

## A REAPPRAISAL OF THE PLEISTOCENE MAMMALS FROM THE KARST INFILLING DEPOSITS OF THE MAGLIE AREA (LECCE, APULIA, SOUTHERN ITALY)

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To cite this article: 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. It. Paleontol. Strat.*, 127(2): 355-382.

*Keywords:* Biochronology; Mammals; Aurelian; karst fissures; southern Italy.

*Abstract.* The karst fissures known as “ventarole”, located in the Salentine Peninsula (southernmost part of Apulia, Italy), were first studied by Mirigliano in 1941. These fissures are generally filled with reddish sediments or “terre rosse” in the lower part, and with brownish sediments or “terre brune” in the upper one. Both deposits are particularly rich in vertebrate remains. The mammal assemblages collected within the “terre rosse” from Melpignano and San Sidero are chronologically referred to the early Late Pleistocene (MIS 5), whereas those from the “terre brune” are referred to the Late Pleistocene – Early Holocene (MIS 2/1) transition. These ages were estimated from correlation with the similarly reddish and brownish sediments cropping out in Grotta Romanelli and with other Apulian local faunal assemblages. However, no detailed textural or mineralogical characterization has been carried out on the “ventarole” deposits. Moreover, the presence of several species led to hypothesize a persistence of Middle Pleistocene taxa during the Late Pleistocene in Apulia. In addition, the fauna of Melpignano was proposed as a Faunal Unit of the late Aurelian Land Mammal Age. In the last two decades, a team from the Department of Earth Sciences of Sapienza University of Rome have carried out fieldwork in this fossiliferous area. The rich fossil sample recovered is here presented, coupled with a reassessment of the remains collected since the 1900s. The updated faunal lists of Melpignano and San Sidero include several new species here identified for the first time, in particular *Dama clactoniana*, *Equus mosbachensis* and *Lynx pardinus*. New biochronological and paleoenvironmental data for southern Italy are presented, deriving from the analyses of the mammal remains from Melpignano and San Sidero and their comparison with those from other Middle-Late Pleistocene Apulian sites. Finally, textural and mineralogical analyses performed on several “ventarole” samples allow for a better description of the characteristics of the “terre rosse” and “terre brune”.

## INTRODUCTION

The Salentine Peninsula (the southernmost part of Apulia) is well known since the 19<sup>th</sup> century for its Quaternary vertebrate record coming from

caves on both Salentine coasts (e.g., Grotta Romanelli, Grotta Zinzulusa, Grotta del Cavallo) and from karst fissures, locally known as “ventarole”, concentrated in the area of Maglie (Lecce; Di Stefano et al. 1992; Bologna et al. 1994). The occurrence of fossil remains in the “ventarole” around Maglie was first reported by Mirigliano (1941). Since

*Received: June 10, 2020; accepted: April 20, 2021*

then, the Salentine Peninsula has been investigated by several institutions, including the Italian Institute of Human Paleontology (IsIPU) and the Italian Institute of Prehistory and Protohistory (IIPP), with the support of the Salentine Speleological Group (de Lorentiis 1962; Cardini 1962; De Giuli 1980, 1983). Beginning in 1990, this area has been investigated by a research team of the Department of Earth Sciences of “Sapienza, University of Rome” (Bologna & Petronio 1994; Bologna et al. 1994; Petronio & Pandolfi 2008; Pandolfi & Petronio 2011; Iurino et al. 2013, 2015; Vinuesa et al. 2016; Pandolfi et al. 2017). A large number of fossils have been collected, mainly from the localities of Melpignano and San Sidero and dispersed in different museums and institutions since the early stages of the excavations.

The Melpignano-San Sidero (MSS) karst fissures are generally filled in the lower part by reddish sediments also known as “terre rosse”, and in the upper part by brownish sediments also known as “terre brune” (De Giuli 1983; Di Stefano et al. 1992; Bologna et al. 1994). Both are particularly rich in vertebrate fossil remains (De Giuli 1983; Di Stefano et al. 1992; Bologna et al. 1994; Pandolfi et al. 2017). The vertebrate assemblage recovered from the “terre rosse” of MSS was considered chronologically homogeneous by different authors and referred to the earliest Late Pleistocene (MIS 5) (Mirigliano 1941; De Giuli 1983; Bologna et al. 1994). The assemblage recovered from the “terre brune” was instead referred to the latest Pleistocene or Early Holocene (De Giuli 1980; Pandolfi et al. 2017). The above mentioned putative ages of the “ventarole” mammal faunas were obtained by correlation with those studied at Grotta Romanelli. This cave is considered the most relevant site for stratigraphic and faunal correlations of the south-eastern part of the Italian Peninsula, with its lowermost level generally referred to MIS 5e (early Late Pleistocene; Blanc 1920). In fact, the correlation between the deposits of MSS and Grotta Romanelli was simply based on sediment color; indeed, the succession of Grotta Romanelli, similarly to the MSS “ventarole”, includes reddish sediments (“terre rosse”) in the lower part, and brownish sediments (“terre brune”) in the upper part. From a paleontological viewpoint, the only data available for Grotta Romanelli is a faunal list reported by Blanc (1920).

Formal descriptions and studies of selected material of the MSS fossil collection have been reported in a number of papers: equids (Mecozzi & Strani 2021); rhinocerotids (Petronio & Pandolfi 2008; Pandolfi & Petronio 2011; Iurino et al. 2020); bovids (Bologna & Petronio 1994); suids (Iannucci et al. 2020); hyaenids (Iurino & Sardella 2015; Vinuesa et al. 2016); canids (Iurino et al. 2013; Sardella et al. 2014; Mecozzi & Bartolini Lucenti 2018; Mecozzi et al. 2020) and mustelids (Iurino et al. 2015; Mecozzi 2021).

Despite this, the taxonomic composition and exact stratigraphic and geographic provenance of the remains are still unclear, and several issues remain unsolved, such as:

- The possible persistence of some Middle Pleistocene taxa in southern Italy during the earliest Late Pleistocene, such as the small-sized wolf *Canis mosbachensis* Soergel, 1925, as suggested by Masini et al. (1991) and Sala et al. (1992). According to other authors (De Giuli 1983; Bologna et al. 1994), the taxonomic attribution of the canid remains from these sites is uncertain.

- The taxonomic attribution of bovines remains based only on teeth and/or limb bones is a difficult task, due to the strong morphological similarities between *Bos primigenius* Bojanus, 1827 and *Bison priscus* Bojanus, 1827. The occurrence of the latter species is reported from MSS by Bologna & Petronio (1994) based on a right astragalus, a right calcaneum, a left naviculocuboid and a fragmented right metatarsal.

- The validity of the Melpignano Faunal Unit (FU). Petronio et al. (2007) proposed the establishment of two FUs, Melpignano and Ingarano, for the late Aurelian Land Mammal Age (LMA) of the Italian biochronological scale (Gliozzi et al. 1997). The Melpignano FU would correspond to the beginning of the early Late Pleistocene (MIS 5e) (Petronio et al. 2007), recording the first occurrences of the two nominal subspecies of *Cervus elaphus* Linnaeus, 1758 and *Dama dama* (Linnaeus, 1758). Nevertheless, other authors preferred not to recognize any FUs for the late Aurelian, especially if the bioevents are represented by the first occurrence of subspecies that are difficult to distinguish (e.g., *D. dama dama*) (Gliozzi et al. 1997; Masini & Sala 2011).

- The hypothesis that several species recognized in MSS evolved peculiar anatomical features during the Late Pleistocene, due to the peninsular

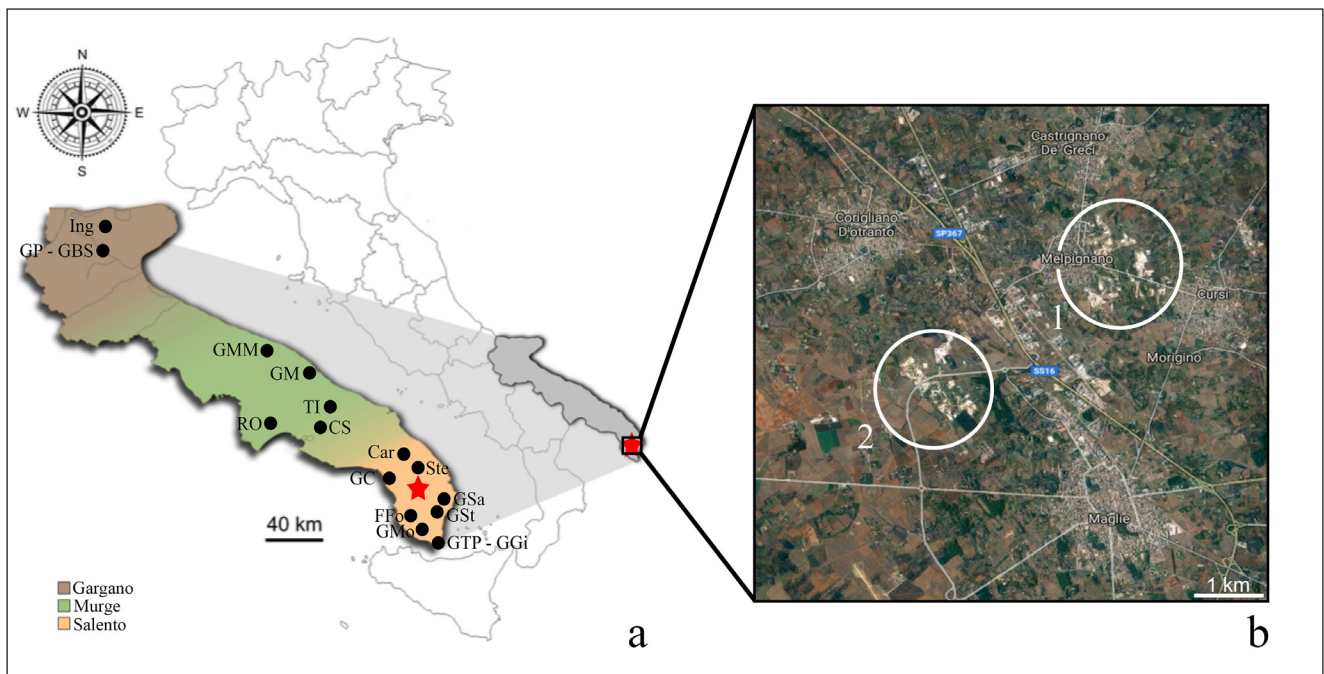


Fig. 1 - a) Location of Apulia (grey area) along the Italian Peninsula. The Gargano, Murge and Salento area are indicated. The red star indicates the position of the studied sites (Melpignano and San Sidero) and neighboring Fondo Cattie. The bold points indicate other Late Pleistocene localities: Ingarano (Ing), Grotta Paglicci (GP), Grotta B di Spagnoli (GBS), Grotta della Masseria del Monte (GMM), Grotta delle Mura (GM), Tana delle Iene (TI), Riparo l'Oscuruscio (RO), Cava Spagnulo (CS), Cardamone (Car), Sternatia (Ste), Grotta del Cavallo (GC), Grotta del Sarcofago (Gsa), Grotta delle Striare (GSt), Santa Cesarea Terme (SCT), Fondo Focone (Ffo), Grotta Montani (Gmo), Grotta delle Tre Porte (GTP) and Grotta dei Giganti (Ggi). b) Location of the Melpignano (1) and San Sidero (2) quarrying areas.

context and the physiography of Apulia (Di Stefano et al. 1992; Sala et al. 1992; Bologna et al. 1994). For example, some specialists hypothesized that the decrease in body size of some Apulian mammals (e.g., cervids, rhinos) during the Late Pleistocene could be due to a sort of “insularism” (Di Stefano 1994; Petronio & Pandolfi 2008; Pandolfi & Petronio 2011; Iurino 2014; Di Stefano et al. 2015).

In this work, new fossil mammals from MSS are presented. In addition, the fossil collections published by Mirigliano (1941) and Bologna et al. (1994) from Melpignano, and Bedetti et al. (2004) and part of the sample of Cardini (1962) from San Sidero are revised. In addition, an overview of recent paleontological works focused on MSS fossils is provided.

The analysis of the mammal fauna from the “terre rosse”, compared with the Middle-Late Pleistocene faunal assemblages from other Apulian sites, led us to provide a new biochronological and paleoenvironmental framework of the area. In addition, textural and mineralogical analyses on the MSS “terre rosse” and “terre brune” are performed to better characterize the sedimentary infilling.

## GEOLOGICAL AND PALEONTOLOGICAL FRAMEWORK

The Salentine Peninsula is the southernmost emerged part of the Adria Plate which constitutes the foreland of both Apennine and Dinaric orogens (Bosellini 2017). It consists of a Variscan basement covered by a 3-5 km-thick Mesozoic carbonate sequence overlain by thin, discontinuous deposits represented by organogenic and/or calcarenitic facies of Paleocene-Oligocene age, and by carbonate-terigenous deposits of Neogene and Quaternary age (Doglioni et al. 1994).

In the fossiliferous area of Maglie (Fig. 1), the bedrock is the 600 m-thick Altamura Limestone Formation (Upper Cretaceous; Ricchetti et al. 1988), made up of well-bedded limestone, dolomitic limestone and dolostone. This unit is overlaid by the widespread Pietra Leccese Formation (Miocene), a marly calcarenites. Its thickness is about 35 m in the Cursi-Melpignano area (Sansò 2017), where it has been and still is extensively quarried. Along the quarry fronts, numerous karst cavities are exposed (Figs. 2-3). During the Middle Pleis-



Fig. 2 - “Ventarole” developed within Pietra Leccese Formation in the Melpignano area. Arrows indicate the “ventarole” from which samples were collected for textural and mineralogical characterization. Labels of samples are also shown.

tocene, the uplift of the Apulian foreland started (Doglioni et al. 1996) and subaerial exposure affected the carbonate formations triggering karstification processes. Karst activity often developed along pre-existing fracture sets and normal faults, formed since the Pliocene (Ciaranfi et al. 1983) parallel to the bulging orientation (NW-SE) of the Apulia Platform (Billi & Salvini 2003). Karstification produced an articulated fissured network, with predominant vertical orientation (Selleri et al. 2003; Selleri 2007). The most common karst types are sub-vertically or funnel-shaped fissures, locally known as “ventarole”, located within the Pietra Leccese Formation. Average width and height of the cavities are <1 m and 10 m, respectively; in some cases, up to 5-6 m-wide cavities were recognized (Pandolfi et al. 2017) (Figs. 2-3). The infilling sediments of the “ventarole” preserve very abundant remains of fossil vertebrates, which were deposited in the cavities together with superficial soil (Pandolfi et al. 2017).

### Melpignano site

The Melpignano site (40°09'22" N, 018°17'30" E; Fig. 1), is located along road SP36 between the towns of Melpignano and Cursi (Lecce). The first description of the Melpignano faunal assemblage was by Mirigliano (1941) (Tab. 1). Further excavations were carried out by IsIPU in the “ventarole” of Cava Motta under the direction of Cardini (1962) (Tab. 1). In the 1990s, a mammal assemblage coming from the “ventarole” of Cava Nuzzo, including an upper third premolar of *Homo neanderthalensis* King, 1864, was reported by Bologna et al. (1994) (Tab. 1). Recently, the Mirigliano paleontological collection was revised by Barbera et al. (2006) (Tab. 1).

### San Sidero site

The San Sidero site (40°08'02" N, 18°16'23" E; Fig.1) is located along road SS16 between Corigliano d'Otranto and Maglie (Lecce). The first description of the faunal assemblage was by Cardini (1962) from the “ventarole” of Sant'Isidoro (Tab.



Fig. 3 - “Ventarole” developed within Pietra Leccese Formation in the San Sidero area. Arrows indicate the “ventarole” from which samples were collected for textural and mineralogical characterization. Labels of samples are also shown.

1). The fossil catalogue of the Paleontology and Paleoethnology Civic Museum of Maglie “Decio de Lorentiis” (PPCMM) has been updated (Muci 1998); in this Museum is stored part of the remains collected by Cardini. A detailed study of the faunal assemblage from Cava L (also known as “S.S.3”) of San Sidero was provided by De Giuli (1980, 1983) (Tab. 1). Bettetti et al. (2004) later described new fossil remains from Cava L (Tab. 1). Recently, new taxa were added to the San Sidero assemblage, such as the dhole *Cuon alpinus* Pallas, 1811 (Petrucci et al. 2012; Iurino et al. 2013) and the badger *Meles meles* Linnaeus, 1758 (Iurino et al. 2015; Mecozzi 2021). Finally, Pandolfi et al. (2017) gave an account of the faunal assemblage recovered from the “terre brune” of Cava Donno (Corigliano d’Otranto) that includes few bones referable to *Homo sapiens* Linnaeus, 1758 (Tab. 1).

#### Fondo Cattie and Sternatia sites

In the Salentine Peninsula, besides MSS, other mammal assemblages have been reported from the

“terre rosse” of Fondo Cattie and Sternatia (Lecce) (Fig. 1).

A sinkhole infilling deposit, named Fondo Cattie, was described by Cremonesi (1980). The stratigraphy includes four levels rich in fossil remains and artefacts ascribed to the Mousterian (Cremonesi 1980; Corridi 1987, 1989). An isolated lower tooth of *Homo neanderthalensis* was found in the deposit (Borgognini Tarli 1983). The Fondo Cattie faunal assemblage was biochronologically referred to MIS 3 (Corridi 1987, 1989) on the basis of the presence of *Dama dama* and *Equus ferus* Boddaert, 1785 and the absence of *Palaeoloxodon antiquus* Falconer & Cautley, 1847, *Stephanorhinus hemitoechus* Falconer, 1868 and *Hippopotamus amphibius* Linnaeus, 1758.

Another well-known faunal assemblage was collected from the karst fissures of Sternatia, biochronologically referred to MIS 3 based on the occurrence of *D. dama*, *E. ferus* and large-sized *Canis lupus* Linnaeus, 1758 and the absence of *P. antiquus*, *S. hemitoechus* and *H. amphibius* (Rustioni et al. 1994).



Sample	"Ventarola"	Description	Clay (%)	Silt (%)	Very fine sand (%)	Fine sand (%)	Medium sand (%)	Coarse fraction (%)	Mineralogy	Organic carbon content wt. %
<b>Melpignano</b>										
Mel3	V1 (Fig. 2a)	"terre brune"	14,2	55,9	5,9	19,7	2,7	1,6	Qzt, Kln, Ha	0,47
Mel4	V2 (Fig. 2b)	"terre brune"	27,9	56,7	3,1	10,5	1,5	0,4		
Mel5			30,8	60,4	2,2	3,3	2,2	1,1		
Mel9	V3 (Fig. 2c)	"terre rosse"	28,2	70,4	0,8	0,6	0	0		
Mel10	V4 (Fig. 2d)	"terre rosse"	38,9	45,9	1,8	10,6	2,5	0,3	Qzt, Kln, Ill, Mnt, Ha	0,08
Mel11			29,4	46	3	17,7	3,5	0,4		
Mel12	V5 (Fig. 2e)	"terre rosse"	30,4	47	2,1	16,6	2,8	1,2		
<b>San Sidero</b>										
SS1	V6 (Fig. 3a)	"terre brune"	18,1	60,1	4,9	11,3	3,1	2,6		
SS13			30,3	54,2	2,1	10,4	1,9	1,1	Qzt, Kln, Ha	0,53
SS14	V7 (Fig. 3a)	"terre brune"	15	60,4	8,1	9,1	6,9	0,5		
SS9			13,7	59,3	9,2	9,6	4,9	3,3		
SS10	V8 (Fig. 3b)	"terre rosse"	26,9	65,4	3,2	3	0,7	0,8		
SS11			27,5	57,5	3,9	7,6	2,2	1,3		
SS12	V9 (Fig. 3c)	"terre rosse"	22,4	59,4	6,8	6,9	2	2,5		
SS6			31,8	54,9	2,4	8	2	0,9		
SS7	V10 (Fig. 3d)	"terre rosse"	42,9	49,5	1,5	4,6	1,1	0,4		
SS8			39,1	59,2	0,7	0,7	0,3	0,1		
SS2			13,1	30,3	6,1	44,4	6	0,1	Qzt, Kln, Ha	0,09
SS3	V11 (Fig. 3d)	"terre rosse"	18,8	31,4	7,3	38,8	3,3	0,3		
SS4			33,1	45,3	3,8	15,2	1,8	0,8		
SS5			30,2	42,5	0,4	6,9	18,2	1,7		

Tab. 2. - Texture, mineralogy and organic carbon content in "terre brune" and "terre rosse" from Melpignano and San Sidero. Abbreviations: Qzt, quartz; Kln, kaolinite; Ill, illite; Mnt, montmorillonite; Ha, hydroxyapatite.

## MATERIALS AND METHODS

### Texture, mineralogy and organic carbon content

A total of 21 samples were collected from eleven cavities (Tab. 2; Figs 2-3). Cavities V1-V2 from Melpignano and V6-V7 from San Sidero were filled by "terre brune"; the other cavities were filled by "terre rosse" (Figs. 2-3). The samples from "terre brune" were less numerous than those from "terre rosse" because of the scarce preservation of the brownish sediments due to both natural erosion and intensive quarrying activity. Samples were analyzed for textural and mineralogical characterization. Grain sizes were determined using a Sympatec HELOS laser diffraction particle size analyzer (range from 0.9 to 100  $\mu\text{m}$ ). Samples, dried at 75°C for 24 hours and mechanically dry sieved at 100  $\mu\text{m}$ , were dispersed in distilled water; ultrasound was also used to avoid particle aggregation. The grain size fractions >100  $\mu\text{m}$  were determined by manual wet sieving. The textural classes follow Wentworth (1922), namely: clay (0.04–4  $\mu\text{m}$ ), silt (4–63  $\mu\text{m}$ ), very fine sand (63–125  $\mu\text{m}$ ), fine sand (125–250  $\mu\text{m}$ ) and medium sand (250–500  $\mu\text{m}$ ). Mineralogy was determined on bulk sediment of selected samples using a Bruker Advance D8 diffractometer operating in Bragg-Brentano geometry

and equipped with a solid-state Sol-X detector. Iron oxides were separated from sediment by suspending the sample in water and picking up magnetic particles with a magnetic stir bar. Identification of the mineral phases was made with the X Powder12 software.

Total organic carbon percentage content was determined using the elemental analyzer EAFlash 1112-Thermo. Samples were dried at 90°C prior to analysis and pretreated with HNO<sub>3</sub> 1M to remove carbonate. Then, 3.0–3.5 mg of sample was weighed, put into tin capsules, and analyzed in triplicate. Results are expressed as wt %.

### Fossil mammals

The fossil material from MSS, currently housed in different museums and research institutions, is here comprehensively presented for the first time. In particular:

The Mirigliano collection from Melpignano (catalogue number M-; 149 specimens) stored at the Paleontology Museum of the University of Naples Federico II (Tab. 3).

The collection from Cava Nuzzo of Melpignano (catalogue number Cur-; 175 remains) housed at the PaleoFactory laboratory in the Department of Earth Sciences, Sapienza University of Rome (Tab. 3).

Species	Localities	Melpignano						San Sidero									
		Mirigliano collection	Cava Nuzzo	Cava della Terra	Cava Bianco	J	A	T	San Sidero E	SS6	SS7	Cava L	Cava L		J	A	T
													Fissure 1	Fissure 2			
		PMUNF	PF	PF	PF				IsIPU	MGPUF	MGPUF	PF	PMUT	PMUT			
<i>Palaeoloxodon antiquus</i>		4	3		14	4	17	21									
<i>Stephanorhinus hemitoechus</i>		1			29	8	22	31				1	5		2	4	6
<i>Stephanorhinus</i> sp.										8					8		8
<i>Equus mosbachensis</i>		106	6		59	16	155	171		168		37			24	181	205
<i>Equus hydruntinus</i>		6			31	10	27	37	7			18			9	16	25
<i>Sus scrofa</i>		3	7		44	18	36	54				6	2		2	6	8
<i>Hippopotamus</i> sp.		1			5	3	3	6				1				1	1
<i>Bos primigenius</i>		24	9	5	215	184	70	254	1			14	4	2	4	17	21
<i>Cervus elaphus</i>	X		38	18	169	46	179	225				23	2		3	22	25
<i>Dama clactoniana</i>			68	26	938	109	923	1032				52			14	38	52
<i>Dama dama</i>	X											59		278	593	128	802
<i>Capreolus capreolus</i>			6	21	31	10	48	58				2			2		2
<i>Mustela putorius</i>		1					1	1									
<i>Meles meles</i>			1		2		3	3				1	1			2	2
<i>Canis lupus</i>		2	11		117	7	123	130				25	42	38	2	103	105
<i>Cuon alpinus</i>												2				2	2
<i>Vulpes vulpes</i>		1	2		18	4	17	21				6	2	4	3	9	12
<i>Crocota spelaea</i>			5		68	1	72	73	1			9	4	1		15	15
<i>Panthera pardus</i>												7	6			13	13
<i>Lynx pardinus</i>									1								
<i>Lynx</i> sp.			1		2		3	3				6	9	2	1	17	18
<i>Felis silvestris</i>												8				8	8
<i>Lepus europaeus</i>			15		204	27	192	219				9	3			12	12
<i>Oryctolagus cuniculus</i>	X		2	16	1625	302	1341	1643	21			11	146	56	10	224	234
<b>Totale</b>		149	174	86	3571	749	3232	3982	31	176	59	230	512	696	212	1492	1704

Tab. 3 - List of the mammal fossil remains from "terre rosse" of Melpignano and San Sidero sites included in this work. Abbreviations: J, juvenile; A, adult; T, total; X, mammal taxa reported by Mirigliano (1941). PMUNF, Paleontology Museum of the University of Naples Federico II; PF, PaleoFactory laboratory, Sapienza University of Rome; IsIPU, Italian Institute of Human Paleontology; MGPUF, Museum of Geology and Paleontology of the University of Florence; PMUT, Paleontology Museum of the University of Turin.

A few fossil specimens of the Cardini collection (catalogue number IsIPU SS-; 31 remains) from the fissure E of San Sidero (Sant'Isidoro) housed at the IsIPU (Tab. 3).

New material from Cava L of San Sidero (catalogue number SSND-; 230 remains) and from Cava della Terra (catalogue number M05-; 86 specimens) and Cava Bianco (catalogue number MPND-; MPSD-; 3571 specimens) of Melpignano stored at the PaleoFactory laboratory in the Department of Earth Sciences, Sapienza University of Rome (Tab. 3).

New material from Fissure 1 and 2 of Cava L of San Sidero (catalogue number PU-; Fissure 1: 512 remains and Fissure 2: 696 remains) stored at the Paleontology Museum of the University of Turin (Tab. 3).

New material from the SS6 and SS7 of San Sidero (catalogue number IGF-; SS6: 176 remains and

SS7: 59 remains) housed at the Museum of Geology and Paleontology of the University of Florence (Tab. 3).

In order to provide new taphonomic data, the surface of the bones has been examined to detect bite marks, rodent gnaw marks or human butchering and exploitation traces. To identify age classes, we have evaluated the degree of fusion of the proximal and distal epiphyses and the dental wear (Laws 1953; Ferrara 1965; Lowe 1967; Morris 1972).

The MSS faunal assemblages were compared to those of the following Middle-Late Pleistocene Apulian sites (Fig. 1): (i) Gargano promontory: Grotta B di Spagnoli (Sala 1978) and Grotta Paglicci (Boscato 1994, 2004); (ii) Murge area: Cava Spagnuolo (Mecozzi et al. 2018); Tana delle Iene (Conti et al. 2010, 2012), Riparo l'Oscurusciuto (Boscato & Crezzini 2012; Spagnolo et al. 2016) and Grotta delle Mura (Bon & Boscato 1993) and (iii) Salentine



Peninsula: Grotta del Sarcofago (Di Stefano et al. 1992), Grotta delle Striare (Malviglia 1955; Di Stefano et al. 1992), Grotta delle Tre Porte (Cardini 1962), Grotta Montani (Cremonesi 1980); Grotta del Cavallo (Sarti et al. 1998, 2002; Sala & Berto 2020), Fondo Cattìe (Corridi 1987, 1989), Sternatia (Rustioni et al. 1994) and Cardamone (Rustioni et al. 2003).

We also studied the mammal remains from Grotta dei Giganti, Grotta delle Tre Porte and Fondo Focone stored at the IsIPU and from Cardamone stored at the Commercial Technical Institute Galilei-Costa (Lecce).

### Overview of paleontological research at MSS localities

In the last decades, several authors carried out morphological and biometric studies on the fossil remains from the “terre rosse” of MSS (Petronio & Pandolfi 2008; Pandolfi & Petronio 2011; Petrucci et al. 2012; Iurino et al. 2013, 2015; Di Stefano et al. 2015; Iurino & Sardella 2015; Vinuesa et al. 2016; Iannucci et al. 2020; Iurino et al. 2020; Mecozzi et al. 2020; Mecozzi 2021; Mecozzi & Strani 2021).

*Equus* specimens from San Sidero were previously attributed to the large-sized *Equus chosaricus* Gromova, 1949 by Eisenmann (1991) and *E. ferus* by De Giuli (1983) and Rustioni (1998), while specimens from Melpignano were referred to *E. ferus*. Recently, *Equus* fossils from Cava Nuzzo, Cava Bianco and Mirigliano Collection of Melpignano, SS6 and Cava L of San Sidero have been reconsidered by Mecozzi & Strani (2021) and attributed to *Equus mosbachensis* von Reichenau, 1915.

Rhinoceros remains from MSS were classified as *Stephanorhinus kirchbergensis* (Jäger, 1839) by different authors (Tab. 1). Most of the samples from Cava Nuzzo and Cava Bianco of Melpignano were revised by Petronio & Pandolfi (2008) and Pandolfi & Petronio (2011), who referred them to *S. hemitoechus*. These remains show several diagnostic features of *S. hemitoechus*, such as the absence of antecrochet, the closing of the mediofossette, the absence of the protocone constriction and a wavy lingual wall with a weak paracone fold in the upper fourth premolar, a distinct distal cingulum and a rough enamel in lower molars. The authors noted the small size of the rhinoceros remains from MSS, which are biometrically close to the Italian (e.g., Torre del Pagliacetto, Malagrotta; MIS 10-8) and French (e.g., Lunel-Viel;

MIS 9-7) Middle Pleistocene specimens, but smaller than other remains from the Italian late Middle Pleistocene (e.g., Vitinia, Grotta Lina; MIS 7-6) and Late Pleistocene (e.g., San Colombano al Lambro) sites (Pandolfi & Petronio 2011).

Recently, a partial braincase and its natural endocast recovered from Cava Bianco were analyzed with Computed Tomography (CT) methods, but due to the young age of the specimen it was referred only to Rhinocerotinae (Iurino et al. 2020).

A recent study focused on the size shift in the late Middle Pleistocene to Early Holocene *Sus scrofa* Linnaeus, 1758 of Apulia (Iannucci et al. 2020) in order to test the existence of a trend toward small dimensions in the species as generally stated in the literature (e.g., Faure & Guérin 1983). Two distinct groups of wild boars were recognized: small-sized specimens from glacial stages and large-sized ones from interglacials. The latter includes the sample from Melpignano (Cava Nuzzo, Cava Bianco, Mirigliano Collection).

Two neurocrania of a hyaenid have been studied with digital techniques and ascribed to *Crocota spelaea* (Goldfuss, 1823) (Iurino & Sardella 2015; Vinuesa et al. 2016). The endocranial morphology of these specimens was closer to that of the nearly coeval (late Middle-Late Pleistocene) *Crocota ultima* (Matsumoto, 1915) from Asia and the extant *Crocota crocuta* (Erxleben, 1777) than to that of other extant bone-cracking taxa (Vinuesa et al. 2016).

The revision of the canid sample from MSS led to the identification of *Cuon alpinus* (Petrucci et al. 2012; Iurino et al. 2013; Mecozzi et al. 2020); in particular, a fragment of left maxillary and a left hemimandible from Cava L of San Sidero were affected by periodontitis (Iurino et al. 2013). The fossils from MSS were also included in a large revision carried out by Mecozzi et al. (2020). The results of this study revealed no significant difference between Middle and Late Pleistocene European dholes, suggesting that the whole fossil record of this canid should be assigned to *Cuon alpinus*.

A partial left hemimandible of *Meles meles* from San Sidero was described by Iurino et al. (2015). As reported by the authors, the specimen shows an evident pathology, probably an injury from a porcupine. This hemimandible from San Sidero and other remains from Cava Bianco and Cava Nuzzo from Melpignano have been recently studied by Mecozzi (2021), confirming their taxonomic attribution.

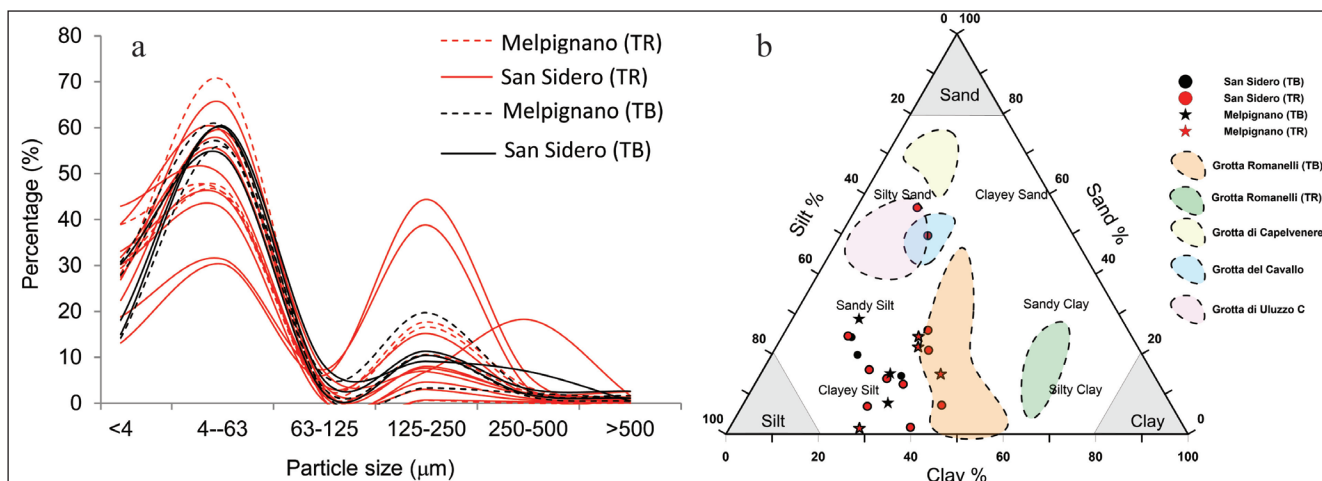


Fig. 4 - a) Particle size distribution of “terre brune” (TB – black line) and “terre rosse” (TR – red line) from Melpignano (dotted line) and San Sidero (solid line); b) Grain size classification of “terre brune” and “terre rosse” data from San Sidero and Melpignano sites. The fields drawn with dashed lines represent the grain size data from Grotta di Uluzzo C (Borzatti von Löwestern & Magaldi 1969), Grotta del Cavallo (Palma di Cesnola 1963), Grotta di Capelvenere (Patriarchi 1980) and Grotta Romanelli (“terre rosse” from Cortesi 1958; “terre brune” from Giustini et al. 2018).

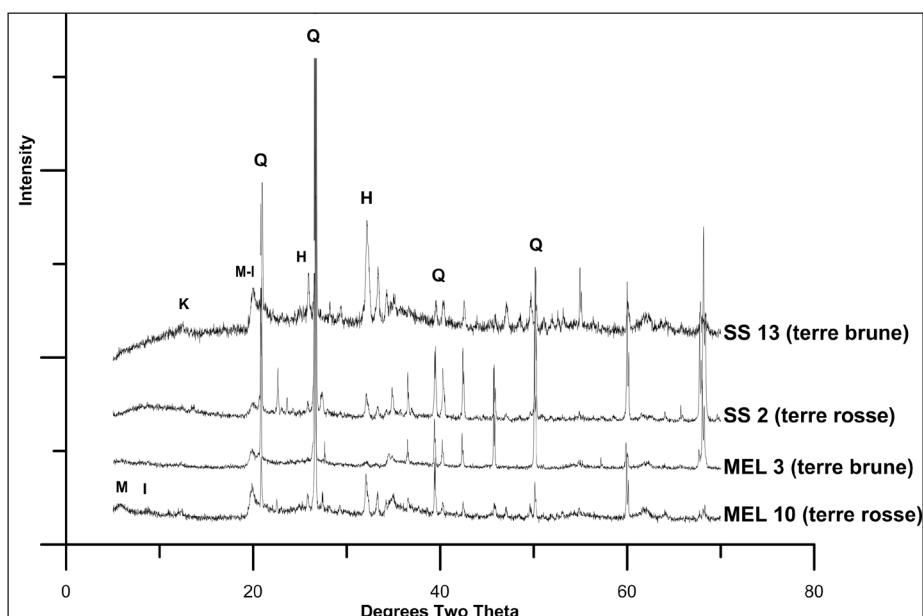


Fig. 5 - Composition of “terre brune” (TB) and “terre rosse” (TR) in samples from Melpignano (MEL3 and MEL10) and San Sidero (SS2 and SS13) from X-ray diffraction. Abbreviations: Q, quartz; K, kaolinite; I, illite; M, montmorillonite; H, hydroxyapatite.

At Cava Nuzzo, together with skeletal elements referable to a juvenile fallow deer, an isolated tooth belonging to a young individual of *Homo neanderthalensis* was found and described by Bologna et al. (1994).

## RESULTS

### Texture, mineralogy and organic carbon content of the “ventarole” infilling sediment

The MSS “ventarole” have variable width, from less than 1 m up to 10 m; they can reach depths of more than 10 m from the soil surface (Figs. 2-3).

Four cavities are filled with “terre brune” sediment, seven with “terre rosse”. In the eleven cavities, the direct contact between “terre brune” and “terre rosse” was never observed, although it was described in the literature (e.g., Pandolfi et al. 2017). In all studied “ventarole”, no definite sedimentary structures were recognizable.

Results of textural and mineralogical analyses are reported in Tab. 2. The “ventarole” sediments are mainly constituted of clayey silt and sandy silt, with the exception of two samples of “terre rosse” from San Sidero which are constituted of silty sands (Fig. 4 a-b). Marked differences are evident among samples, although no clear relationship can be de-

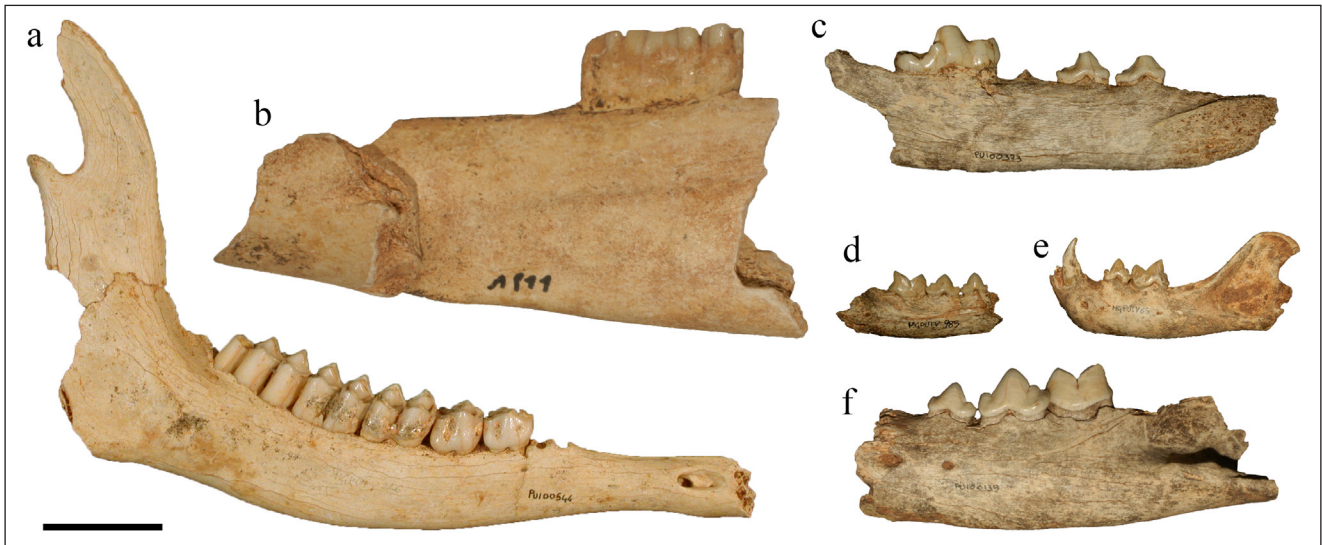


Fig. 6 - Fossil specimens from “terre rosse” of San Sidero: a) PU100544, right hemimandible of *Dama clactoniana* in labial view; b) SSND50, fragment of right hemimandible of *Equus mosbachensis* in lingual view; c) PU100373, fragment of left hemimandible of *Canis lupus* in lingual view; d) PU102849 (ex. MGPUTV985), fragment of right hemimandible of *Felis silvestris* in labial view; e) PU102936 (ex. MGPUTV65), left hemimandible of *Lynx pardinus* in lingual view; f) PU100139, fragment of left hemimandible of *Panthera pardus* in labial view. Scale bar 3 cm.

tected between grain size and sites. The grain size distributions are bimodal (Fig. 4a), with one mode coarser than 125  $\mu\text{m}$  and another finer than 63  $\mu\text{m}$ . The fine and medium sand fractions are characterized by sub-rounded grains of quartz. The coarse fraction ( $>500 \mu\text{m}$ ) is mainly constituted of splinters of Pietra Leccese, fragments of bones, shells, and rodent teeth.

XRD analyses show a mineralogical composition dominated by quartz and to a lesser extent kaolinite and hydroxyapatite; illite and montmorillonite were detectable only in sample MEL10 from “terre rosse” (Fig. 5). Iron oxides (e.g., goethite and hematite), not detectable by the XRD method, were identified because they adhere to the magnetic stir bar and are visualized as black particles.

The organic carbon content ranges from 0.57 wt %, measured in “terre brune”, to 0.08 wt %, measured in “terre rosse” (Tab. 2).

### Notes on taphonomy

Most of the specimens from “terre rosse” of Melpignano and San Sidero are taxonomically identifiable, 3982 out of 5364 and 1704 out of 2139 respectively (Fig. 6-7). Many indeterminate elements are long bone shaft fragments of large- and medium-sized ungulates. The mammal fauna from MSS is dominated by cervids (Melpignano = 32.9%; San Sidero = 57.9%) and the European rabbit *Oryctola-*

*gus cuniculus* (Linnaeus, 1758) (Melpignano = 41.2%; San Sidero = 13.5%). Bovids and equids are well represented, whereas elephants, rhinos and hippos are very scarce. Among the carnivorans, the most abundant species is *Canis lupus*, mustelids are represented only by a few specimens.

The material is generally well preserved, rarely covered by a thin reddish limestone crust. Some remains were found in partial anatomical connection, but most of them are isolated elements. Part of the sample was referred to juvenile individuals, such as deciduous teeth and long bones with both proximal and distal epiphyses disarticulated or unfused suture lines (Melpignano = 16.3%; San Sidero = 12.4%).

Most of the bones show no evidence of surface abrasion or flutination, excluding a long transport process before the final deposition, whereas a few specimens display clear signs of weathering, such as exfoliation or micro-fractures on the surface. Traces of manganese occur in many specimens, while there is no evidence of bite marks, human butchering and exploitation, except for a fragment of left tibia (MPND556), a fragment of right tibia (MPND557) and a right calcaneum (MPND464) referred to *Bos primigenius* with clear bite marks (Fig. SD1). Only a right radius of a young individual of *Stephanorhinus hemitoechus* (SSND147) from San Sidero displays rodent gnaw marks (Fig.

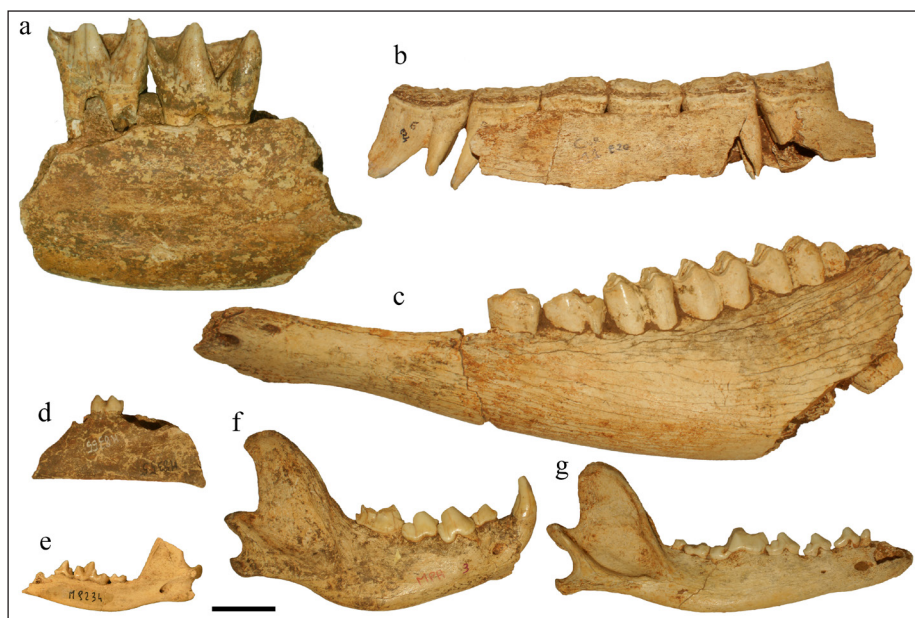


Fig. 7 - Fossil specimens from "terre rosse" of Melpignano: a) MPND1030, fragment of right hemimandible of *Stephanorhinus bemtoechus* in lingual view; b) MPND396 (ex. Cur11), fragment of left hemimandible of *Equus mosbachensis* in lingual view; c) MPND605, fragment of left hemimandible of *Bos primigenius* in labial view; d) M8355, fragment of left hemimandible of *Sus scrofa* in labial view; e) M8234, fragment of right hemimandible of *Vulpes vulpes* in lingual view; f) MPND942, right hemimandible of *Crocuta spelaea* in labial view; g) MPND859 (ex. MPC1), right hemimandible of *Canis lupus* in labial view. Scale bar 3 cm.

SD1). Therefore, it is possible to exclude the action of carnivorans and humans in the accumulation of the fossil remains at MSS.

#### Revised taxonomy of selected species

In order to clarify several open issues on the MSS faunal assemblage, we revised the taxonomic attribution of selected species.

#### *Hippopotamidae*

De Lorenzo & D'Erasmo (1935) reported the occurrence of some isolated hippopotamus teeth from the Melpignano area and referred them to *H. amphibius*. Since then, all the hippo remains from the Salentine Peninsula have been attributed to this taxon, even if Mazza (1995) suggested that an isolated lower molar recovered from Melpignano, stored at PPCMM, could be instead referred to *Hippopotamus* cf. *antiquus* Desmarest, 1822. The hippopotamus is one of the most common species in the European Pleistocene large mammal record, but there are conflicting opinions on its systematics and evolution (e.g., Mazza 1995; Mazza & Bertini 2013; van der Made et al. 2017). However, the hippo material from MSS comprises fragmented postcranial elements and isolated canines of poor diagnostic value, which are therefore referred to *Hippopotamus* sp. (Tab. 3).

#### *Bovidae*

The Bovidae material from the old and new collections (248 specimens from Melpignano; 21

from San Sidero) was reassessed, including a few postcranial elements previously attributed to *Bison prisus* (Bologna & Petronio 1994). The bovid remains from MSS display morphological features clearly indicative of *Bos primigenius*, among which are: a well-developed entostyle and a more columnar and hypsodont appearance (swelling is absent) of the upper molars; V-shaped enamel around the central cavity of both the upper and the lower molars; the two main lobes are more developed mesio-distally in the lower molars; presence of a small accessory styloid between hypoconid and hypoconulid in the lower third molar.

Four remains were attributed to *B. prisus* by Bologna & Petronio (1994), and are here re-described in detail (Fig. SD2). MPND909 is a complete right astragalus. In posterior view, the lateral trochlear crest is more proximally elongated than the medial one, with a deep trochlear pit. The proximal profile of the sustentacular surface is sinuous, with a lateral margin that is more proximally developed. A large foramen, proximo-distally elongated, occupies a central part of the distal pit and extends up to the lateral margin of the bone. The distal trochlea is deep. Laterally, the distal trochlear surface is oval in shape, the lateral crest of the proximal trochlea is flat. The profile of the distal pit is semicircular along the posterior margin, the latter displays a marked protuberance posteriorly projected at the level of the distal margin of the calcaneal-malleolar articular surface. In dorsal view, the trochlear pit is marked with the lateral artic-

ular surface well developed, but it does not reach the distal trochlea. The medial tubercle is located just above the distal trochlea, which shows a nearly straight proximal margin. MPND457 is a complete right calcaneus. Medially, the sustentaculum surface is flattened, whereas the posterior sustentaculum margin is rounded. In posterior view, the articular surface for the naviculocuboid is proximally elongated. The sustentaculum is projected almost perpendicularly to the main axis of the bone, while its medial-anterior extension is not visible. MPND471 is a complete left naviculocuboid. In proximal view, the anterior margin is sinuous. Two foramina are present but are well separated, with both the inner and the external astragal articular surfaces reaching the medial process. The calcaneal articular surface has the same breadth across its antero-posterior depth. In distal view, the anterior cuneal articular surface reaches the posterior one, with the two separated by a weak crest. The anterior cuneal articular surface posteriorly diverges by the anterior-external metatarsal articular surface. The latter is well separated by the posterior-external metatarsal articular surface and is much expanded laterally. The deep foramen opens in the central part of the bone, at the level of the posterior cuneal articular surface. MPND522 is an incomplete right metatarsal which preserves only part of the diaphysis and the distal epiphysis. In both anterior and posterior views, the diaphysis spreads out slightly towards the distal epiphysis and no medial and lateral swellings are present at the level of the distal epiphysis. The interarticular incisure is V-shaped and is more proximally extended in relationship to the margin of both condyles. The suture is completely obliterated. Posteriorly, a large and deep longitudinal furrow reaches the condyles, while the medial and lateral intercondylar crests diverge slightly. Distally, the depth of the medial and lateral condyles is similar. In both anterior and posterior views, the greatest width corresponds to the level of the distal portion, and is greater than the supracondylar width.

Most of the features described above are generally recognized in *Bos*, even if the morphology of the bovine skeleton shows a large variability, with a variable percentage at which each trait is observed in extant specimens (e.g., Sala 1986; Balkwill & Cumbaa 1992).

### *Cervidae*

Taxonomic attribution of fossil European deer is mainly based on antler morphology (e.g., Di Stefano 1994, 1996; Di Stefano et al. 1998; Lister 1996; Pfeiffer 1998; Breda & Lister 2013; Breda 2015; Breda et al. 2015), explaining the difficulty in classification, especially when the antlers are not present. This applies in particular to the identification of late Middle Pleistocene fallow deer specimens, because *Dama clactoniana* (Falconer, 1868) shares many morphological features with *D. dama*. In previous studies, fallow deer remains were attributed to *D. dama* (Di Stefano 1994; Bologna et al. 1994). The antler MPD296 from Cava Bianco, even if not completely preserved, shows a posterior tine on the beam (Fig. 8) which is a diagnostic character of *D. clactoniana*. The morphology of MPD296 is close to that of specimens from the basal gravel and lower loam from Swanscombe (England), classified as *D. clactoniana* (plate II – III in Leonardi & Petronio 1976). In the samples from Cava Nuzzo, Cava della Terra and Cava Bianco of Melpignano and Cava L of San Sidero, the following cranial and postcranial features have been detected: in the P<sub>3</sub>, paraconid and parastylid not always separated; in the P<sub>4</sub>, the metaconid and paraconid are joined to



Fig. 8 - MPD296, antler of *Dama clactoniana* from Melpignano (left); IGF731V, antler of *Dama dama* from San Sidero (right). Scale bar 5 cm.

Region	Taxon	Site	Age	Reference	P <sup>4</sup> L	M <sup>1</sup> L	M <sup>1</sup> B	M <sub>1</sub> L	
Italy	<i>Canis lupus</i>	La Polledrara di Cacabibbio	Middle Pleistocene	Anzidei et al. (1989)	23,0				
	<i>Canis lupus</i>	Melpignano - Cava Bianco	Middle Pleistocene	This work	19.6 (17.5 - 25.8; n=11)	14.1 (14.0 - 14.3; n=5)	16.7 (15.5 - 17.6; n=5)	23.8 (21.6 - 25.8; n=3)	
	<i>Canis lupus</i>	Melpignano - Cava Nuzzo	Middle Pleistocene	This work				25.7 (25.5-26.0; n=2)	
	<i>Canis lupus</i>	Melpignano - Mirigliano collection	Middle Pleistocene	This work				22,2	
	<i>Canis lupus</i>	San Sidero - Cava L	Middle Pleistocene	This work	22.1 (22.0 - 22.3; n=3)	15.0 (15.0 - 15.1; n=2)	18.9 (18.2-19.5; n=2)	23.3 (21.9 - 24.7; n=2)	
	<i>Canis lupus</i>	San Sidero - Fissure 1	Late Pleistocene	This work				25,4	
	<i>Canis lupus</i>	San Sidero - Fissure 2	Late Pleistocene	This work	23,6				
	<i>Canis lupus</i>	Grotta Romanelli - level G	Late Pleistocene	This work	22.1 (21.5 - 22.7; n=5)	13.9 (13.4 - 14.4; n=7)	17.0 (16.4 - 17.7; n=7)	23.9 (23.7 - 24.0; n=4)	
	<i>Canis lupus</i>	Ingarano	Late Pleistocene	This work	23.5 (21.6 - 24.6; n=5)	14.4 (14.0 - 15.9; n=6)	18.1 (17.5 - 19.7; n=6)	25.4 (22.9 - 27.0; n=7)	
	<i>Canis lupus</i>	Avetrana	Late Pleistocene	This work	23.0 (20.8 - 26.4; n=8)	16.0 (14.0 - 17.5; n=11)	19.5 (18.4 - 21.4; n=11)	27.9 (25.8 - 31.1; n=19)	
	<i>Canis lupus</i>	Broion	Late Pleistocene	Bertè (2013)	24.9 (25.0 - 24.9; n=2)	15.9 (15.5 - 15.9; n=2)	18.8 (18.8 - 18.9; n=2)	30.2 (29.6 - 30.5; n=2)	
	<i>Canis lupus</i>	Buco del Frate	Late Pleistocene	Bertè (2013)	26.1 (22.7 - 31.0; n=2)	16.9 (15.1 - 16.9; n=12)	21.9 (18.0 - 21.0; n=12)	28.4 (25.2 - 31.0; n=27)	
	<i>Canis lupus</i>	Cardamone	Late Pleistocene	This work	24.7 (20.5 - 26.7; n=13)	15.6 (13.7 - 17.3; n=13)	18.5 (15.9 - 20.1; n=13)	28.2 (25.0 - 31.0; n=18)	
	<i>Canis lupus</i>	Covoli di Velo	Late Pleistocene	Bertè (2013)	25.4 (20.1 - 25.4; n=2)	17.0	19.5		
	<i>Canis lupus</i>	Grotta di Ladrenizza	Late Pleistocene	Bertè (2013)	23.9 (23.7 - 24.1; n=2)	15.2 (15.2 - 15.2; n=2)	18.1 (18.0 - 18.3; n=2)		
	<i>Canis lupus</i>	Grotta della Jena	Late Pleistocene	This work	25.3 (25.3 - 25.4; n=2)	17,5	21,8	29.2 (29.2 - 29.3; n=2)	
	<i>Canis lupus</i>	Grottadi Sant'Agostino	Late Pleistocene	Tozzi (1970)	24.5 (23.0 - 26.0; n=2)	17.3 (17.0 - 18.0; n=3)	22.0 (21.0 - 23.0; n=3)	27.8 (25.7 - 30.0; n=5)	
	France	<i>Canis lupus lunellensis</i>	Aven I de La Fage	Middle Pleistocene	Boudadi-Maligne (2010)	21.7 (20.5 - 22.8; n=3)	14.8 (14.4 - 15.4; n=3)	19.4 (18.7 - 20.3; n=3)	25.5 (24.3 - 26.7; n=7)
		<i>Canis lupus lunellensis</i>	Igue des Rameux	Middle Pleistocene	Boudadi-Maligne (2010)	23.1 (20.0 - 26.3; n=57)	15.1 (13.1 - 19.1; n=51)	19.7 (16.7 - 21.8; n=51)	25.4 (21.7 - 28.6; n=83)
<i>Canis lupus lunellensis</i>		Lunel-Viel 1	Middle Pleistocene	Boudadi-Maligne (2010)	22.6 (20.1 - 24.5; n=23)	14.4 (12.3 - 15.6; n=20)	19.2 (16.9 - 20.4; n=20)	25.0 (22.9 - 26.8; n=24)	
<i>Canis lupus santenaisiensis</i>		Coudoulous I	Middle Pleistocene	Boudadi-Maligne (2010)	23.2 (22.6 - 23.9; n=8)	14.5 (13.8 - 14.8; n=6)	19.7 (18.8 - 21.7; n=6)	26.0 (23.3 - 27.5; n=9)	
<i>Canis lupus santenaisiensis</i>		Aven de l'Arquet	Late Pleistocene	Boudadi-Maligne (2010)	26.4 (22.7 - 29.0; n=26)	16.3 (14.7 - 17.9; n=19)	21.4 (19.5 - 23.0; n=19)	28.2 (25.0 - 31.3; n=28)	
<i>Canis lupus maximus</i>		Grotte de Jaurens	Late Pleistocene	Boudadi-Maligne (2010)	27.8 (23.8 - 29.9; n=6)	16.6 (16.0 - 17.5; n=5)	21.9 (20.6 - 22.4; n=5)	29.6 (26.5 - 33.4; n=19)	
<i>Canis lupus maximus</i>		Igue du Gral	Late Pleistocene	Boudadi-Maligne (2010)	26.7 (23.5 - 29.0; n=10)	16.8 (15.6 - 18.4; n=12)	22.5 (20.8 - 24.1; n=12)	29.3 (27.3 - 32.0; n=10)	
<i>Canis lupus maximus</i>		Maldidier	Late Pleistocene	Boudadi-Maligne (2010)	28.6 (28.5 - 28.8; n=3)	16.2 (16.0 - 16.4; n=2)	21.9 (21.9 - 22.0; n=2)	30.3 (30.2 - 30.4; n=3)	

Tab. 4 - Middle-Late Pleistocene canids from selected localities of France and Italy. P<sup>4</sup>L – Length of upper fourth premolar; M<sup>1</sup>L – Length of upper first molar; M<sup>1</sup>B – Breadth of upper first molar; M<sub>1</sub>L – Length of lower first molar.

form a closed lingual wall, aligned with the long axis of the tooth; in the lower molars, variable development of the ectostylids; in the M<sub>3</sub>, variable presence of the additional stylid between hypoconid and talonid; in the scapula, the tuberosity of the coracoid process is slightly downturned, but not distinctly hooked, in proximal view; in the humerus, variable development of the radial and coronoid fossa; in the metatarsal, the articular surface of the posterior side is variable, but generally less proximally extended. These characters are generally observed in *D. clactoniana* (Tab. 3). The samples from SS7, Fissure 1 and 2 from San Sidero show a different morphology. As can be observed in Figure 8, in the antler from SS7 the posterior tine on the beam and

the third anterior tine are absent. Craniodental and postcranial remains show the paraconid and parastylid well separated in the P<sub>3</sub>; the metaconid and paraconid separated in the P<sub>4</sub>; the presence of the additional stylid between hypoconid and talonid in the M<sub>3</sub>; the radial fossa wider than the coronoid one in the humerus. According to several authors (e.g., Di Stefano 1996; Lister 1996), these features resemble those of *D. dama* (Tab. 3).

#### Canidae

The canid sample (130 specimens from Melpignano; 105 from San Sidero) shows craniodental features referable to *Canis lupus*, such as the reduced protocone and a weak lingual cingulum of

P<sup>4</sup>, a weak buccal cingulum, a lingual cingulum that is subdued and often incomplete across paracone, and reduced hypocone basin of M<sup>1</sup>. In addition, the P<sup>4</sup>, the M<sup>1</sup> and the M<sub>1</sub> of *C. lupus* from Cava Bianco and Mirigliano Collection of Melpignano and from Cava L of San Sidero are biometrically closer to those from Middle Pleistocene French localities (e.g., Lunel-Viel, Igue des Rameux; *Canis lupus lunellensis* Bonifay, 1971), and smaller than those from Late Pleistocene Italian localities (e.g., Avetrana, Cardamone) (Tab. 4). On the other hand, isolated teeth from Cava Nuzzo of Melpignano and Fissure 1 and 2 of San Sidero are slightly larger than those from Middle Pleistocene French sites, and similar to those from Late Pleistocene Italian ones (Tab. 4).

#### *Felidae*

*Lynx* remains from MSS were referred to *Lynx lynx* (Linnaeus, 1758) by Bologna et al. (1994) and Bedetti et al. (2004) (Tab. 1). A recent study focused on lynx craniodental remains from Ingarano (southern Italy) has revealed the diagnostic characters that allow identification of *Lynx pardinus* (Temminck, 1827) (Mecozi et al. 2021a). At present, morphological features useful for lynx classification are found in the cranial and dental remains, while no clear skeletal character has yet been identified. The lynx remains from MSS are quite scarce, represented by postcranial material with the exception of a juvenile hemimandible from the Fissure 1 of San Sidero (Fig. 6e). These remains have a poor taxonomic value, and therefore we refer them to *Lynx* sp. (Tab. 3). The only dental specimen of *Lynx* was recovered from San Sidero E and is the first specimen reported from this deposit (Fig. 9; Tab.1). The IsIPU SS24 specimen consists of a lower left first molar (M<sub>1</sub>), and it clearly lacks the metaconid on the distal margin of the protoconid blade. The M<sub>1</sub> metaconid is generally absent or barely developed in fossil and extant *L. pardinus* (e.g., Ingarano, absent - 70.4%; weak metaconid - 29.6%; Mecozi et al. 2021a; extant specimens, absent - 83%; weak metaconid - 14%; García-Perea et al. 1985). A distinct M<sub>1</sub> metaconid has been observed in extant and fossil *L. lynx* (Kurtén 1963; Werdelin 1981, 1987). Following this, the IsIPU SS24 from San Sidero can be referred to *L. pardinus*.

Our review of the earliest published paleontological sample from Melpignano, namely the

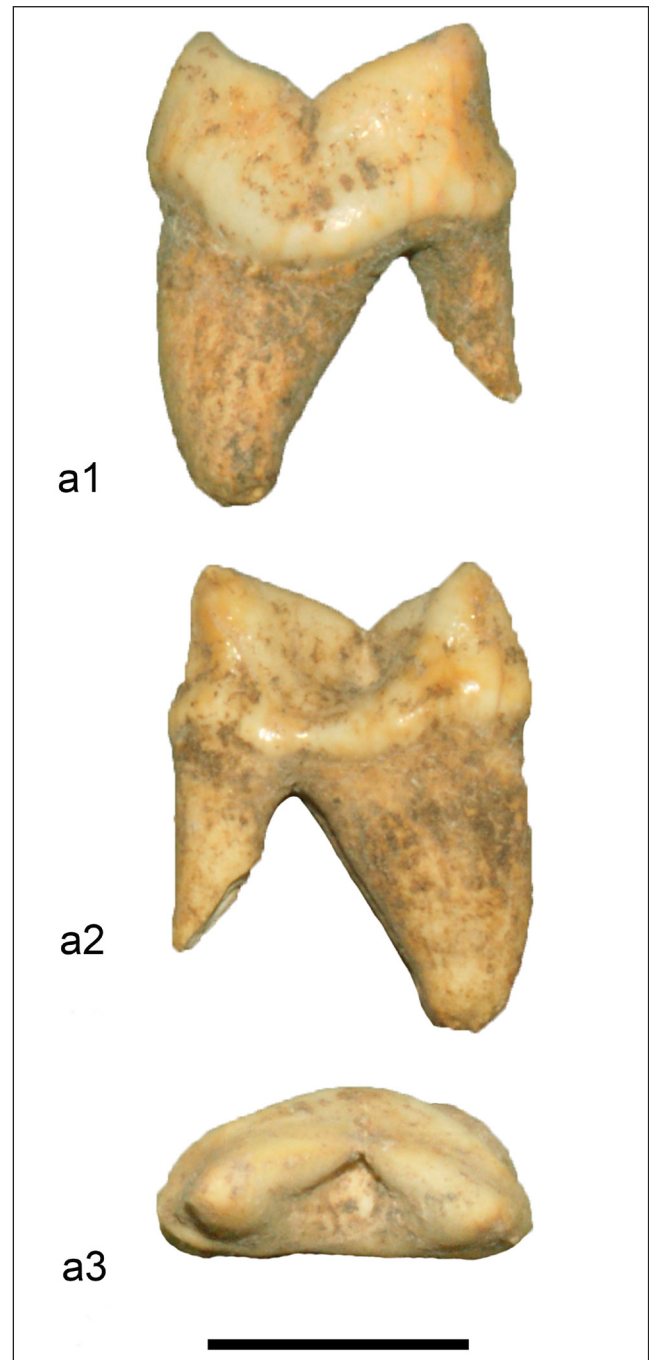


Fig. 9 - a) IsIPU SS24, lower first molar of *Lynx pardinus* from San Sidero E in labial (1), lingual (2) and occlusal (3) views. Scale bar 1 cm.

Mirigliano Collection, highlights that part of the material was recently lost and several species are no longer represented, such as *Lepus* sp. Pallas, 1775, *O. cuniculus*, *Ovis* sp. Linnaeus, 1758 and *Cervus elaphus*. In particular, *C. elaphus* was the most represented species reported by Mirigliano (1941) (Tab. 1), with 35 fossil remains (32%). Moreover, part of the samples of *S. hemitoechus*, *H. amphibius*, *Mustela putorius* (Linnaeus, 1758) and *C. lupus* are lost.

We also considered a small part of the Cardini Collection stored at the IsIPU, almost 50 years after its description (Cardini 1962). The material coming from “Cava Motta” of Melpignano, as well as most of the sample from San Sidero (=Sant’Isidoro), is stored at PPCMM and, unfortunately, it was not possible to include it in this work. Cardini (1962) reported a preliminary analysis of the vertebrate fossil materials recovered from these deposits, in which the most common species were *D. dama*, *B. primigenius* and *E. ferus* (Tab. 1). However, Cardini (1962) reported many fossils from the MSS deposit, while we have studied only a few specimens. This clearly limits our interpretation of these historical collections.

## DISCUSSION

### The infilling sediments of “ventarole”

Despite the consensus in considering “terre rosse” and “terre brune” as two distinct sedimentary units at MSS, there is no clear separation between the analyzed samples, either in particle size (Fig. 4), or in mineralogical composition (Fig. 5). Macroscopic observations did not allow us to distinguish different facies. On the basis of the performed analyses, the most relevant difference between “terre rosse” and “terre brune” is the organic carbon content, which may be responsible of the different coloring. In “terre brune”, the relatively large percentage of measured organic carbon (0.47-0.53 wt. %) could give the brownish color to the deposit; this could be related to a cool and relatively dry paleoclimate phase when slow decomposition of organic matter allowed the storage of organic material. The lower content of organic carbon measured in “terre rosse” (0.08-0.09 wt. %) may suggest a pedogenic process referable to a hot and relatively humid paleoclimate phase.

The XRD analysis (Fig. 5) of the infilling sediments shows that they are composed of quartz and a minor amount of kaolinite and hydroxyapatite. Illite and montmorillonite are also present and particularly abundant in one sample (Mel10, from “terre rosse”) which is characterized by a marked clayey texture (Tab. 2). Hydroxyapatite is probably derived from deterioration of the vertebrate remains. For comparison, mineralogical composition of soil and sediment from different Apulian sites are reported in Table 5. The infilling sediments of “ventarole” are

compositionally comparable to the local soil, Terra Rossa-type (Cortesi 1958) or Red Mediterranean soils (Vingiani et al. 2018 and reference therein), suggesting local derivation of the “ventarole” sediments by re-sedimentation of the overlying soil. Soil can be transported inside the cavities as a result of diverse processes, such as vertical colluviation and runoff. In the case of the “ventarole”, the sedimentation is attributed to vertical colluviation of the soil from the surface within the karst features (Pandolfi et al. 2017). The lack of other kinds of sediments (e.g., speleothems, coarse gravel) and of definite sedimentary structures suggests that sedimentation from running water has been of limited importance.

In the relevant literature (e.g., Bologna et al. 1994), the correlation between the “ventarole” deposits and other stratigraphic sequences (in particular that of Grotta Romanelli), which allowed their chronological definition, was mainly based on the coloration of sediments. Therefore, a direct comparison between mineralogy and texture of the “ventarole” sediments and infilling sediments of Grotta Romanelli (Cortesi 1958; Giustini et al. 2018) was performed (Tab. 5 and Fig. 4b). The mineralogical composition of Grotta Romanelli sediments, mainly consisting of quartz, grossly matches that of the “ventarole”, whereas the grain size is slightly enriched in clay. In Grotta Romanelli the grain size selection is probably linked to runoff processes from the exterior of the cave.

Therefore, the chronological definition of the “ventarole” cannot be made merely on the basis of correlation with this stratigraphic sequence but should be evaluated on the basis of the study of their faunal assemblages.

### Faunal assemblages from the “ventarole”

Despite decades of research on the mammal faunal remains from the fossiliferous area of Maglie, two main issues remain unresolved. The first is about the specific attribution of the bovid remains, due to the strong morphological similarities between *Bos primigenius* and *Bison priscus*. Revision of the old collections, including the fossils described by Bologna & Petronio (1994), and the study of the new ones do not support the presence of *B. priscus*, as previously reported.

The second concerns the possible persistence of Middle Pleistocene taxa in southern Italy during the earliest Late Pleistocene, including *Canis mosba-*



Site	Sample description	Site description	Mineralogy	Reference
Melpignano	"terre brune" sediment (sample Mel3)	"ventarola"	dominated by quartz, with minor amount of kaolinite, hydroxyapatite	This work
Melpignano	"terre rosse" sediment (sample Mel10)	"ventarola"	dominated by quartz, with minor amount of kaolinite, illite, montmorillonite, hydroxyapatite	This work
San Sidero	"terre brune" sediment (sample SS13)	"ventarola"	dominated by quartz, with minor amount of kaolinite, hydroxyapatite	This work
San Sidero	"terre rosse" sediment (sample SS2)	"ventarola"	dominated by quartz, with minor amount of kaolinite, hydroxyapatite	This work
Grotta Romanelli	"terre rosse" sediment (Pleistocene)	Grotta Romanelli (Apulia)	dominated by quartz, with minor amount of chalcedony, glauconite, feldspars, kaolinite, oxides, hydroxides	Cortesi (1958)
	"terre brune" sediment (Late Pleistocene-Early Holocene)		dominated by quartz, with minor amount of calcite, plagioclase, feldspar, clay minerals of the illite and kaolinite groups	Giustini et al. (2018) Calcagnile et al. (2019)
Santa Cesarea	Local red soil	Non-cultivated area, 15km SE of Melpignano-San Sidero	dominated by quartz, with minor amount of chalcedony, glauconite, feldspars, kaolinite, oxides, hydroxides	Cortesi (1958)
Several sites	82 samples of carbonate-free terra rossa, from deep deposits (entirely enclosed in Cretaceous carbonate rocks, or covered by Pliocene-Pleistocene calcarenites) and superficial deposits	Murge, Salento and Gargano areas (Apulia)	dominated by kaolinite, illite, Fe-oxides, with minor amount of quartz, feldspar, mica, Al-oxides and hydroxides, Ti-oxides	Moresi & Mongelli (1988)
Several sites	69 samples of insoluble residue from Cretaceous carbonate rocks	Murge and Salento areas (Apulia)	dominated by illite, kaolinite, Fe-oxides, with minor amount of quartz, feldspar, mica, Al-oxides and hydroxides, Ti-oxides	Moresi & Mongelli (1988)

Tab. 5 - Mineralogical compositions of soil and sediment from different Apulian sites.

*chensis* (Masini et al. 1991; Sala et al. 1992). The taxonomic attribution of the canid remains from MSS and other early Late Pleistocene sites of southern Italy (e.g., Grotta Romanelli) has been debated among paleontologists (Masini et al. 1991; Sala et al. 1992; Sardella et al. 2014; Mecozzi & Bartolini Lucenti 2018; among others). According to Sardella et al. (2014), the wolf specimens from the late Middle to Late Pleistocene deposits of Apulia can be referred to *C. lupus* (fossils from MSS are part of the "Apulian wolves" group). Our analysis confirms this hypothesis, excluding the presence of *Canis mosbachensis* in MSS deposits. The medium-sized wolf specimens from Cava Bianco and Mirigliano Collection of Melpignano and from Cava L of San Sidero fall within the range of variation of the late Middle Pleistocene *C. lupus lunellensis*, and are the earliest representatives of this species in Europe (Brugal & Boudadi-Maligne 2011). In contrast, the fossils from Cava Nuzzo of Melpignano and Fissure 1 and Fissure 2 of San Sidero are slightly larger than those

from Middle Pleistocene French sites and other cavities of MSS and are more similar to those from Late Pleistocene Italian sites (e.g., Brugal & Boudadi-Maligne 2011; Mecozzi & Bartolini Lucenti 2018; Tab. 4).

Our review has for the first time identified the Clacton deer *Dama clactoniana* from the "terre rosse" of Cava Nuzzo, Cava della Terra and Cava Bianco of Melpignano and Cava L of San Sidero, while other remains from "terre rosse" of SS7, Fissure 1 and 2 from San Sidero are referred to the fallow deer *D. dama*. Although two fallow deer species are here recognized, no coexistence hypothesis is proposed. In fact, the fossils from Cava Nuzzo, Cava della Terra and Cava Bianco of Melpignano and Cava L of San Sidero are biochronologically attributed to late Middle Pleistocene, while those from SS7, Fissure 1 and 2 from San Sidero are attributed to Late Pleistocene (see Biochronological framework of Apulia).

Another taxon identified for the first time from the "terre rosse" of MSS is the pardel lynx,

*L. pardinus* represented by IsIPU SS24 from San Sidero E. The occurrence of this carnivoran in MSS deposits represents its southernmost record in the Italian Peninsula and the easternmost in Europe. This also confirms that the paleoecological conditions along the coast of the Adriatic and Ionian Sea, which were probably dominated by Mediterranean ecosystems (shrublands with scrub-pasture ecotones), were favorable to the presence of the pardel lynx. However, the review of San Sidero E fossils is needed to obtain clear information on its biochronological and paleoecological context.

Finally, the taxonomy of the hippopotamus remains has been revised. Fossils from MSS have been previously classified as *H. amphibius* (De Lorenzo & D'Erasmus 1935) or *Hippopotamus* cf. *antiquus* (Mazza 1995). Unfortunately, the sample from MSS consists of quite fragmentary fossils with poor diagnostic value, and therefore are conservatively referred to *Hippopotamus* sp.

#### Biochronological framework of Apulia

Previous studies hypothesized that the faunal assemblage from “terre rosse” of the MSS “ventarole” can be referred to the early Late Pleistocene (MIS 5e) (Mirigliano 1941; De Giuli 1983). Other authors suggested instead that this faunal assemblage could be slightly younger (MIS 5c-5a; Bologna 1992; Bologna et al. 1994; Bedetti et al. 2004). The chronological attribution of the MSS mammal fauna has been linked to the stratigraphic scheme defined for the Grotta Romanelli sequence as described by Blanc (1920), in which the lower complex – including “terre rosse” – was referred to the beginning of the Late Pleistocene because it directly overlies a “Tyrrhenian” beach” (MIS 5e). In 2015, a new field campaign started on this key site, with the aim to define a more accurate chronological scheme for the sequence, and a possible Middle Pleistocene age for the lower complex cannot be ruled out (Sardella et al. 2018, 2019; Mecozzi et al. 2021b).

The fossil sample from MSS “terre rosse” include two species referable to the Middle Pleistocene, *D. clactoniana* and *E. mosbachensis* (Palombo 2018). The Clacton fallow deer is a typical form of the Galerian LMA, and its last occurrence is recorded in the Torre in Pietra FU (early Aurelian) (Gliozzi et al. 1997; Palombo 2018). Unfortunately, the taxonomy of European Middle-Late Pleistocene *Equus* is still debated (Forstén 1991; van Asperen 2012).

Despite this, based on the European fossil record, *E. mosbachensis* is the first caballine equid that appears in the early Middle Pleistocene (Eisenmann et al. 1985; Langlois 2005). In the Italian fossil record, late Middle Pleistocene horses are usually referred to *E. mosbachensis*, whereas the Late Pleistocene ones are referred to *E. ferus germanicus* (Rustioni 1998). Although the debate is still ongoing, mtDNA analysis has revealed that *E. ferus* originated during the late Middle Pleistocene (George & Ryder 1986) thus supporting the validity of an archaic form, *E. mosbachensis*. However, Orlando et al. (2013) confirmed the separation of the modern *Equus* forms during the early Middle Pleistocene, and the position of *E. mosbachensis* and its relationship with Middle Pleistocene horses therefore needs to be clarified.

During the late Middle Pleistocene, a global climatic cooling trend started, culminating in the Last Glacial Maximum (MIS 2; Ramstein et al. 1997; Kahlke 2014), producing drastic environmental changes that deeply affected the structure of the faunal assemblages (Gliozzi et al. 1997). In the Late Pleistocene, mammal assemblages are relatively less diversified than those of earlier times (Gliozzi et al. 1997; Petronio et al. 2007). Several mammal remains from the Middle to Late Pleistocene deposits of Apulia are described in the literature (Tab. 6). Among these, the fossils from the karst filling of Contrada Monticelli are the only ones that have been biochronologically referred to the early Middle Pleistocene (Mazza & Varola 1999; Mecozzi et al. 2017; Stefanelli et al. 2021). The mammal list from this site includes the straight-tusked elephant, equids, bovids, *Dama* cf. *roberti* Breda & Lister, 2013, *Stephanorhinus hundsheimensis* Toula, 1902 and *C. mosbachensis*.

However, due to impoverishment of mammal communities during the late Middle Pleistocene to Early Holocene, only a few bioevents may be useful for biochronological correlations, such as the disappearance of *Hippopotamus* and *Palaeoloxodon*. In fact, the presence of the hippo and the straight-tusked elephant in the Italian Peninsula has been mainly reported from localities chronologically related to the late Middle Pleistocene (Mazza 1995; Caloi et al. 1998; Braun & Palombo 2012; Mazza & Bertini 2013; Petronio & Pandolfi 2015; Pandolfi et al. 2018; Palombo 2018). Doubtful occurrences of these taxa after MIS 5 have been reported from few Italian deposits: the co-occurrence of hippo

and elephant was recognized at Grotta Romanelli lower complex (Blanc 1920), Ingarano (Petronio & Sardella 1998), Canale Mussolini (=Canale della Acque Alte; Caloi & Palombo 1995; Farina 2011) and Grotta Guattari (Stiner 1992; Caloi & Palombo 1995; Alhaique & Tagliacozzo 2000), whereas only hippo specimens were found at Avetrana (beds 1-7; Salari et al. 2019 and references therein) and Grotta dei Moscerini (Alhaique & Tagliacozzo 2000). As mentioned above, a late Middle Pleistocene age of the lower complex of Grotta Romanelli cannot be ruled out (Sardella et al. 2018, 2019). The specimens from Ingarano were recovered outside the stratigraphic context of the site, and therefore their age is uncertain (Petronio & Sardella 1998). The fossil collection from the historical site of Canale Mussolini includes different species from the Late Pleistocene to the Holocene, with no exact stratigraphic provenance (Farina 2011). However, radiometric dating provided an age older than 54 ka for the lower part of the succession (Farina 2011; Braun & Palombo 2012). The data on the fossil material from Grotta Guattari are difficult to interpret, complicated by the lack of stratigraphic information (Stiner 1992). The radiometric (U-series) and ESR dating performed by Schwarcz et al. (1991) are also problematic, with different ages obtained for samples from the same level. Caloi & Palombo (1995) referred the faunal assemblage to MIS 5a or to the beginning of MIS 4. Finally, according to Marra et al. (2020) the new radiometric dating and stratigraphic data suggest that the deposit can be mainly referred to early Late Pleistocene. Recently, an early Late Pleistocene age was confirmed by Salari et al. (2019) for Avetrana. The site of Grotta dei Moscerini also has been recently constrained to the early Late Pleistocene by Marra et al. (2020). According to this evidence, the persistence of *Hippopotamus* and *Palaeoloxodon* later than MIS 5 is questionable (Masini & Sala 2011; Braun & Palombo 2012). On the other hand, the occurrence of these taxa, often associated with *S. hemitoechus* and fallow deer species (*D. clactoniana* or *D. dama*), characterized the late Middle Pleistocene - earliest Late Pleistocene mammal assemblages of the Mediterranean area (e.g., Grotta del Sarcofago, Grotta delle Striare) (Tab. 6).

In sum, the literature reveals that the mammal assemblages from the Apulian fossiliferous sites considered could confirm a Middle to earliest Late Pleistocene (MIS 5) presence of the straight-

tusked elephant and hippopotamus (Tab. 6). The disappearance of these two taxa is probably due to the progressive climatic deterioration of the Last Glacial period. Furthermore, in the Apulian deposits chronologically referred to MIS 4 – MIS 3, the rhinoceros and fallow deer do not occur or are less frequent, and no record of these taxa are reported during the MIS 2 (Tab. 6).

In this scenario, our results suggest that the age of the mammal fauna from “terre rosse” of the MSS “ventarole” can be chronologically referred to a wide timespan, contrary to what was previously supposed. The presence of *E. mosbachensis*, *D. clactoniana* and medium-sized *C. lupus* (*C. lupus lunellensis sensu* Bonifay 1971), together with *P. antiquus* and *Hippopotamus*, allows us to ascribe the mammal assemblages from “terre rosse” of Mirigliano Collection, Cava Nuzzo, Cava della Terra and Cava Bianco of Melpignano and Cava L and SS6 of San Sidero to the late Middle Pleistocene (Torre in Pietra FU; MIS 9-8). On the other hand, the faunal assemblages from “terre rosse” of other karst deposits, such as Fissure 1 and 2 of San Sidero, are similar to those reported from Fondo Cattie and Sternatia, both chronologically referred to MIS 3. These faunal assemblages include *D. dama*, *E. ferus* and large-sized *C. lupus*, whereas *P. antiquus* and *Hippopotamus* are absent. Therefore, these latter faunal assemblages can be referred to the Late Pleistocene (MIS 3). Finally, the mammal fauna from “terre rosse” differs from that described by Pandolfi et al. (2017) for the “terre brune”, which include *Homo sapiens*, *Bos taurus* Linnaeus, 1758, *Ovis aries* Linnaeus, 1758 vel *Capra hircus* Linnaeus, 1758, and *Canis* sp. (Tab. 6). Radiometric dating carried out on human and faunal remains from “terre brune” deposits revealed an Early Holocene age (Pandolfi et al. 2017).

### The “Melpignano Faunal Unit”

The Aurelian LMA of the Italian biochronological scale based on large mammals was established by Gliozzi et al. (1997) and includes the FUs of Torre in Pietra (MIS 9) and Vitinia (MIS 7). During the Aurelian LMA, a marked renewal of the mammal fauna occurred, where several Galerian taxa became extinct, such as for example the large-sized deer *Praemegaceros* (Gliozzi et al. 1997). In the Torre in Pietra FU, the core of the modern European mammal fauna appeared for the first time with the first occurrence of *C. lupus*, *Ursus spelaeus* Rosen-

Species	Gargano Promontory		Murge		Salentine Peninsula																			
	GBS	GP	CS	TI	RO	Car	Stie	GC			Salentine Peninsula						Mel	FC	Gsa	Gst	GM	GTP		
Level	22-24		8	1-9	Car	Stie	N-M	L-I	H	F	E	Mel Coll. Mirigliano	Mel Cava Nuzzo	Mel Cava Bianco	SS Cava L.	SS Fissure 1	SS Fissure 2	SS SS6	Mel Cava Donnò	FC Gsa	Gst	GM	GTP	
Dating	Lower	Upper	< 6000	42724	> 39000	> 109100	> 45700	> 39850	> 109100	> 45700	> 39850	> 109100	> 45700	> 39850	> 109100	> 45700	> 39850	> 109100	> 45700	> 39850	> 109100	> 45700	> 39850	> 109100
	26500 ± 300	26500 ± 300	> 39000	± 716	> 39000	> 109100	> 45700	> 39850	> 109100	> 45700	> 39850	± 900	± 1000	± 140	± 900	± 1000	± 140	± 900	± 1000	± 140	± 900	± 1000	± 140	± 900
<i>Palaeoxodon antiquus</i>						X						X	X	X	X	X	X	X				X	X	X
<i>Mammuthus primigenius</i>												X	X	X	X	X	X	X				X	X	X
<i>Stephanorhinus hemitoechus</i>												X	X	X	X	X	X	X				X	X	X
<i>Stephanorhinus kirchbergensis</i>												X	X	X	X	X	X	X				X	X	X
<i>Stephanorhinus sp.</i>												X	X	X	X	X	X	X				X	X	X
<i>Coelodonta antiquitatis</i>												X	X	X	X	X	X	X				X	X	X
<i>Equus hydruntinus</i>												X	X	X	X	X	X	X				X	X	X
<i>Equus mosbacherensis</i>												X	X	X	X	X	X	X				X	X	X
<i>Equus ferus</i>												X	X	X	X	X	X	X				X	X	X
<i>Sus scrofa</i>												X	X	X	X	X	X	X				X	X	X
<i>Hippopotamus sp.</i>												X	X	X	X	X	X	X				X	X	X
<i>Hippopotamus amphibius</i>												X	X	X	X	X	X	X				X	X	X
<i>Capra ibex</i>												X	X	X	X	X	X	X				X	X	X
<i>Ovis aries vel Capra hircus</i>												X	X	X	X	X	X	X				X	X	X
<i>Rupicapra rupicapra</i>												X	X	X	X	X	X	X				X	X	X
<i>Rupicapra sp.</i>												X	X	X	X	X	X	X				X	X	X
<i>Bos primigenius</i>												X	X	X	X	X	X	X				X	X	X
<i>Bos taurus</i>												X	X	X	X	X	X	X				X	X	X
<i>Carviidae</i>												X	X	X	X	X	X	X				X	X	X
<i>Capreolus capreolus</i>												X	X	X	X	X	X	X				X	X	X
<i>Dama clactoniana</i>												X	X	X	X	X	X	X				X	X	X
<i>Dama dama</i>												X	X	X	X	X	X	X				X	X	X
<i>Canis elaphus</i>												X	X	X	X	X	X	X				X	X	X
<i>Ursus spelaeus</i>												X	X	X	X	X	X	X				X	X	X
<i>Canis lupus</i>												X	X	X	X	X	X	X				X	X	X
<i>Canis sp.</i>												X	X	X	X	X	X	X				X	X	X
<i>Canis alpinus</i>												X	X	X	X	X	X	X				X	X	X
<i>Vulpes vulpes</i>												X	X	X	X	X	X	X				X	X	X
<i>Felis silvestris</i>												X	X	X	X	X	X	X				X	X	X
<i>Lynx pardinus</i>												X	X	X	X	X	X	X				X	X	X
<i>Lynx lynx</i>												X	X	X	X	X	X	X				X	X	X
<i>Lynx sp.</i>												X	X	X	X	X	X	X				X	X	X
<i>Panthera pardus</i>												X	X	X	X	X	X	X				X	X	X
<i>Panthera spelaea</i>												X	X	X	X	X	X	X				X	X	X
<i>Panthera leo</i>												X	X	X	X	X	X	X				X	X	X
<i>Crocodylus spelaea</i>												X	X	X	X	X	X	X				X	X	X
<i>Crocodylus crocota</i>												X	X	X	X	X	X	X				X	X	X
<i>Mustelidae</i>												X	X	X	X	X	X	X				X	X	X
<i>Meles meles</i>												X	X	X	X	X	X	X				X	X	X
<i>Mustela putorius</i>												X	X	X	X	X	X	X				X	X	X
<i>Mustela nivalis</i>												X	X	X	X	X	X	X				X	X	X
<i>Martes martes</i>												X	X	X	X	X	X	X				X	X	X
<i>Hystrix brachyura vinogradovi</i>												X	X	X	X	X	X	X				X	X	X
<i>Oryctolagus cuniculus</i>												X	X	X	X	X	X	X				X	X	X
<i>Lepus europaeus</i>												X	X	X	X	X	X	X				X	X	X
<i>Lepus timidus</i>												X	X	X	X	X	X	X				X	X	X
<i>Lepus sp.</i>												X	X	X	X	X	X	X				X	X	X

Tab. 6 - Late Pleistocene mammal taxa from selected localities of the Apulian Peninsula: GBS, Grotta B di Spagnoli; GP, Grotta Paglicci; CS, Cava Spagnoli; TI, Tana delle Iene; RO, Riparo l'Oscurasciuto; Car, Cardamone; Ste, Sternatia; GC, Grotta del Cavallo; Mel, Melipignano; SS, San Sidero; FC, Fondo Cattìe; Gsa, Grotta del Sarcofago; Gst, Grotta delle Strate; GM, Grotta Montani; GTP, Grotta delle Tre Porte.

müller, 1794 and *Megaloceros giganteus* Blumenbach, 1799 (Gliozzi et al. 1997). The Vitinia FU is marked by the first occurrence of *Dama dama tiberina* Di Stefano & Petronio, 1997 and *Equus hydruntinus* Regalia, 1907 (Gliozzi et al. 1997). Palombo et al. (2004) carried out a stratigraphic re-assessment of the outcrops in the urban area of Rome attributed to the Vitinia FU (Sedia del Diavolo, Monte delle Gioie), where *D. dama tiberina* and *E. hydruntinus* occurred. In addition to the description of these new outcrops and new radiometric dating, the authors suggested a revision of the Aurelian biochronological scheme. In fact, the revision of Sedia del Diavolo and Monte delle Gioie provided an age between 355 and 285 ka (Palombo et al. 2004). The comparative analysis of the faunal complexes ascribed to the Torre in Pietra and Vitinia FUs highlighted strong similarities, especially the coexistence of *D. clactoniana* and *D. dama tiberina* (Palombo et al. 2004). Recently, the mammal fauna of Ponte Molle (Rome, central Italy), type locality of *D. dama tiberina* Di Stefano & Petronio, 1997 has been revised by Mecozzi et al. (2021c). In this revision, the material from Ponte Molle has been attributed to *D. clactoniana*, which makes the use of *D. dama tiberina* subspecies inconsistent (Mecozzi et al. 2021c).

Petronio et al. (2007) proposed a revision of the late Aurelian biochronological scheme, with the introduction of two new FUs, Melpignano and Ingarano. In particular, the former FU would be marked by the first occurrences of *C. elaphus elaphus* and *D. dama dama* (Petronio et al. 2007), corresponding to the beginning of the Late Pleistocene. However, there is consensus in avoiding the use of the FU concept in the late Aurelian, due to monotonous taxonomic composition of fossil mammal assemblages with a sporadic occurrence of taxa of cold environments (*Mammuthus* and *Coelodonta*) (Gliozzi et al. 1997; Palombo 2009; Masini & Sala 2011). During the Pleistocene, the Italian Peninsula was characterized, as it is today, by marked regional climatic differences due to its peculiar physiography (see Manzi et al. 2011 for discussion). These factors resulted in a heterogeneity of climatic and environmental conditions, which led to asynchrony in mammal dispersal events (Gliozzi et al. 1997; Masini & Sala 2011).

The revision of several mammal fossil collections from “terre rosse” of MSS reveals the presence of assemblages of different ages that can be

biochronologically placed in a time span between the late Middle Pleistocene (MIS 9-8) and the Late Pleistocene (MIS 3). Therefore, our results further discourage the use of the Melpignano FU as a formal biochron (Fig. 10).

Finally, some authors have advocated a weak effect of endemism, even “insularism”, given the relatively isolated position of Apulia, to explain size differences observed in some species (Petronio & Pandolfi 2008; Pandolfi & Petronio 2011; Iurino 2014). In particular, an insularism effect has been proposed for small-sized *S. hemitoechus*, since the age of the remains was considered to be early Late Pleistocene (Pandolfi & Petronio 2011). However, in the light of the revised chronology of the MSS faunal assemblages from “terre rosse”, “insularism” or endemism for the Apulian mammals should be carefully tested. For example, the size of *S. hemitoechus* from “terre rosse” of Cava Nuzzo and Cava Bianco is perfectly consistent with the revised Middle Pleistocene age.

## CONCLUSIONS

Karst fissures, locally called “ventarole”, are located in the Maglie area where several quarries, still working today, are used for the extraction of the Miocene Pietra Leccese. Through the Quaternary the “ventarole” were progressively filled by vertebrate bone remains and sediments. In the paleontological literature, a simple differentiation based on color of the sediment was commonly accepted: “terre rosse” deposited during the early Late Pleistocene and “terre brune” during the Late Pleistocene – Early Holocene. Textural and mineralogical analyses performed on the infilling sediments of the “ventarole” indicate no clear separation between “terre rosse” and “terre brune” samples, either in particle size or in composition, and thus led us to reject this color-based division. The only difference between “terre rosse” and “terre brune” sediment is the organic carbon content, with the latter characterized by highest values.

The study of new fossil materials, as well as the re-evaluation of the old collections, allowed us to update the faunal list of the Melpignano and San Sidero sites, confirming the occurrence of *Bos primigenius*, *Canis lupus*, *Lynx pardinus* and two non-coeval species of fallow deer, *Dama dama* and *Dama clac-*

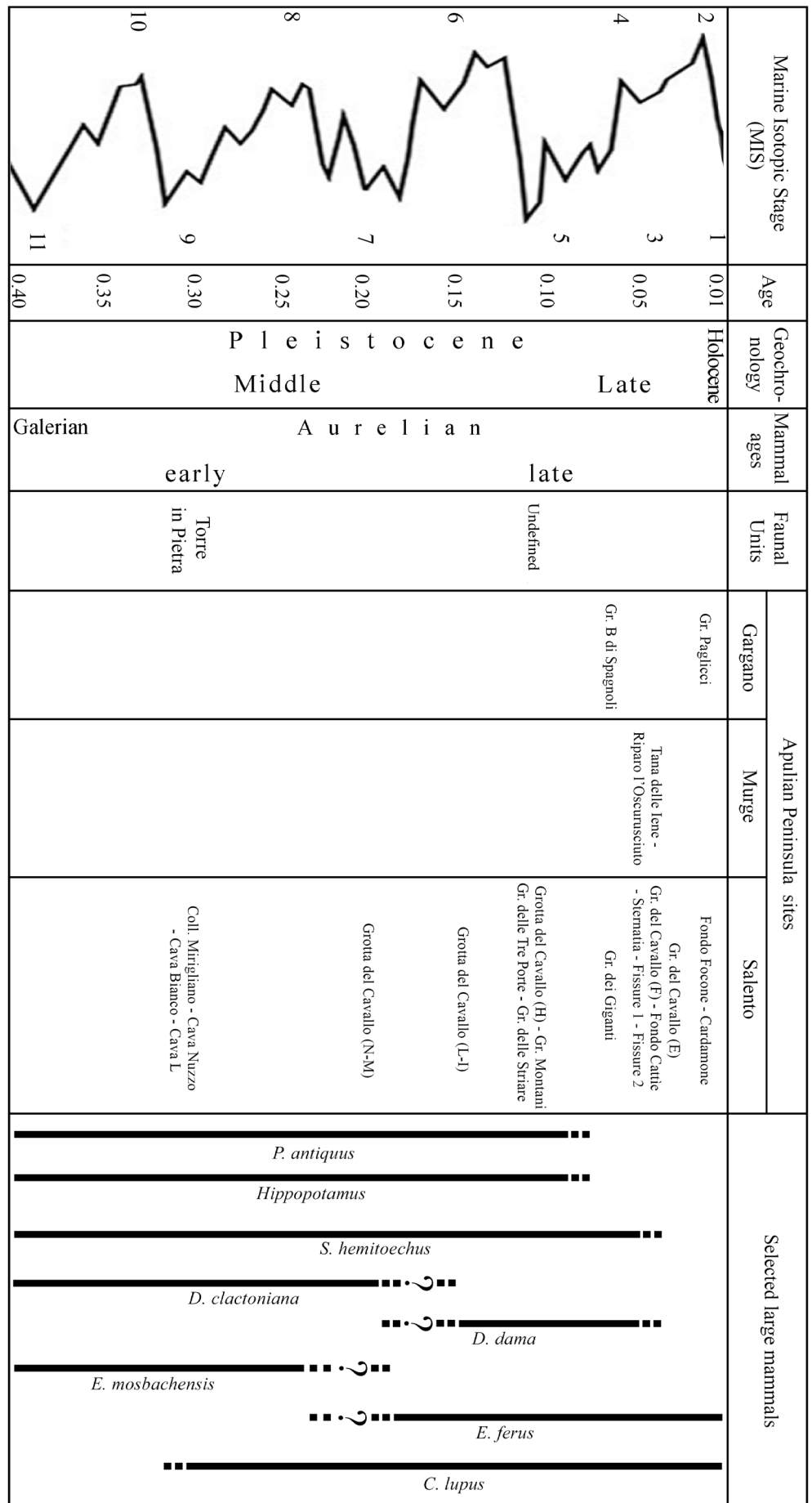


Fig. 10 - Biochronological scheme of the Middle-Late Pleistocene sites of Apulia.

*toniana*. The hippopotamus remains have been also revised and conservatively referred to *Hippopotamus* sp. since the sample from MSS consists of quite fragmentary fossils of poor diagnostic value.

The taphonomic analysis of the MSS fossils from “terre rosse” suggests no evidence of human activity, nor modifications by carnivores or rodents, except for three remains of *Bos primigenius* and one of *Stephanorhinus hemitoechus*.

The study and comparison of the mammal fauna from MSS allow to redefine the chronology of these deposits, taking into account that the fossil remains from each “ventarola” (karst fissure) should be considered as a single assemblage. For a long time the subdivision of MSS deposit into “terre rosse” and “terre brune” has been used. As such, the fossil remains from different “ventarole” have been considered as part of two distinct stratigraphical levels, “terre rosse” and “terre brune”, with a well-defined chronological framework. Our results highlight that the mammal assemblages from these karst fissures encompass a chronological time span longer than generally supposed. If some faunal assemblages are certainly referable to the Late Pleistocene (MIS 3), as Fissure 1 and Fissure 2 from San Sidero, others include taxa such as *D. clactoniana* and *E. mosbachensis*, thus suggesting a Middle Pleistocene age (MIS 9-8), as in the cases of Mirigliano Collection, Cava Nuzzo, Cava Bianco, Cava della Terra of Melpignano and Cava L and SS6 of San Sidero. Our revision finally underlines that the faunal assemblages from the MSS “ventarole” can be attributed to a long-time deposition (late Middle Pleistocene to Late Pleistocene), which implies the rejection of Melpignano as a valid FU for the Aurliean LMA.

*Acknowledgments:* The Soprintendenza Archeologia, Belle Arti e Paesaggio delle province di Brindisi, Lecce e Taranto provides the permission to study the fossils.

We are grateful to Maria Carmela Del Re (Paleontology Museum of the University of Naples Federico II), Elisabetta Cioppi (Museum of Geology and Paleontology of the University of Florence) and Marco Pavia (Paleontology Museum of the University of Turin), for the access to museum collections and for their precious technical support. The authors wish to thank the IsIPU (Istituto Italiano di Paleontologia Umana, Anagni) and in particular Luciano Bruni and Stefano Grimaldi for the access to fossil collection. Special thanks are due to Daniele Passeri and Francesca Trapasso (CNR-IGAG) for grain size and XRD analyses, respectively. Finally, we wish also to thank Eugenio Cerilli, Jacopo Conti, Luca Forti, Alessia Leggio and Antonio Profico for their useful suggestions and help. A special thank to Carmelo Petronio for conducting several fieldwork activities in the fossiliferous area of Maglie.

This work was supported by Grandi Scavi 2016 (ref. SA116154CD9592F3), Grandi Scavi 2017 (ref. SA11715C81468801), Grandi Scavi 2018 (ref. SA1181642D3B3C58), Grandi Scavi 2019 (ref. SA11916B513E7C4B) of Sapienza University of Rome, resp. Raffaele Sardella.

We thank Barthelemy Giannetti, Federico Ciavatta, Cristina Tosca, Gianluigi Neri, Angelo Perfetto and Edoardo Terranova for their valuable help in laboratory activities and preliminary classification of fossils from Melpignano and San Sidero localities. Finally, we would like to thank the editor, Lars Werdelin, and two anonymous reviewers for their constructive and useful comments.

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