 99–104.

Sala, B., Masini, F., Ficcarelli, G., Rook, L., Torre, D., 1992. Mammal dispersal events in the middle and late pleistocene of Italy and western Europe. Cour. Forsch.Inst. Senckenberg 153, 59–68.

Sardella, R., Bertè, D., Iurino, D.A., Cherin, M., Tagliacozzo, A., 2014. The wolf from grotta Romanelli (Apulia, Italy) and its implications in the evolutionary history of *Canis lupus* in the late pleistocene of southern Italy. Quat. Int. 328, 179–195.

Sarti, L., Boscato, P., Lo Monaco, M., 1998. Il Musteriano finale di Grotta del Cavallo nel Salento: studio preliminare. Origini: Preistoria e protostoria delle civiltà antiche 22, 45–110.

Sauqué, V., Cuenca-Besćos, G., 2013. The Iberian peninsula, the last European refugium of *Panthera pardus* Linnaeus 1758 during the upper pleistocene. Quaternaire 24 (1), 35–48.

Schulz, E., Kaiser, T.M., 2007. Feeding strategy of the urus *Bos primigenius* BOJANUS, 1827 from the Holocene of Denmark. Cour. Forsch.Inst. Senckenberg 259, 155–164.

Shipman, P., Foster, G., Schoeninger, M., 1984. Burnt bones and teeth: an experimental study of color, morphology, crystal structure and shrinkage. J. Archaeol. Sci. 11, 307–325.

Slott-Moller, R., 1990. La faune. In: Jaubert, J., Lordblanchet, M., Laville, H., Slott-Moller, R., Turc, A., Brugal, J.-P. (Eds.), Les chasseurs d'aurochs de La Borde. Un site du Paléolithique moyen (Livernon, Lot), vol. 27. DAF, pp. 33–68.

Sommer, R.S., 2020. Late pleistocene and Holocene history of mammals in Europe. In: Hackländer, K., Zachos, F.E. (Eds.), Mammals of Europe-Past, Present, and Future. Springer, Cham, Switzerland, pp. 83–98.

Sommer, R.S., Nadachowski, A., 2006. Glacial refugia of mammals in Europe: evidence from fossil records. Mamm. Rev 36 (4), 251–265.

Spagnolo, V., Aureli, D., Martini, I., Ekberg, I., Boschin, F., Crezzini, J., Poggi, G., Boscato, P., Ronchitelli, A., 2020. Short and close in time: overlapped occupation from the layer 56 of the Molare Rock shelter (Southern Italy). Archaeol. Anthropol. Sci. 12, 1–35.

Stevens, R.E., Jacobi, R., Street, M., Germonpré, M., Conard, N.J., Münzel, S.C., Hedges, R.E.M., 2008. Nitrogen isotope analyses of reindeer (*Rangifer tarandus*), 45,000 BP to 9,000 BP: palaeoenvironmental reconstructions. Palaeogeogr. Palaeoclimatol. Palaeoecol. 262, 32–45.

Stewart, J.R., Cooper, A., 2008. Ice Age refugia and Quaternary extinctions: an issue of Quaternary evolutionary palaeoecology. Quat. Sci. Rev. 27 (27–28), 2443–2448.

Stewart, J.R., Lister, A.M., Barnes, I., Dalèn, L., 2010. Refugia revisited: individualistic responses of species in space and time. P. Roy. Soc. B-Biol. Sci 277, 661–671.

Szuma, E., 2003. Microevolutionary trends in the dentition of the red fox (*Vulpes vulpes*). J. Zool. Syst. Evol. Res. 41, 47–56.

Szuma, E., 2004. Evolutionary implications of morphological variation in the lower carnassial of red fox Vulpes vulpes. Acta Theriol. 49 (4), 433–447.

Szuma, E., 2007. Geography of dental polymorphism in the red fox *Vulpes vulpes* and its evolutionary implications. J. Zool. 90, 61–84.

Szuma, E., 2011. Ecological and evolutionary determinants of dental polymorphism in the arctic fox *Vulpes (Alopex) lagopus*. Ann. Zool. Fenn. 48 (4), 191–213.

Tagliacozzo, A., 2003. Archeozoologia dei livelli dell'Epigravettiano finale di Grotta Romanelli (Castro, Lecce) strategie di caccia ed economia di sussistenza. In: Fabri, P., Ingravallo, E., Mangia, A. (Eds.), Grotta Romanelli Nel Centenario Della Sua Scoperta (1900-2000). Congedo Editore, Lecce, pp. 169–216.

Tagliacozzo, A., Zeppieri, F., Fiore, I., Spinapolice, E., Del Lucchese, A., 2012. Archaeozoological evidence of subsistence strategies during the Gravettian at riparo Mochi (Balzi Rossi, Ventimiglia, Imperia-Italy). Quat. Int. 252, 142–154.

Terlato, G., Livraghi, A., Romandini, M., Peresani, M., 2019. Large bovids on the Neanderthal menu: exploitation of *Bison priscus* and *Bos primigenius* in northeastern Italy. J. Archaeol. Sci.: Reports 25, 129–143.

Ungar, P.S., 2010. Mammal Teeth: Origin, Evolution, and Diversity. Johns Hopkins University Press, Baltimore, pp. 1–303.

Vacca, E., Coppola, D., 1993. The Upper Paleolithic burials at the cave of Santa Maria di Agnano (Ostuni, Brindisi): preliminary report. Riv. Antropol. 71, 275–284.

Vacca, E., Novotny, V., Pesce-Delfino, V., 1992. Note anthropologiche preliminari sui resti della gestante paleolitica di Santa Maria di Agnano (Ostuni, Brindisi). Riv. Sci. Preist. 44, 1–2.

van Asperen, E.N., Stefaniak, K., Proskurnyak, I., Ridush, B., 2012. Equids from Emine-Bair-Khosar Cave (Crimea, Ukraine): co-occurrence of the stenonid *Equus hydruntinus* and the caballoid *E. ferus latipes* based on skull and postcranial remains. Palaeontol. Electron. 15 (1), 5A.

Villa, P., Mahieu, E., 1991. Breakage patterns of human long bones. J. Hum. Evol. 21, 27–48.

Villaret, J.C., Bon, R., Rivet, A., 1997. Sexual segregation of habitat by the alpine ibex in the French Alps. J. Mammal. 78 (4), 1273–1281.

Vismara, P., 2012. Il genere *Lepus* in Italia: chiavi diagnostiche morfo-odontologiche e contributi paleobiogeografici. PhD Thesis, Università di Milano, pp. 1–376.