


Human occupation continuity in southern Italy towards the end of the Middle Palaeolithic: a palaeoenvironmental perspective from Apulia

FRANCESCO BOSCHIN,^{1,2} ANDREA COLUMBU,^{3*}  VINCENZO SPAGNOLO,^{1,2} JACOPO CREZZINI,^{1,2} JEAN-JACQUES BAHAIN,⁴ CHRISTOPHE FALGUÈRES,⁴ STEFANO BENAZZI,⁵ PAOLO BOSCATO,¹ ANNAMARIA RONCHITELLI,¹ ADRIANA MORONI^{1,2} and IVAN MARTINI¹

¹Dipartimento di Scienze Fisiche, della Terra, e dell'Ambiente, Università Degli Studi di Siena, Siena, Italy

²Centro Studi sul Quaternario, Sansepolcro, Arezzo, Italy

³Dipartimento di Scienze Biologiche, Geologiche e Ambientali, Università di Bologna, Bologna, Italy

⁴HNHP, UMR7194 'Histoire naturelle de l'Homme préhistorique', MNHN-CNRS-UPVD, Département Homme et Environnement du Muséum National d'Histoire Naturelle 1, Paris, France

⁵Dipartimento di Beni Culturali, Università di Bologna, Ravenna, Italy

Received 12 August 2020; Revised 7 January 2021; Accepted 9 April 2021

ABSTRACT: After the last interglacial [Marine Isotope Stage (MIS) 5e] Europe was affected by several harsh climatic oscillations. In this context southern Italy acted, like the rest of peninsular Mediterranean Europe, as a 'glacial refugium', allowing the survival of various species, and was involved in the spread of 'cold taxa' (e.g. woolly mammoth and woolly rhino) only during the coldest phases (MIS 4 and MIS 2). Both late Mousterian and early Upper Palaeolithic sites testify to a human occupation continuity in southern Italy and especially in Apulia in this time span. Here we present a focus on three key Apulian Palaeolithic sequences (Grotta di Santa Croce, Riparo L'Oscurusciuto and Grotta del Cavallo – layers F-E) jointly spanning from the late MIS 4 to the demise of Neanderthals around 43 ka. Novel chronological, sedimentological and zooarchaeological data are discussed for the first time in the light of the palaeoenvironmental information provided by recent analyses carried out on a speleothem from Pozzo Cucù cave (Bari) and the results of the magnetic susceptibility analysis from Riparo L'Oscurusciuto. This integrated reading allows a better understanding of the role played by the Apulian region as both a refugium for late Neanderthals and a suitable habitat for the early settling of modern humans. © 2021 The Authors. *Journal of Quaternary Science* Published by John Wiley & Sons Ltd.

KEYWORDS: Middle to Upper Palaeolithic transition; MIS 3; refugia; southern Italy

Introduction

Recent genetic studies indicate that European Neanderthals faced drastic demographic crises during the last phases of their history. Genetics points to possible local extinctions of some Neanderthal lineages and to a later spread of other groups into the newly unpopulated areas. Since available data are still scarce, the dynamics of population turnovers after 60 ka BP are still unclear (Hajdinjak *et al.*, 2018), but the proposed scenarios imply a demographic reduction during Marine Isotope Stage (MIS) 3, when Europe experienced rapid climatic oscillations on millennial to centennial scale (Hemming, 2004; Long and Stoy, 2013). Regardless of what the more reliable re-colonization scenario is, the existence of one or more refugia – which fostered resilience of Neanderthal populations – must be postulated. Refugia guaranteed survival of taxa and preservation of biodiversity when Pleistocene glacial–interglacial cycles shaped the European ecological setting (Ordonez and Svenning, 2017; Morales-Barbero *et al.*, 2018). Several areas, like Iberia, the Italian peninsula, southern Balkans, the Carpatian basin and the Atlantic French margin, are considered to have acted as important refugia for more thermophilous/temperate species, whose geographical distribution contracted southwards during the coldest phases (e.g. Sommer and Zachos, 2009). Noteworthy, refugia should have also guaranteed the persistence of the species during warmer phases (e.g. Bennett *et al.*, 1991).

The Italian peninsula played this role during MIS 2 both for flora (Petit *et al.*, 2002) and for fauna (Sommer and Benecke, 2005), and available data (although scanty) suggest similar circumstances also in earlier phases (MIS 5–3). For instance, the persistence and survival of several arboreal taxa occurred during the whole Late Pleistocene during both stadial and interstadial phases (e.g. Allen *et al.*, 2000; Ricci Lucchi, 2008; Allen and Huntley, 2009). Considering continental large mammals, on which data are more abundant, Late Pleistocene faunal associations from Italy fall within the Late Aurelian age, an assemblage difficult to define due to the regional fragmentation and the lack of representative faunal units (Masini and Sala, 2011). In a first phase, corresponding to the Last Interglacial and to the first MIS 5 cooling stages, species more adapted to warm conditions spread throughout the Italian territory. Hippo (*Hippopotamus amphibius*) and straight-tusked elephant (*Palaeoloxodon antiquus*) were recognized in northern Italy at Grotta della Madonna dell'Arma (Liguria, archaeological cave site, Valensi and Psathi, 2004), in central Italy at Campo Verde (Latium, archaeological open-air site, Marra *et al.*, 2018) and in southern Italy at Grotta Grande (Campania, archaeological cave site, Ronchitelli *et al.*, 2011) and Contrada Iannì (Calabria, archaeological open-air site, Marra, 2009). Hippo was also found in layers 1 and 6 at Avetrana (Apulia, stratified karstic infill deposit, Petronio *et al.*, 2008). Fallow deer (*Dama dama*) was attested to in all the above-mentioned sites, as well as in northern Italy, at Caverna degli Orsi (Venezia Giulia, archaeological cave site, Berto and Rubinato, 2013) and possibly at Ciota Ciara, an archaeological cave site in

*Correspondence: Andrea Columbu, as above.
E-mail: andrea.columbu2@unibo.it

Piedmont (identified as 'cf. *Dama*' in Berto *et al.*, 2016) (Fig. 1). Data related to MIS 4 are scanty and less clear, also due to the lack of a good framework of chronometric studies. Commonly, this phase is said to be characterized by the decline and disappearance of hippo and straight-tusked elephant, and by the appearance of cold stenothermal taxa: woolly rhino (*Coelodonta antiquitatis*) and woolly mammoth (*Mammuthus primigenius*). Regretfully, most remains of these large mammals are from undated open-air sites, or from contexts whose chronological attribution is uncertain (e.g. for the woolly mammoth, MIS 4–3 at Riparo Tagliente, an archaeological cave site in Veneto – northern Italy, Reggiani and Sala, 1992; age >41 ka BP at Buca della lena, archaeological cave site in Tuscany – central Italy, Pitti *et al.*, 1976). Evidence tentatively associated with MIS 4 seems to be present in the southernmost part of Apulia (southern Italy, woolly rhino at Grotta Romanelli, Pandolfi and Tagliacozzo, 2013). Warm climate taxa are also tentatively reported for this period, as for instance *Palaeloxodon antiquus* at Grotta Guattari (Latium, central Italy) associated with an age of 57 ± 6 ka

(Schwarcz *et al.*, 1991a; Stuart, 2005) or fallow deer at Arna delle Manie (Liguria, northern Italy, Valensi, 2009). MIS 3 well-dated woolly rhino and mammoth specimens have been detected so far only in north-eastern Italy at Grotta di Fumane (Veneto, archaeological cave site, layer A3, Tagliacozzo *et al.*, 2013) and Settepolesini di Bondeno (alluvial deposits in Emilia, eastern Po valley, Beta-128160: 40 884–35 912 cal BP; Gallini and Sala, 2001), respectively. Thus, during MIS 3, the area north-east of the Apennine chain was still influenced by the arrival of cold taxa, while in the area stretching from the north-western Tyrrhenian belt to southern Italy the presence of more thermophilous fallow deer was quite constant (Fig. 1). This taxon was found in archaeological cave sites from Liguria (Riparo Bombrini, Holt *et al.*, 2019), Tuscany (Buca della lena, Grotta La Fabbrica, Pitti *et al.*, 1976; Grotta dei Santi, Spagnolo *et al.*, 2020a), Latium (Grotta Breuil and Grotta del Fossellone, Alhaique and Tagliacozzo, 2000), Campania (Grotta di Castelcivita, Masini and Abbazzi, 1997; Grotta della Cala, Benini *et al.*, 1997; Riparo del Poggio, Boscato *et al.*, 2009) and Apulia

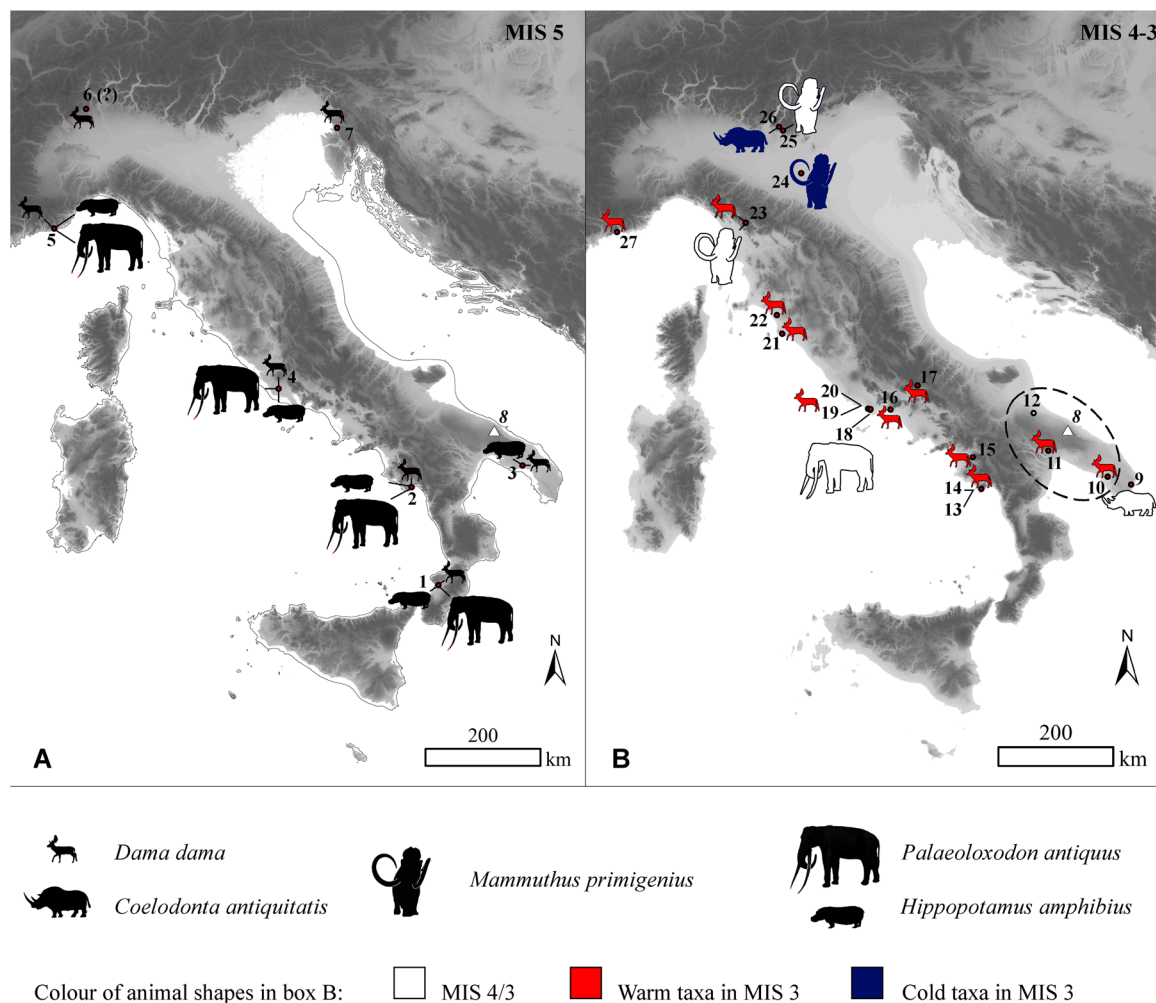


Figure 1. 'Warm' (*Dama*, *Palaeloxodon* and *Hippopotamus*) and 'Cold' (*Coelodonta* and *Mammuthus*) large mammal taxa in Italy during MIS 5 and MIS 4–3. Circled area: geographical position of the archaeological sites analysed in this work (Nos. 10–12) and Grotta di Pozzo Cucù, (speleotheme, No. 8, white triangle). The digital elevation model is the European digital elevation model from the GMES RDA project (https://www.eea.europa.eu/data-and-maps/data/eu-dem#tab-originaldata/eudem_hlsd_3035_europe). The bathymetric model is from the European Marine Observation and Data Network. The map was generated using ArcGIS version 10.5. In A are represented both the minimum extension of the coastline during MIS 5e and a mean of the maximum estimated extension of the coastline (grey line) during the cooler oscillations of MIS 5. Sites: A (MIS 5): (1) Contrada Ianni, (2) Grotta Grande, (3) Avetrana, (4) Campoverde, (5) Grotta della Madonna dell'Arma, (6) Ciota Ciara, (7) Caverna degli Orsi, (8) Grotta di Pozzo Cucù. B (MIS 4–3): (8) Grotta di Pozzo Cucù, (9) Grotta Romanelli, (10) Grotta del Cavallo, (11) Riparo L'Oscurusciuto, (12) Grotta Santa Croce, (13) Grotta della Cala, (14) Riparo del Poggio, (15) Grotta di Castelcivita, (16) Grotta di Sant'Agostino, (17) Grotta Reali, (18) Grotta Guattari, (19) Grotta del Fossellone, (20) Grotta Breuil, (21) Grotta dei Santi, (22) Grotta la Fabbrica, (23) Buca della lena, (24) Settepolesini di Bondeno, (25) Riparo Tagliente, (26) Grotta Fumane, (27) Riparo Bombrini. See text for references and explanations. [Color figure can be viewed at wileyonlinelibrary.com]

(Grotta del Cavallo, Boscato and Crezzini, 2012a; Riparo L'Oscurusciuto, Boscato and Crezzini, 2012b). Fallow deer made its last appearance at Grotta della Cala (Campania, southern Italy) in the Aurignacian layers (Benini *et al.*, 1997). Its extinction is in line with the reduction of the signal of temperate forests from the pollen record of central–southern Italy, which is counterbalanced by the increase of steppe-related herbaceous taxa (Allen *et al.*, 2000; Badino *et al.*, 2020). The presence of cold taxa restricted to north-eastern Italy makes the Italian Peninsula quite different from Iberia, where woolly mammoth was able to reach the southernmost regions during some of the coldest MIS 3 oscillations (Álvarez-Lao *et al.*, 2009).

In this scenario, a number of dated contexts testify to Neanderthals' persistence in peninsular Italy during the Late Pleistocene. Among the main sites attributed to MIS 5 are Riparo del Poggio (Boscato *et al.*, 2009), Grotta Grande di Scario (Ronchitelli *et al.*, 2011) and Riparo di Santa Caterina (Gambassini and Ronchitelli, 1998) in Campania. An MIS 5–4 site is Grotta Guattari (Schwarcz *et al.*, 1991a) in Latium. Sites dated to MIS 3 are present in Tuscany (Grotta dei Santi, Moroni *et al.*, 2019; Spagnolo *et al.*, 2020a), Latium (Grotta dei Moscerini, Kuhn, 1995; Sant'Agostino, Tozzi, 1970; Schwarcz *et al.*, 1991b), Campania (Riparo del Poggio, Boscato *et al.*, 2009), Molise (Grotta Reali, Peretto *et al.*, 2020) and Apulia (Grotta Romanelli, Sardella *et al.*, 2014; Grotta di Santa Croce, Arrighi *et al.*, 2009; Riparo L'Oscurusciuto, Boscato *et al.*, 2011; Grotta del Cavallo, Zanchetta *et al.*, 2018). From about 45k to 39k cal a BP (Higham *et al.*, 2014), Neanderthals were replaced in Europe by Modern Humans (MHs). According to the current state of knowledge, the early dispersal of MHs into Europe followed two penecontemporaneous routes: the first, perhaps slightly older, through the inner part of the Balkan peninsula, is attested to by the recent identification of MH bone remains in association with an Initial Upper Palaeolithic

assemblage at Bacho-Kiro Cave in Bulgaria (Hublin *et al.*, 2020). The other, towards Apulia (possibly along the Ionian fringe of the southern Balkan peninsula – Greece and across the Adriatic Sea), is related to the spreading of the Uluzzian technocomplex, whose occurrence is testified to in several localities. The main sites are located in Greece (Higham *et al.*, 2014), Apulia (southern Italy, Ionian area, Benazzi *et al.*, 2011; Moroni *et al.*, 2013, 2018), Campania (southern Italy, Tyrrhenian area Martini *et al.*, 2018; Collina *et al.*, 2020; Marciani *et al.*, 2020a), Latium (central Italy, Villa *et al.*, 2018), Tuscany (central Italy, Villa *et al.*, 2018) and Veneto (northern Italy, Peresani *et al.*, 2019). When MHs reached southern Apulia (Grotta del Cavallo), the last Neanderthals were still present in the central part of the region (Riparo L'Oscurusciuto, Fig. 1) and the co-existence of the two groups possibly lasted for several hundred years (Higham *et al.*, 2014). Thus, Southern Italy, and more specifically Apulia, is a key region for studying the role of the environment in relation to both late Neanderthals and the newcomers. The aim of this work is to refine our knowledge about the ecological setting of Apulia during the last part of MIS 4 and the first half of MIS 3, by integrating faunal, chronological and palaeoclimatic data from four sites: Grotta di Santa Croce, Grotta del Cavallo, Riparo L'Oscurusciuto and Grotta di Pozzo Cucù (Fig. 1). We test the possible role that the Apulian region played, initially as a refugium for late Neanderthals, and later as the scenario of their replacement by MHs.

The sites

Grotta di Santa Croce (Bisceglie – Barletta-Andria-Trani)

Grotta di Santa Croce (Fig. 2) is a horizontal cave containing a rich archaeological deposit mainly located

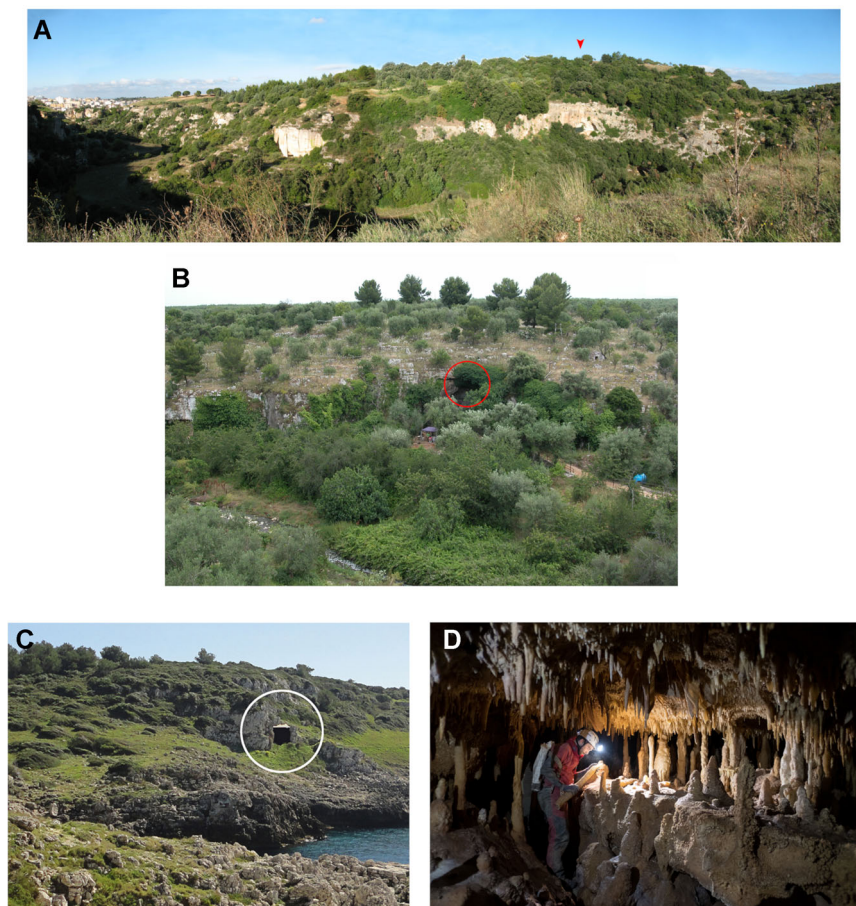


Figure 2. The studied sites. A: Riparo L'Oscurusciuto (photo by Paolo Boscato); B: Grotta di Santa Croce (photo by Paolo Boscato); C: Grotta del Cavallo (photo by Vincenzo Spagnolo); D: Grotta di Pozzo cucù (photo by Orlando Lacarbonara). [Color figure can be viewed at wileyonlinelibrary.com]

immediately in front of its entrance. Early research at this site was carried out between 1939 and 1958 (Cardini, 1954; Segre and Cassoli, 1987). In 1997, fieldwork was resumed by the University of Siena in collaboration with the local Heritage Office. Except for a test trench carried out inside the cave, the main excavation activity was focused on the talus of the external deposit, with an 18-m-wide and 1.5-m-deep trench (Fig. 3). Excavations did not reach the bottom of the archaeological deposit. Even if the peripheral part of the talus is about 40 m far from the present-day cave entrance, in Palaeolithic times, the rocky vault most probably covered a large part of the extant outer deposit. Moving from the bottom of the already excavated part of the stratigraphy, the external sequence is subdivided into three main lithostratigraphic units: (i) reddish sandy levels yielding a rich assemblage of Mousterian lithic

implements and animal remains, which is characterized by large limestone blocks testifying to the episodic collapse of the vault – the lithic assemblage is characterized by a discoidal reduction sequence; (ii) pinkish sandy layers affected by erosive events, with a combination of Mousterian and Protoaurignacian evidence; and (iii) greyish sandy/silty layers with few Gravettian implements (AMS Beta 147996: 29 526–28 446 cal a BP) (Boscato *et al.*, 2006a, 2010; Arrighi *et al.*, 2009; Ranaldo *et al.*, 2017) (Fig. 3).

The presence of the Protoaurignacian in the pinkish sandy layers is also confirmed by a ¹⁴C date (AMS Beta 181166: 36 755–34 277 cal a BP). No structures, such as fireplaces, were found. Small mammals, birds and molluscs are very scarce (or even absent) as well as the vegetal remains.

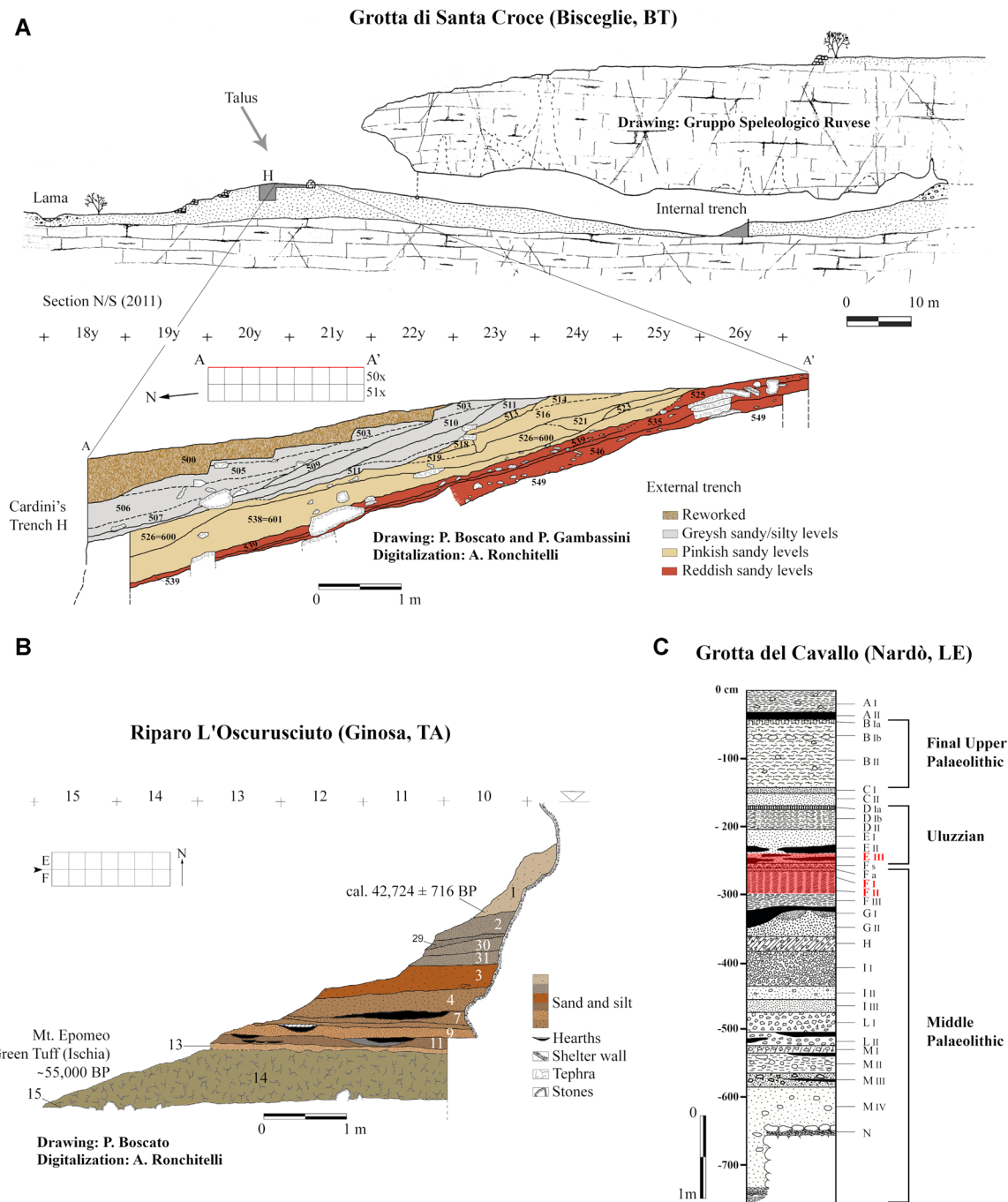


Figure 3. Stratigraphic sequences of the studied archaeological sites (C modified after Palma di Cesnola, 2001). [Color figure can be viewed at wileyonlinelibrary.com]

Grotta del Cavallo (Nardò – Lecce)

Grotta del Cavallo (Fig. 2) opens in the Uluzzo bay. The cave is formed by a main chamber with a wide entrance facing NE. Excavations were directed by A. Palma di Cesnola (University of Siena) from 1961 to 1979, and later by other colleagues of the same University until 2019. A thick stratigraphic continental deposit lies on a marine beach and includes the Middle Palaeolithic, the Uluzzian, the Late Upper Palaeolithic (Romanellian) and the Neolithic (Palma di Cesnola, 1967). The upper part of the Mousterian sequence (layer FI-III) lies between two tephra layers dated, respectively to 108.7 ± 0.9 ka (X-6, layer G) and ~ 45.5 ka (Y-6, layer Fa) (Zanchetta *et al.*, 2018). Layer FII, which has been ^{14}C -dated to $47\,900\text{--}42\,100$ cal a BP, yielded a Neanderthal deciduous tooth (Fabbri *et al.*, 2016; Sarti *et al.*, 2017). The Uluzzian sequence (layers E–D) is sandwiched between the tephra layer Fa and another tephra corresponding to the Campanian Ignimbrite (Y-5, 39.85 ± 0.14 ka). The chronology of the Uluzzian package at Cavallo is also confirmed by ^{14}C dates obtained in the Oxford laboratory (Benazzi *et al.*, 2011; Higham *et al.*, 2014). In layer EIII (Fig. 3) two deciduous teeth were found (Benazzi *et al.*, 2011; Moroni *et al.*, 2018). These represent the early evidence for MHs in Italy and one of the oldest in Europe. No data are available so far from bird, mollusc and vegetal remains, while the only data available for small mammals are from Dalla Valle (2008).

Riparo L'Oscurusciuto (Ginosa – Taranto)

Riparo L'Oscurusciuto (Fig. 2) is a key site for the study of late Neanderthal groups in southern Italy. It is located at the bottom of the ravine of Ginosa. Excavations (which are still underway) started in 1998 under the direction of the University of Siena in collaboration with the local Heritage Office. This site has a long-term stratigraphic sequence in which the archaeological evidence is exclusively related to the Mousterian occupation (Fig. 3). The part of the deposit already excavated is dated between 55 ka (volcanic tephra, layer 14) and $45\,335\text{--}40\,711$ cal a BP (^{14}C date, bottom of layer 1) (Marciani *et al.*, 2020b and references therein). Some extensively excavated layers have yielded important information about settlement strategies and space organization patterns of late Neanderthals. Layer 11 is a long-term palimpsest characterized by the presence of several hearths, whose diameters range from about 25 to 50 cm. They have an SW–NE alignment and are associated with areas devoted to knapping and butchering. A possible sleeping area, connected to this phase, was detected in the NW corner of the shelter. Layer 9 displays a similar alignment of hearths allocated in sub-circular shallow pits. By contrast, layer 8 does not show clear structures and was probably affected by slight erosional phenomena. The phase represented by layers 5–7 is characterized by a change in the space management: a single large hearth (about 2 m in diameter) was set in the NW corner of the shelter. Layer 4 is a thick palimpsest very rich in faunal and lithic remains. Several stones, some of them intentionally imported into the site, were found in the upper part of the layer (Boscato and Ronchitelli, 2007; Spagnolo *et al.*, 2016, 2019, 2020b; Martini *et al.*, 2020). Small mammal, bird, mollusc and vegetal remains are sporadic.

Grotta di Pozzo Cucù (Castellana Grotte – Bari)

This cave (not an archaeological site) opens into the Cretaceous limestone plateau belonging to the Calcare di Altamura Formation, and is located around 10 km from the Adriatic coastline (Fig. 2). The modern entrance, a narrow

~ 8 -m-deep pit at ~ 270 m a.s.l., leads to a sub-horizontal environment that stretches for ~ 300 m. A ~ 50 -cm-long stalagmite from this cave has recently produced the first continuous Western European speleothem palaeoclimate record for the last glacial period (Columbu *et al.*, 2020). By applying high-resolution U–Th dating ($n = 27$) and $\delta^{13}\text{C}\text{--}\delta^{18}\text{O}$ ($n = \sim 2700$), the Pozzo Cucù (PC) record allowed the determination of rainfall amount, moisture circulation and soil bio-productivity from 106.0 ± 2.8 to 26.6 ± 0.9 ka, with average $\pm 2\sigma$ age model uncertainty of around 1.3 ka. Average $\pm 2\sigma$ age model uncertainty drops below ~ 1 ka over the period between ~ 50 and ~ 40 ka.

Materials and methods

Chronology at Santa Croce

Three herbivorous teeth recovered in the external talus of Santa Croce cave were analysed by the ESR/U-series method. The following analytical protocol was used (Bahain *et al.*, 2010): after its extraction, enamel was cleaned of any track of sediment or dentine using a dental drill, crushed and sieved to retrieve the $100\text{--}200\text{-}\mu\text{m}$ grain-size fraction, which was then split into 10 aliquots. One aliquot was kept as a natural reference and the nine others were irradiated using a panoramic source of ^{60}Co (LNHB, CEA, CEN, Saclay, France) at doses ranging between 25 and 11 700 Gy. These aliquots were then measured by ESR spectrometry with a Bruker EMX spectrometer (band X, frequency modulation 100 kHz) at room temperature. The following parameters were used: microwave power of 1 mW, modulation amplitude of 0.1 mT, scan range of 10 mT, scan time of 4 min. At least four measurements for each aliquot were performed on different days. The ESR intensities of the $g = 2.0018$ enamel ESR signal were measured according to Grün (2000) and the equivalent doses D_e were then extrapolated from the obtained dose–response data sets using an exponential + linear function (according to Shao *et al.*, 2015).

U-series analyses were performed on each dental tissue using the chemical protocol treatment described by Shao *et al.* (2011). Measurements were performed on a Neptune Multi-Collector Inductively Coupled Plasma Mass Spectrometer at Nanjing Normal University, China (Shao *et al.*, 2015). The radioelement contents of sediments associated with the teeth were measured by high-purity low-background gamma spectrometry, and conversion contents–doses factors of Guérin *et al.* (2011) were used for the age calculation. For each dental tissue, Rn loss was estimated from both gamma and alpha/inductively coupled plasma measurements (Bahain *et al.*, 1992). Additional *in situ* gamma measurements were performed with an Inspector 1000 Canberra gamma spectrometer using an NaI detector. The cosmic dose rate was estimated for each sample by the formula of Prescott and Hutton (1994) considering the depth of the samples in the sequence.

ESR/U-series ages (Table 1) were estimated from the whole data set as well as dose-rate contributions and U-uptake parameters considering the US model (Grün *et al.*, 1988) and using the 'USESR' software (Grün, 2009).

Magnetic susceptibility analysis

Magnetic susceptibility (MS) analysis was performed at Riparo L'Oscurusciuto to obtain palaeoclimatic information, especially for the lower part of the succession currently not excavated. A huge part of siliclastic sediments in caves and rock shelters derive from infiltration processes, through which

Table 1. ESR/U-series data and ages of teeth from Santa Croce.

Samples	Tissue	U content (p.p.m.) (2σ)	²³⁴ U/ ²³⁸ U (2σ)	²³⁰ Th/ ²³⁴ U (2σ)	²²² Rn/ ²³⁰ Th	Initial thickness (μm)	Removed	
							thickness internal side (μm)	Removed thickness external side (μm)
SC535	Dentine	20.01 ± 0.69	1.025 ± 0.049	0.066 ± 0.009	0.191	1339 ± 167	35 ± 4	29 ± 4
	Enamel	0.43 ± 0.03	1.033 ± 0.092	0.130 ± 0.029	1.000			
SC546	Dentine	94.88 ± 2.71	1.075 ± 0.059	0.109 ± 0.011	0.110	1467 ± 183	38 ± 5	26 ± 3
	Enamel	1.76 ± 0.08	0.952 ± 0.059	0.133 ± 0.013	0.261			
SC549	Dentine	6.42 ± 0.26	1.068 ± 0.061	0.403 ± 0.080	1.000	1246 ± 156	29 ± 4	27 ± 3
	Enamel	0.28 ± 0.03	1.005 ± 0.128	0.403 ± 0.080	1.000			

Samples	Tissue	<i>D_e</i> (Gy) (2σ)	U uptake parameter <i>p</i>	Dose rate (μGy a ⁻¹) [†]				ESR/U-series ages US or AU models (ka) (2σ) [§]
				<i>D_a</i> α*	<i>D_a</i> β [‡]	<i>D_a</i> (γ + cosm)	<i>D_a</i> total	
SC535	Dentine	58.81 ± 2.45	4.0165 ± 0.3893	19 ± 69	210 ± 60	1049 ± 39	1278 ± 60	46 ± 3
	Enamel		0.9174 ± 0.1852					
SC546	Dentine	78.66 ± 3.02	5.4440 ± 0.5191	87 ± 75	292 ± 66	1001 ± 45	1380 ± 110	57 ± 4
	Enamel		1.5962 ± 0.2468					
SC549	Dentine	63.37 ± 2.07	6.2265 ± 1.1697	104 ± 182	144 ± 16	1045 ± 47	1293 ± 189	49 ± 7
	Enamel		0.0873 ± 0.4086					

*A *k*-value (α efficiency) of 0.13 ± 0.02 (Grün and Katzenberger-Apel, 1994).

[†]The water content of the sediments was estimated after 1 week of drying in a 40 °C oven but, as the sampled section has been open for a long time, the obtained values were considered as minima and a representative value of 15 ± 5% was assumed for the age calculations. Water contents of 0 wt% in the enamel and 7 wt% in the dentine were used.

[‡]The beta dose attenuation was evaluated from the enamel part destroyed on each side of the enamel layer during the preparation process (according to Brennan *et al.*, 1997).

[§]The age uncertainty was calculated with a Monte Carlo approach (Shao *et al.*, 2014).

fine-grained sediments are carried from overlying soils (Iacoviello and Martini, 2012, 2013; Martini *et al.*, 2018, 2020). In turn, pedogenesis during cool and arid climates produces sediments with low MS magnitudes, while warmer and humid climates yield higher MS magnitudes. As a consequence, MS data in cave and shelter sites can be an excellent palaeoclimatic proxy (Ellwood *et al.*, 1998).

Samples (*n* = 22) were collected in the 5.7-m thick siliciclastic succession (i.e. low-resolution sampling). Two samples were not considered in this palaeoclimatic-orientated study because they were exclusively made of volcanic ash (i.e. not providing palaeoclimatic information). Samples were sieved in the laboratory at 1 mm, following the procedure proposed by Ellwood *et al.* (2001): 10 g of the <1-mm fraction of each sample is placed in a cylindrical bottle and MS is measured with a Bartington Instrument MS-2 susceptibility meter combined with an MS2B dual frequency sensor. The instrument operates at 465 and 4650 Hz, thus providing the opportunity to measure low-frequency (LF) and high-frequency (HF) MS values (χ_{mass}). The difference between these LF and HF χ_{mass} values corresponds to the χ_{fd} (χ_{fd} = χ_{mass}LF – χ_{mass}HF), a value that has a close positive relationship with pedogenesis and highlights the MS signal of minerals produced during pedogenesis (cf. Maher, 1986; Liu *et al.*, 2003).

Data elaboration and presentation follow the suggestion of Ellwood (2007), even if raw data are not smoothed using splines due to the low-resolution sampling. Palaeoclimatic trends are expressed with the bar log format; that is, changes are assumed to be significant if the MS cyclical trends increase/decrease by a factor of two or more and if the change is represented by two or more data points, and consequently the highs and lows associated with these cycles are differentiated by filled (high MS values) or open (low MS values) bar logs (Ellwood, 2007).

Faunal remains

The study focuses on the already published faunal remains from Grotta di Santa Croce (excavation fieldwork 1998–2005), Grotta del Cavallo (excavation fieldwork 1980–1986) and

Riparo L'Oscurusciuto (excavation fieldwork 1998–2011). All these sites were stratigraphically investigated with modern methodologies and sediments were water-sieved with 1-mm size mesh. In addition to the already published data (Bosco and Crezzini, 2006, 2012a,b; Bosco, 2017; Spagnolo *et al.*, 2020b) new samples from Grotta di Santa Croce (layer 549, Ciullo, 2016) and Riparo L'Oscurusciuto (layers 4–7, Batini, 2018) are presented. The sample from Grotta di Santa Croce is from the 2011 fieldwork and is composed of 789 bone fragments. The sample from Riparo L'Oscurusciuto was recovered during the 2017 fieldwork, carried out in a stratigraphic baulk located in the northernmost part of the shelter. This sample is composed of 8659 bone fragments. Specimens were identified using the osteological reference collection at the University of Siena. The number of identified specimens (NISP) is used to describe the abundance of taxa. The calculation of the minimum number of individuals has not been carried out due to the ongoing debate about its validity (Lyman, 2008, 2018). Ecological considerations on ungulate taxa are from Heptner *et al.* (1988).

Results

Chronology at Santa Croce

The obtained ages range between 57 ± 4 and 46 ± 3 ka. A Bayesian treatment of these results including stratigraphical and radiocarbon constraints was also realized using Chronomodel software (Lanos *et al.*, 2016) (Fig. 4). It suggests that the Mousterian occupation levels are clearly younger than MIS 5 and were coeval with MIS 4 to early MIS 3.

Magnetic susceptibility

Raw MS data from Oscurusciuto are presented in Supporting Information Table S1 and the results are synthesized in Fig. 5. HF and LF values display a similar trend over the entire succession, and absolute values for each sample show only slight differences. The same trend is also expressed when

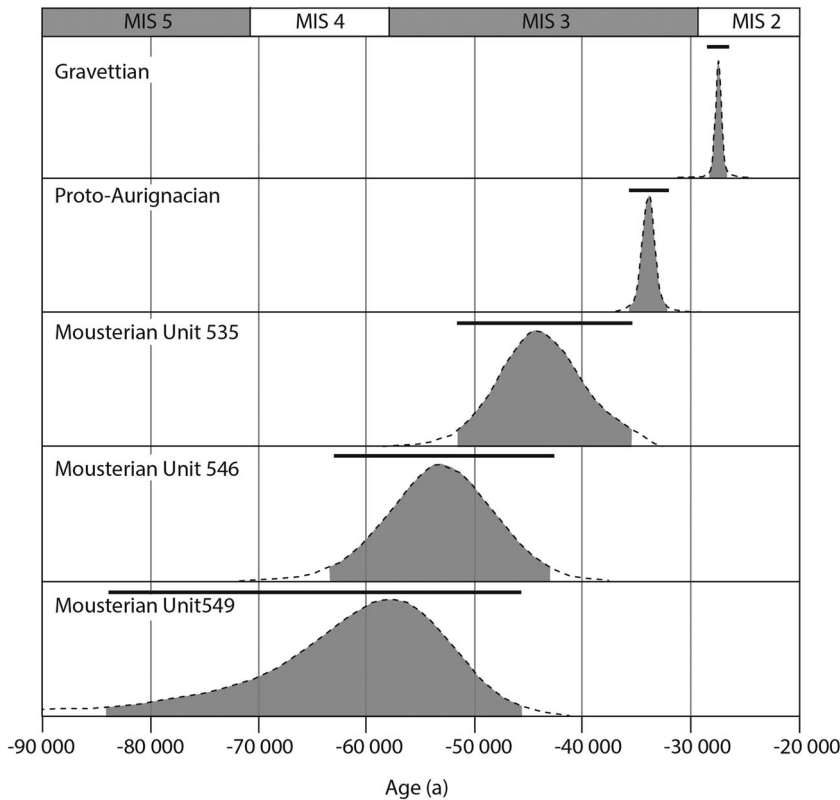


Figure 4. Bayesian age model of the Santa Croce external deposits (performed with Chronomodel). The very young age of the modelled end of the Mousterian sequence is probably biased by erosional events.

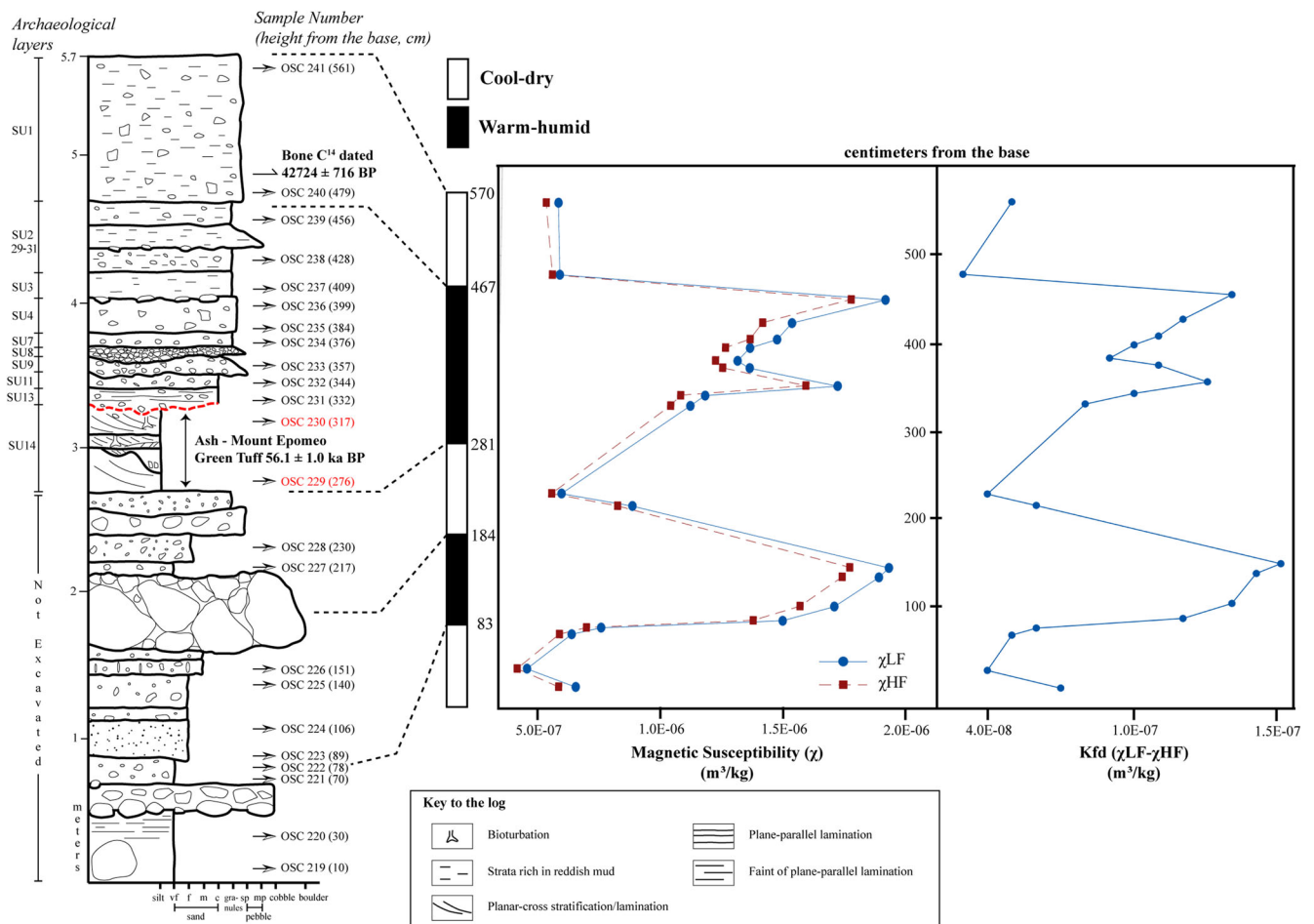


Figure 5. Sedimentary log of the Oscurusciuto succession with the locations of samples collected for magnetic susceptibility (MS) analysis. Results of MS measurement are reported and accompanied by bar logs that highlight the main palaeoclimate fluctuations as deduced by MS data. Samples OSC 229 and 230 have not been analysed due to their composition, almost exclusively represented by volcanic ash. χ_{LF} and χ_{HF} : low- and high-frequency MS values. [Color figure can be viewed at wileyonlinelibrary.com]

plotting χ_{fd} values; indeed, the bar log format obtained for χ_{massLF} , χ_{massHF} and χ_{fd} are the same. This result could be partially influenced by the low resolution of sampling, but surely highlights the high influence of climate-driven pedogenetic processes in the observed MS values.

The data suggest that the deposition of the succession started in relatively cool/dry settings (from the base of the succession up to 83 cm), followed by a period of warm/humid climate (interval 83–184 cm), in turn overlaid by sediments deposited during cool/arid settings (interval 184–281 cm). This part of the stratigraphic sequence has still not been investigated; therefore, these data are – so far – the only available proxies for palaeoclimatic reconstructions.

The upper part of the succession, which has already been excavated, shows a more monotonous situation with MS values, suggesting a warm and humid setting in the interval between 281 and 467 cm, corresponding to the archaeological layers 14–3. Only the samples collected in the upper layers (SU1 and possibly a part of SU2, i.e. the interval from 467 to 570 cm) show MS values documenting a rapid shift towards more cool/arid settings (Fig. 5).

Faunal remains

Faunal remains are listed in Table 2. The oldest sample, referred to the final phase of MIS 4 to early MIS 3, is from Grotta di Santa Croce. The mammal assemblage is poor in terms of biodiversity and points to a quasi-exclusive predation upon horse and aurochs in all the layers. Zooarchaeology on the new sample from layer 549 shows the same pattern already observed in the other layers (Bosco et al., 2006b; Bosco and Crezzini, 2006; Bosco, 2017): isolated teeth count for the 75% of the identified remains (NISP = 72), long bones are represented only by diaphysis fragments and no phalanges have been identified. Considering NISP and the unidentified fragments together (total specimens = 789), diaphysis and compact bone fragments account for 74.6% of the whole sample. Only 0.5% of the remains are spongy bones/epiphyses. Anthropogenic modifications (impact marks, cone flakes and burned bones) account for 2.3% of the faunal remains, while carnivore-induced modifications were not observed. About 92% of teeth belong to adult/elderly individuals.

New data from Oscurusciuto were collected in the northernmost sector of the shelter, layers 4–7 (excavation ongoing). Faunal remains from this area are less affected by concretions than those from the rest of the site (only 2% of them are partially covered by thin calcite films). Bones are usually very fragmented (91% are within the size class 1–3 cm) and only 0.05% are unbroken. Among the 71 specimens taxonomically identified, 56 are from layers 5–7 and 15 from layer 4. They mainly include isolated teeth and diaphysis fragments (93% in layer 4 and 76% in layers 5–7). The only identified epiphyses belong to the proximal metacarpal and to first and second phalanges. Considering also the unidentified sample, spongy elements are represented by 16% of specimens in layer 4 and 17% in layers 5–7. Several specimens are burned (33% in layer 4 and 65.7% in layers 5–7), while other anthropic marks (cut marks, percussion notches and cone flakes) were identified on 1.7% of remains in layer 4 and on 1.6% in layers 5–7. No carnivore-induced bone modifications were identified. These data confirm the picture that has emerged from previously studies (Bosco and Crezzini, 2006, 2012a,b; Bosco, 2017; Spagnolo et al., 2020b).

As far as Oscurusciuto is concerned, this faunal assemblage is distributed across a period between 55k and ~43k cal a BP. Aurochs is almost always the most abundant species. The only

exception is layer 3, where horse counts for the 28% of the faunal remains. Again, taxa well adapted to open environments (steppe and forest steppe) are those showing the highest frequency. Moreover, caprines (ibex and chamois), wild boar and cervids were also identified. In layer 1 cervids account for the 45% of NISP. Fallow deer was identified in all the phases, while rhino and carnivore specimens are very rare.

At Grotta del Cavallo it was possible to consider both Mousterian (Layer F, Sarti et al., 2000) and Uluzzian (Layer E, Bosco and Crezzini, 2012a) data. Generally, cervids are more abundant than at the other sites, but again aurochs is the most targeted prey. Such a faunal association seems to resemble the quasi-contemporaneous upper part of the sequence from Oscurusciuto. A slight increase of taxa related to open environments is visible during the Uluzzian, but the difference with the preceding Mousterian is not remarkable. At Grotta del Cavallo, carnivore and lagomorph remains are consistently very rare. The analysis carried out by Bosco and Crezzini (2012b) points to an anthropogenic accumulation of animal remains without any trace of carnivore activity.

Discussion and conclusions

From a chronological perspective, our data anchor – for the first time – the external deposit of Santa Croce to a period between the end of MIS 4 and early MIS 3.

This result enables us to evaluate human presence over a long time frame that covers some of the harshest phases of the early Late Pleistocene. At Santa Croce, Oscurusciuto and Cavallo, the layers where zooarchaeological and MS analyses were performed are palimpsests. As a consequence, data from these layers represent ‘mean values’ that describe timespans of different duration. This must be considered when they are compared with palaeoenvironmental results from Pozzo Cucù, as the datasets have different scales (Fig. 6).

The new zooarchaeological data from layer 549 of Grotta di Santa Croce and layers 7–4 of Riparo L’Oscurusciuto confirm the pattern outlined by previously published samples: significantly, the Middle Palaeolithic faunal assemblages share similar characteristics in all the considered sites. First, we note the scarcity of remains related to small game and birds. These resources had an extremely marginal – if not absent – role in the subsistence of Apulian Neanderthals, who mainly hunted aurochs and/or horse. Second, zooarchaeology also points to repetitive behaviours in hunting strategies and carcass reduction over time. Carcasses were intensely exploited, including within-bone nutrients (bone and marrow). Epiphyses and spongy bones were probably smashed to extract these substances. However, in spite of the general scarcity (in all sites and layers) of spongy bone fragments, there is no evidence of either the use of bone as fuel (e.g. Spagnolo et al., 2019) or the alteration of osteological samples by carnivores, such as hyenas (Bosco and Crezzini, 2006, 2012a). This could suggest the hypothesis that Neanderthals systematically exploited fat contained in epiphyses and spongy bones. Hunting strategies, as far as for aurochs and horses, were mostly focused on the killing of mature/elderly individuals (Bosco and Crezzini, 2006, 2012b).

The highest representation of these two species together – which are both adapted to open landscapes (forest steppe and steppe, respectively) – is reached in the cold/arid phases at Santa Croce, where cervids are very rare, and fallow deer is completely absent. At Oscurusciuto and Cavallo, although horse and aurochs count for most of the faunal remains, the other species are more abundant compared to Santa Croce.

Table 2. Number of identified specimens (NISP) according to sites and layers.

Site	Layers	Equus		Bos		Capra	Rupicapra sp.	Caprinae	Cervus elaphus	Capreolus capreolus	Dama dama	Cervidae	Sus scrofa	Stephanorhinus sp.	Panthera leo	Crocuta crocuta	Canis lupus	Vulpes vulpes	Lepus sp.	Total
		Equus ferus	Equus hydruntinus	Equus sp.	Equus primigenius															
GC	EIII5	53	1	1	86	/	/	/	52	/	/	/	3	/	/	1	2	4	1	204
GC	FI	14	/	/	25	/	/	/	22	/	3	2	/	/	/	/	/	6	4	76
GC	FII	21	/	/	46	/	/	/	26	1	7	2	1	/	/	/	/	7	2	113
RO	1	2	/	/	20	/	/	/	11	1	6	/	/	/	/	/	/	/	/	40
RO	2/29/30/31	48	/	/	82	5	/	/	27	8	12	3	/	/	1	/	/	/	/	186
RO	3	16	/	/	15	1	/	/	15	2	1	/	/	7	/	/	/	/	/	57
RO	4	7	/	/	165	1	4	/	26	4	10	2	/	/	/	/	/	/	/	219
RO	5-6-7	1	/	/	160	/	/	/	9	2	20	5	/	1	/	/	2	/	/	201
RO	8	1	/	/	79	/	/	/	4	/	7	/	/	/	/	/	/	/	/	91
RO	9	4	/	/	69	/	/	/	12	4	6	1	/	/	/	/	/	/	/	96
RO	11	3	/	/	61	/	/	/	5	1	3	/	1	/	/	/	/	/	/	74
GSC	525	142	/	/	111	/	/	/	/	/	/	/	/	/	/	/	/	/	/	253
GSC	535	73	/	/	96	/	/	/	/	/	/	/	/	/	/	/	/	/	/	169
GSC	546	68	/	/	131	/	/	/	1	/	/	/	/	/	/	/	/	/	/	200
GSC	549	15	/	/	53	/	/	/	4	/	/	/	/	/	/	/	/	/	/	72

Abbreviations: GC, Grotta del Cavallo; GSC, Grotta di Santa Croce; RO, Riparo L'Oscursciuto.

Fallow deer, which was observed at Avetrana during MIS 5, appears again in Apulia, thus placing this region within the 'warm' belt described in the Introduction and represented in Fig. 1B. The presence of cervid taxa indicates also a more humid habitat in that area, which remained quite constant in the period, thus indicating that the extreme climatic fluctuations of MIS 3 did not affect Apulia. Macromammal data from layer F of Grotta del Cavallo are in line with those from small mammals from the same layer, where the dominant taxon *Microtus savii*, related to open environments in a Mediterranean climate, is accompanied by *Apodemus sylvaticus*, *Apodemus flavicollis* and *Elyomys quercinus*, which attest to more vegetated areas (Dalla Valle, 2008). Even if the dates from Santa Croce show a high degree of uncertainty, the pattern displayed by the faunal remains from this site seems to be in agreement with the evidence from Pozzo Cucù, which attests to a long arid phase within MIS 4 and – after some rapid oscillations that probably are not registered by zooarchaeological analysis – a very harsh peak at ~55 ka followed by another relatively arid phase until about 50 ka. A subsequent more humid phase characterized by quite stable conditions in soil productivity (Columbu *et al.*, 2020) is in line with the data from L'Oscursciuto and Cavallo (Fig. 6). The harshest peak detected in the PC speleothem at about 55 ka, together with all the other rapid climate oscillations provided by this record, is probably too short to be perceived through the faunal record. Even if the faunal composition at Oscursciuto reflects a continuous presence of open environments (with the spotted presence of vegetated areas) between 55 ka and ~43k cal a BP, the increase in horse remains in layers 3 and 2 could testify to local slightly more arid conditions, which were not recorded at Pozzo Cucù. This evidence is supported by MS data, which register a cool/dry phase in layer 1. Such apparent inconsistency can be explained by the fact that the response of animal communities to climate changes is faster than that of pedogenetic processes. Indeed, a certain amount of time is needed for pedogenesis, for the infiltration of fine-grained sediments through the rock massif and finally for their deposition in the environment of the rock-shelter. Similar shifts have already been observed in soils and soil-related loess in China (Liu *et al.*, 2003). Even if shifts in MS detected at Oscursciuto do not provide the exact magnitude of the corresponding climatic oscillations, the two cool/dry phases identified in the unexcavated part of the sequence can be tentatively linked to the peaks in $\delta^{18}\text{O}$ registered in Pozzo Cucù before 55 ka. If so, the oldest part of the sequence of Oscursciuto could be attributed to MIS 4 or to a very early phase of MIS 3. The ecotonal environment of the ravines surrounding Oscursciuto was composed of a mixture of very different habitats (the wet, possibly vegetated, bottom of the ravines, the rock walls and the flat arid uplands) that guaranteed a high biodiversity of ungulates. This feature, along with the availability of lithic raw materials and the presence of (at least seasonal) water streams, was probably the reason why Neanderthals were able to persist in the territory (e.g. Spagnolo *et al.*, 2020b). Even if some more arid phases are indicated by the spread of horse and by MS data, the fairly constant presence of fallow deer indicates the absence of shifts towards very cold conditions.

When MHs reached Apulia about 45k cal a BP, climate and habitats were still the same as those experienced by late Neanderthals. MHs hunted the same taxa as Neanderthals, but showing a different strategy in the exploitation of herds (younger individuals; Sano *et al.*, 2019) and carcasses (less intensive exploitation of spongy bone tissues). This different exploitation

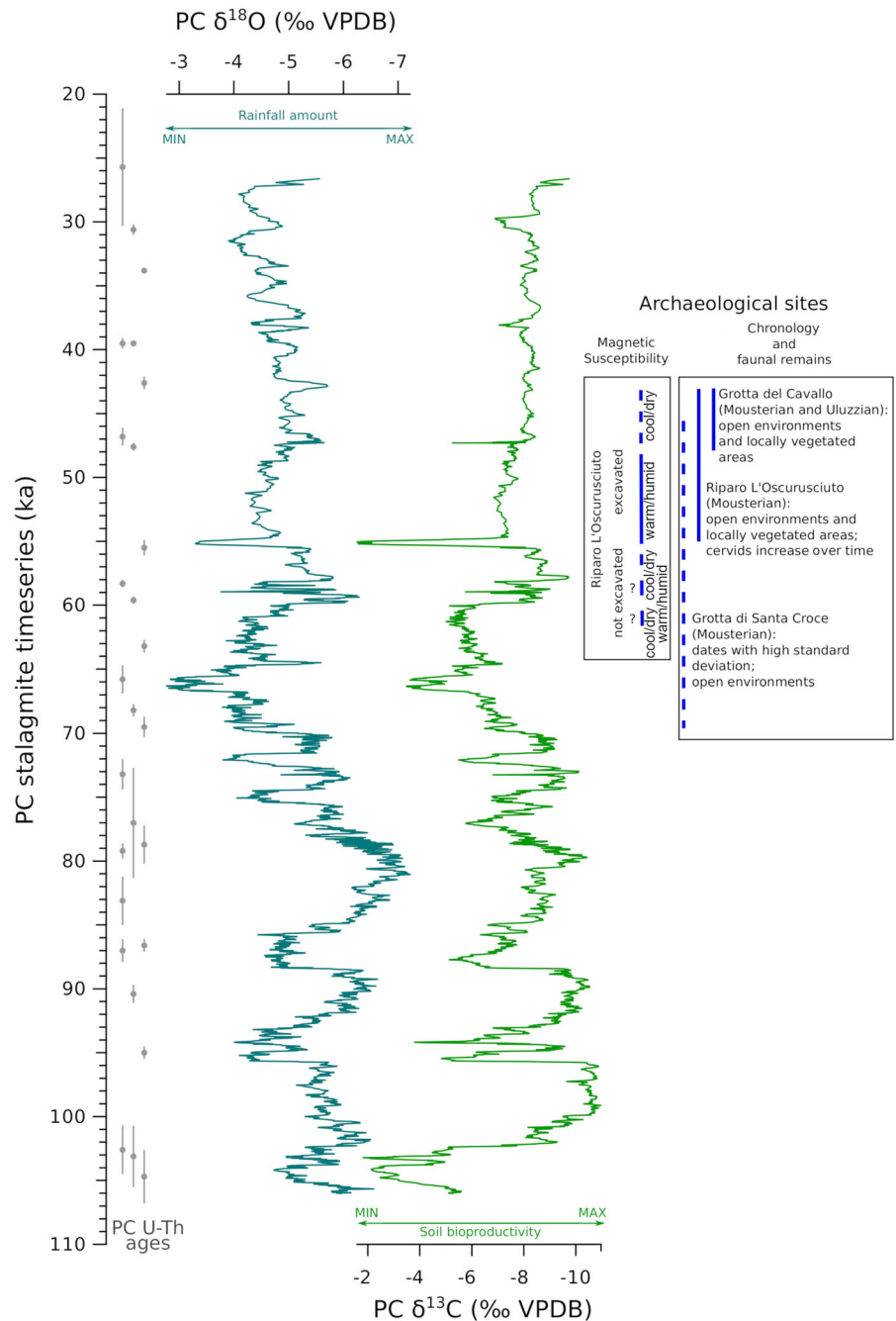


Figure 6. Comparison between palaeoclimate proxies (rainfall amount and soil bioproductivity) from Pozzo Cucù Cave (PC stalagmite, Columbu *et al.*, 2020), magnetic susceptibility data from Riparo L'Oscrusciuto and zooarchaeology from the studied archaeological sites. [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.com)]

model could originate from a diversity in hunting technology and behaviours between the two populations. In particular, Sano *et al.* (2019) demonstrated that MHs were fully equipped with a new projectile technology (bow and arrow or spear-thrower) that allowed them to hunt while maintaining a greater distance from prey. However, further research is needed to understand in detail nutritional patterns displayed by Neanderthals and MHs, as well as any possible diversity between their carcass exploitation strategies. MHs arrived in the Uluzzo bay when Neanderthals had most probably already abandoned this area. The survival of Neanderthals at Oscrusciuto until ~43k cal a BP points to a possible coexistence between the two populations in Apulia for some hundred years, but no evidence of an interaction has been found so far. In conclusion, Apulia offered resources and suitable stable climatic conditions for both late Neanderthal persistence and the early settling of MHs. Data from Pozzo Cucù and zooarchaeology do not support a population replacement due to climatic changes.

Therefore, even if a comprehensive explanation for the abandonment of the Uluzzo bay area by Neanderthals before 45k cal a BP and for their disappearance ~43k cal a BP at Oscrusciuto is still lacking, the possibility that more advanced hunting strategies implemented by MHs could have played a significant role in the replacement between the two groups cannot be excluded (Sano *et al.*, 2019).

Author contributions—F.B.: conceptualization of the paper and analysis of part of the faunal remains; F.B., P.B., A.R. and A.M.: coordination of research and excavation at the three archaeological sites; P.B. and J.C.: identification of faunal remains; I.M.: sedimentological analysis; J.J.B. and C.F.: dating at Grotta di Santa Croce; V.S.: sedimentological sampling and realization of Figures 1 and 2; A.C.: palaeoenvironmental analyses at Pozzo Cucù; all the authors collaborated in writing, reviewing and editing the paper.

Data availability statement

Data are available from the corresponding author upon request.

Supporting information

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Supplementary Table S1. Raw MS data from Oscurusciuto.

Supporting information

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Supplementary Table S1. Raw MS data from Oscurusciuto.

Acknowledgements. We thank Soprintendenze Archeologia, Belle Arti e Paesaggio per le province di Brindisi, Lecce e Taranto and Barletta–Andria–Trani e Foggia for their support in the research at the sites considered in this study. Research at Riparo L'Oscurusciuto is carried out under the Ministerial permission DDG rep. No. 935, 30 August 2019. We are particularly grateful to Vittorio Marras and the Gruppo Speleologico Neretino and to Mimmo Rana (Gruppo Scout di Bisceglie) for their help in the logistic organization of fieldwork at Grotta del Cavallo and Grotta di Santa Croce, respectively. We are particularly grateful to the municipality of Ginosa and to Piero di Canio and his family for the logistic organization and financial support of fieldwork at Riparo L'Oscurusciuto. S.B. is funded by the European Research Council (ERC) under the European Union's Horizon 2020 research and innovation programme (grant agreement No. 724046 – SUCCESS – www.erc-success.eu). The sedimentological and stratigraphic analyses at Riparo L'Oscurusciuto are funded by the National Geographic Society/Exploration Grant Program (grant NGS-61617R-19 to I. Martini). We thank Dr Daniele Aureli for his help in making it possible to carry out chronological measurements at Santa Croce. Finally, we would like to warmly acknowledge Dr Owen Higgins for his fundamental help in proofreading the English text. Last but not least, we thank two anonymous reviewers for their insightful comments.

Abbreviations. HF, high frequency; LF, low frequency; MHs, Modern Humans; MIS, Marine Isotopic Stage; MS, magnetic susceptibility; NISP, number of identified specimens; PC, Pozzo Cucù.

References

- Alhaique F, Tagliacozzo A. 2000. L'interpretazione dei dati faunistici nella ricostruzione delle strategie di sussistenza nel Paleolitico medio: l'esempio del Lazio. *Atti del 2° Convegno Nazionale di Archeozoologia* 111–124.
- Allen JRM, Huntley B. 2009. Last Interglacial palaeovegetation, palaeoenvironments and chronology: a new record from Lago Grande di Monticchio, southern Italy. *Quaternary Science Reviews* **28**: 1521–1538.
- Allen JRM, Watts WA, Huntley B. 2000. Weichselian palynostratigraphy, palaeovegetation and palaeoenvironment; the record from Lago Grande di Monticchio, southern Italy. *Quaternary International* **73–74**: 91–110.
- Álvarez-Lao DJ, Kahlke R-D, García N *et al.* 2009. The Padul mammoth finds – on the southernmost record of *Mammuthus primigenius* in Europe and its southern spread during the Late Pleistocene. *Palaeogeography, Palaeoclimatology, Palaeoecology* **278**: 57–70.
- Arrighi S, Freguglia M, Rinaldo F *et al.* 2009. Production and use in the Lithic Industry of the Mousterian in Santa Croce (Bisceglie, Italy). *Human Evolution* **24/2**: 91–106.
- Badino F, Pini R, Ravazzi C *et al.* 2020. An overview of Alpine and Mediterranean palaeogeography, terrestrial ecosystems and climate history during MIS 3 with focus on the Middle to Upper Palaeolithic transition. *Quaternary International* **551**: 7–28.

- Bahain J-J, Falguères C, Dolo J-M *et al.* 2010. ESR/U-series dating of teeth recovered from well-stratigraphically age-controlled sequences from Northern France. *Quaternary Geochronology* **5**: 371–375.
- Bahain J-J, Yokoyama Y, Falguères C *et al.* 1992. ESR dating of tooth enamel: a comparison with K–Ar dating. *Quaternary Science Reviews* **11**: 245–250.
- Batini M. 2018. *Il riparo l'Oscurusciuto (Ginosa – Taranto). Studio dei resti faunistici della campagna di cavo 2017, US 4-5-6-7 – Paleolitico Medio*. Bachelor Thesis, University of Siena.
- Benazzi S, Douka K, Fornai C *et al.* 2011. Early dispersal of modern humans in Europe and implications for Neanderthal behaviour. *Nature* **479**: 525–528. [PubMed: 22048311]
- Benini A, Boscato P, Gambassini P. 1997. Grotta della Cala (Salerno): industrie litiche e faune uluzziane ed aurignaziane. *Rivista di Scienze Preistoriche* **48**: 37–95.
- Bennett KD, Tzedakis PC, Willis KJ. 1991. Quaternary refugia of north European trees. *Journal of Biogeography* **18**: 103–115.
- Berto C, Bertè D, Luzi E *et al.* 2016. Small and large mammals from the Ciota Ciara cave (Borgosesia, Vercelli, Italy): an Isotope Stage 5 assemblage. *Comptes Rendus Palevol* **15**: 669–680.
- Berto C, Rubinato G. 2013. The Upper Pleistocene mammal record from Caverna degli Orsi (San Dorligo della Valle e Dolina, Trieste, Italy): A faunal complex between eastern and western Europe. *Quaternary International* **284**: 7–14.
- Boscato P. 2017. Ambienti ed economia nel Paleolitico medio della Puglia: lo studio delle faune. *Studi di Preistoria e Protostoria* **4**: 119–124.
- Boscato P, Boschian G, Caramia F *et al.* 2009. Il Riparo del Poggio a Marina di Camerota (Salerno): cultura ed ambiente. *Rivista di Scienze Preistoriche* **LIX**: 5–40.
- Boscato P, Crezzini J. 2006. The exploitation of ungulate bones in *Homo neanderthalensis* and *Homo sapiens*. *Human Evolution* **21**: 311–320.
- Boscato P, Crezzini J. 2012a. Middle-Upper Palaeolithic transition in Southern Italy: Uluzzian macromammals from Grotta del Cavallo (Apulia). *Quaternary International* **252**: 90–98.
- Boscato P, Crezzini J. 2012b. Il deposito musteriano del Riparo l'Oscurusciuto (Ginosa -TA): la fauna a grandi mammiferi delle UUSS 1:9. In *Atti del 6° Convegno Nazionale di Archeozoologia*, De Grossi Mazzorin J, Saccà D, Tozzi C (eds). Lucca; 25–32.
- Boscato P, Crezzini J, Freguglia M *et al.* 2010. Activités de subsistance et exploitation des ressources de l'environnement à S. Croce (Bisceglie – Bari – Italie du Sud): les unités stratigraphiques 546 et 535 du Paléolithique moyen. In *Settlement Dynamics of the Middle Paleolithic and Middle Stone Age Vol. III*, Conard NJ, Delagnes A (eds). Kerns Verlag: Tübingen; 265–282.
- Boscato P, Crezzini J, Pellegrini A. 2006b. Le parti mancanti: faune del Paleolitico medio nel deposito esterno della Grotta di Santa Croce, Bisceglie (BA). In *Archaeozoological Studies in Honour of Alfredo Riedel*, Tecchiati U, Sala B (eds). Bolzano; 39–50.
- Boscato P, Gambassini P, Rinaldo F *et al.* 2011. Management of Palaeoenvironmental Resources and Raw materials Exploitation at the Middle Paleolithic Site of Oscurusciuto (Ginosa, Southern Italy): Units 1 and 4. In *Neanderthal Lifeways, Subsistence and Technology*, Conard NJ, Richter J (eds). Springer: Berlin; 87–98.
- Boscato P, Gambassini P, Ronchitelli A. 2006a. Grotta di Santa Croce di Bisceglie (Prov. di Bari). *Rivista di Scienze Preistoriche* **LVI** 614–615.
- Boscato P, Ronchitelli A. 2007. Le strutture di combustione al Riparo l'Oscurusciuto (Ginosa – TA). *Studi di Preistoria e Protostoria* **4**: 175–180.
- Brennan BJ, Rink WJ, McGuire EL *et al.* 1997. Beta doses in tooth enamel by “one-group” theory and the ROSY ESR dating software. *Radiation Measurements* **27**: 307–314.
- Cardini L. 1954. Scoperte e scavi paleontologici in Italia 1954: Bisceglie. *Bari. Rivista di Scienze Preistoriche* **IX**: 230–231.
- Ciullo S. 2016. *Archeozoologia nella Grotta di Santa Croce (Bisceglie – BT)*. Le unità stratigrafiche 538–549. Bachelor Thesis, University of Siena.
- Collina C, Marciani G, Martini I *et al.* 2020. Refining the Uluzzian through a new lithic assemblage from Rocca San Sebastiano (Mondragone, southern Italy). *Quaternary International* **551**: 150–168. <https://doi.org/10.1016/j.quaint.2020.03.056>
- Columbu A, Chiarini V, Spötl C *et al.* 2020. Speleothem record attests stable environmental conditions during Neanderthal-Modern

- Human turnover in Southern Italy. *Nature Ecology and Evolution*. **4**: 1188–1195.
- Dalla Valle C. 2008. *I micromammiferi dei livelli musteriani e romanelliani della Grotta del Cavallo (Lecce)*. Bachelor Thesis, University of Venezia.
- Ellwood BB. 2007. Magnetic susceptibility (MS), low-field. In *Encyclopedia of Geomagnetism and Paleomagnetism*, Gubbins D, Herrero-Bervera E (eds). Springer: Berlin; 566–571.
- Ellwood BB, Harrold FB, Benoist SL *et al.* 2001. Paleoclimate and intersite correlations from Late Pleistocene/Holocene cave sites: results from southern. *Europe. Geoarchaeology* **16**: 433–463.
- Ellwood BB, Zilhão J, Harrold FB *et al.* 1998. Identification of the Last Glacial Maximum in the Upper Paleolithic of Portugal using magnetic susceptibility measurements of Caldeirão cave sediments. *Geoarchaeology* **13**: 55–71.
- Fabbri PF, Panetta D, Sarti L *et al.* 2016. Middle Paleolithic human deciduous incisor from Grotta del Cavallo, Italy. *American Journal of Physical Anthropology* **161**: 506–512. [PubMed: 27365292]
- Gallini V, Sala B. 2001. Settepolesini di Bondeno (Ferrara – eastern Po Valley): the first example of mammoth steppe in Italy. In *The World of Elephants Proceedings of the First International Congress*, Cavaretta G (ed.), Gioia P, Mussi M, Palombo MR (eds). Consiglio Nazionale Delle Ricerche: Roma; 272–275.
- Gambassini P, Ronchitelli A. 1998. Linee di sviluppo dei complessi del Paleolitico inferiore-medio nel Cilento. *Rivista di Scienze Preistoriche* **XLIX**: 357–378.
- Grün R. 2000. Methods of dose determination using ESR spectra of tooth enamel. *Radiation Measurements* **32**: 767–772.
- Grün R. 2009. The DATA program for the calculation of ESR age estimates on tooth enamel. *Quaternary Geochronology* **4**: 231–232.
- Grün R, Katzenberger-Apel O. 1994. An alpha irradiator for ESR dating. *Ancient TL* **12**: 35–38.
- Grün R, Schwarcz HP, Chadam JM. 1988. ESR dating of tooth enamel: coupled correction for U-uptake and U-series disequilibrium. *International Journal of Radiation Applications and Instrumentation. Part D. Nuclear Tracks and Radiation Measurements* **14**: 237–241.
- Guérin G, Mercier N, Adamiec G. 2011. Dose-rate conversion factors: update. *Ancient TL* **29**: 5–8.
- Hajdinjak M, Fu Q, Hübner A *et al.* 2018. Reconstructing the genetic history of late Neanderthals. *Nature* **555**: 652–656. [PubMed: 29562232]
- Hemming SR. 2004. Heinrich Events: massive Late Pleistocene detritus layers of the North Atlantic and their global climate imprint. *Reviews of Geophysics* **42**: 1005.
- Heptner VG, Nasimovich AA, Bannikov AG. 1988. Mammals of the Soviet Union volume I. *Perissodactyla and Arciodactyla*. Smithsonian Institution Libraries, The National Science Foundation, Washington.
- Higham T, Douka K, Wood R *et al.* 2014. The timing and spatiotemporal patterning of Neanderthal disappearance. *Nature* **512**: 306–309. [PubMed: 25143113]
- Holt B, Negrino F, Riel-Salvatore J *et al.* 2019. The Middle-Upper Paleolithic transition in Northwest Italy: new evidence from Riparo Bombrini (Balzi Rossi, Liguria, Italy). *Quaternary International* **508**: 142–152.
- Hublin JJ, Sirakov N, Aldeias V *et al.* 2020. Initial upper Palaeolithic Homo sapiens from Bacho Kiro Cave, Bulgaria. *Nature* **581**: 299–302. [PubMed: 32433609]
- Iacoviello F, Martini I. 2012. Provenance and geological significance of red mud and other clastic sediments of the Mugnano cave (Montagnola Senese, Italy). *International Journal of Speleology* **41**: 317–328.
- Iacoviello F, Martini I. 2013. Clay minerals in cave sediments and terra rossa soils in the Montagnola Senese karst massif (Italy). *Geological Quarterly* **57**: 527–536.
- Kuhn SL. 1995. *Mousterian Lithic Technology and Raw Material Economy: a Cave Study*. Princeton University Press: Princeton.
- Lanos P, Philippe A, Lanos H *et al.* 2016. *Chronomodel: Chronological modelling of archaeological data using Bayesian statistics. (version 1.5)*. <http://www.chronomodel.fr>
- Liu XM, Rolph T, An Z *et al.* 2003. Paleoclimatic significance of magnetic properties on the Red Clay underlying the loess and paleosols in China. *Palaeogeography, Palaeoclimatology, Palaeoecology* **199**: 153–166.
- Long JA, Stoy PC. 2013. Quantifying the periodicity of Heinrich and Dansgaard–Oeschger events during Marine Oxygen Isotope Stage 3. *Quaternary Research* **79**: 413–423.
- Ricci Lucchi M. 2008. Vegetation dynamics during the Last Interglacial–Glacial cycle in the Arno coastal plain (Tuscany, western Italy): location of a new tree refuge. *Quaternary Science Reviews* **27**: 2456–2466.
- Lyman RL. 2008. *Quantitative Paleozoology*. Cambridge University Press: Cambridge.
- Lyman RL. 2019. A critical review of four efforts to resurrect MNI in zooarchaeology. *Journal of Archaeological Method and Theory* **26**: 52–87.
- Maher BA. 1986. Characterisation of soils by mineral magnetic measurements. *Physics of the Earth and Planetary Interiors* **42**: 76–92.
- Marciani G, Ronchitelli A, Arrighi S *et al.* 2020a. Lithic techno-complexes in Italy from 50 to 39 thousand years bp: an overview of lithic technological changes across the Middle-Upper Palaeolithic boundary. *Quaternary International* **551**: 123–149.
- Marciani G, Spagnolo V, Martini I *et al.* 2020b. Neanderthal occupation during the tephra fall-out: technical and hunting behaviours, sedimentology and settlement patterns in SU 14 of Oscurusciuto rock shelter (Ginosa, southern Italy). *Archaeological and Anthropological Sciences* **12**: 152.
- Marra AC. 2009. Pleistocene mammal faunas of Calabria (southern Italy): biochronology and palaeobiogeography. *Bollettino della Società Paleontologica Italiana* **48**: 113–122.
- Marra F, Petronio C, Ceruleo P *et al.* 2018. The archaeological ensemble from Campoverde (Agro Pontino, central Italy): new constraints on the Last Interglacial sea level markers. *Scientific Reports* **8**: 17837. [PubMed: 30546120]
- Martini I, Baucon A, Boschian F. 2020. Depositional processes and environmental settings in rock shelters: the case of the prehistoric Oscurusciuto site (Southern Italy). *Geological Magazine* 1–14.
- Martini I, Ronchitelli A, Arrighi S *et al.* 2018. Cave clastic sediments as a tool for refining the study of human occupation of prehistoric sites: insights from the cave site of la Cala (Cilento, southern Italy). *Journal of Quaternary Science* **33**: 586–596.
- Masini F, Abbazzi L. 1997. L'associazione di mammiferi della Grotta di Castelcivita. In *Il Paleolitico della Grotta di Castelcivita, cultura e ambiente*, Gambassini P (ed.). Materiae 5, Electa: Napoli; 33–57.
- Masini F, Sala B. 2011. Consideration on an integrated biochronological scale of Italian Quaternary continental mammals. *Quaternario, Italian Journal of Quaternary Science* **24**: 193–198.
- Morales-Barbero J, Martinez PA, Ferrer-Castán D *et al.* 2018. Quaternary refugia are associated with higher speciation rates in mammalian faunas of the western Palaeartic. *Ecography* **41**: 607–621.
- Moroni A, Boscato P, Ronchitelli A. 2013. What roots for the Uluzzian? Modern behaviour in Central-Southern Italy and hypotheses on AMH dispersal routes. *Quaternary International* **316**: 27–44.
- Moroni A, Boschian G, Crezzini J *et al.* 2019. Late Neanderthals in central Italy. High-resolution chronicles from Grotta dei Santi (Monte Argentario – Tuscany). *Quaternary Science Reviews* **217**: 130–151.
- Moroni A, Ronchitelli A, Arrighi S *et al.* 2018. Grotta del Cavallo (Apulia – Southern Italy). The Uluzzian in the mirror. *Journal of Anthropological Sciences* **96**: 1–36.
- Ordonez A, Svenning JC. 2017. Consistent role of Quaternary climate change in shaping current plant functional diversity patterns across European plant orders. *Scientific Reports* **7**: 42988. [PubMed: 28230069]
- Palma di Cesnola A. 1967. Il Paleolitico della Puglia. *Memorie del Museo Civico di Storia Naturale di Verona* **15**: 1–84.
- Palma di Cesnola A. 2001. Il Paleolitico inferiore e medio in Italia. Millenni 3; Firenze.
- Pandolfi L, Tagliacozzo A. 2013. Earliest occurrence of woolly Rhino (*Coelodonta antiquitatis*) in Italy (Late Pleistocene, Grotta Romanelli site). *Rivista Italiana di Paleontologia e Stratigrafia* **119**: 125–129.

- Peresani M, Bertola S, Delpiano D *et al.* 2019. The Uluzzian in the north of Italy: insights around the new evidence at Riparo Broion. *Archaeological and Anthropological Sciences* **11**: 3503–3536.
- Peretto C, Arzarello M, Coltorti M *et al.* 2020. Grotta Reali, the first multilayered mousterian evidences in the Upper Volturno Basin (Rocchetta a Volturno, Molise, Italy). *Archaeological and Anthropological Sciences* **12**: 67.
- Petit RJ, Brewer S, Bordács S *et al.* 2002. Identification of refugia and post-glacial colonisation routes of European white oaks based on chloroplast DNA and fossil pollen evidence. *Forest Ecology and Management* **156**: 49–74.
- Petronio C, Bellardini F, Arzarello M *et al.* 2008. The deposit of the late Pleistocene from Avetrana (Taranto, Southern Italy): biochronology and palaeoecology. *Quaternario* **21**: 409–422.
- Pitti C, Tozzi C, Sorrentino C. 1976. *L'industria di tipo paleolitico superiore arcaico della Grotta la Fabbrica (Grosseto): nota preliminare Atti della Società Toscana di Scienze Naturali* **83**: 174–201.
- Prescott JR, Hutton JT. 1994. Cosmic ray contributions to dose rates for luminescence and ESR dating: large depths and long-term time variations. *Radiation Measurements* **23**: 497–500.
- Rinaldo F, Arrighi S, Freguglia M *et al.* 2017. La variabilità tecnica del Musteriano della Grotta di Santa Croce (Bisceglie - BT). *Studi di Preistoria e Protostoria* **4**: 153–158.
- Ronchitelli A, Boscato P, Surdi G *et al.* 2011. The Grotta Grande of Scario (Salerno, Italy): archaeology and environment during the last interglacial (MIS 5) of the Mediterranean region. *Quaternary International* **231**: 95–109.
- Sano K, Arrighi S, Stani C *et al.* 2019. The earliest evidence for mechanically delivered projectile weapons in Europe. *Nature Ecology and Evolution* **3**: 1409–1414. [PubMed: 31558829]
- Sardella R, Bertè D, Iurino DA *et al.* 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. *Quaternary International* **328–329**: 179–195.
- Sarti L, Boscato P, Lo Monaco M. 2000. Il Musteriano finale di Grotta del Cavallo nel Salento: studio preliminare. *Origini* **XXII**: 45–109.
- Sarti L, Romagnoli F, Carmignani L *et al.* 2017. Grotta del Cavallo (scavi Sarti): tradizione e innovazione nella sequenza musteriana sulla base dell'indicatore litico. *Studi di Preistoria e Protostoria* **4**: 131–138.
- Schwarcz HP, Bietti A, Buhay WM *et al.* 1991a. On the reexamination of Grotta Guattari: uranium-series and electron-spin-resonance dates. *Current Anthropology* **32**: 313–316.
- Schwarcz HP, Buhay W, Grün R *et al.* 1991b. Absolute dating of sites in coastal Lazio. *Quaternaria Nova* **1**: 51–67.
- Segre AG, Cassoli PF. 1987. Giacimento preistorico del Pleistocene medio e superiore della grotta Di S. Croce, Bisceglie (Bari). *Atti XXV Riunione Scientifica I.I.P.P., Monopoli 16-19 ottobre* **1984**: 111–118.
- Shao Q, Bahain JJ, Dolo JM *et al.* 2014. Monte Carlo approach to calculate US-ESR age and age uncertainty for tooth enamel. *Quaternary Geochronology* **22**: 99–106.
- Shao Q, Bahain JJ, Falguères C *et al.* 2011. New ESR/U-series data for the early Middle Pleistocene site of Isernia la Pineta, Italy. *Radiation Measurements* **46**: 847–852.
- Shao Q, Chadam J, Grün R *et al.* 2015. The mathematical basis for the US-ESR dating method. *Quaternary Geochronology* **30**: 1–8.
- Sommer RS, Benecke N. 2005. The recolonization of Europe by brown bears *Ursus arctos* Linnaeus, 1758 after the Last Glacial Maximum. *Mammal Review* **35**: 156–164.
- Sommer RS, Zachos FE. 2009. Fossil evidence and phylogeography of temperate species: 'glacial refugia' and post-glacial recolonization. *Journal of Biogeography* **36**: 2013–2020.
- Spagnolo V, Crezzini J, Marciani G *et al.* 2020a. Neanderthal camps and hyena dens. Living floor 150 A at Grotta dei Santi (Monte Argentario, Tuscany, Italy). *Journal of Archaeological Science: Reports* **30** [PubMed: 102249].
- Spagnolo V, Marciani G, Aureli D *et al.* 2016. Between hearths and volcanic ash: The SU 13 palimpsest of the Oscurusciuto rock shelter (Ginosa – Southern Italy): analytical and interpretative questions. *Quaternary International* **417**: 105–121.
- Spagnolo V, Marciani G, Aureli D *et al.* 2019. Neanderthal activity and resting areas from stratigraphic unit 13 at the Middle Palaeolithic site of Oscurusciuto (Ginosa – Taranto, Southern Italy). *Quaternary Science Reviews* **217**: 169–193.
- Spagnolo V, Marciani G, Aureli D *et al.* 2020b. Climbing the time to see Neanderthal behaviour's continuity and discontinuity: SU 11 of the Oscurusciuto Rockshelter (Ginosa, Southern Italy). *Archaeological and Anthropological Sciences* **12**: 54.
- Stuart AJ. 2005. The extinction of woolly mammoth (*Mammuthus primigenius*) and straight-tusked elephant (*Palaeoloxodon anti-quus*) in Europe. *Quaternary International* **126–128**: 171–177.
- Tagliacozzo A, Romandini M, Fiore I *et al.* 2013. Animal exploitation strategies during the Uluzzian at Grotta di Fumane (Verona, Italy). In *Zooarchaeology and Modern Human Origins*, Clark JL, Speth JD (eds). Springer: Dordrecht; 129–150.
- Tozzi C. 1970. La Grotta di S. Agostino (Gaeta). *Rivista di Scienze Preistoriche* **XXV**: 3–87.
- Valensi P. 2009. Evolution des peuplements mammaliens en Europe méditerranéenne occidentale durant le Pléistocène moyen et supérieur. Un exemple régional: les Alpes du Sud françaises et italiennes. *Quaternaire* **20**: 551–567.
- Valensi P, Psathi E. 2004. Faunal Exploitation during the Middle Palaeolithic in South-Eastern France and North-Western Italy. *International Journal of Osteoarchaeology* **14**: 256–272.
- Villa P, Pollarolo L, Conforti J *et al.* 2018. From Neanderthals to modern humans: new data on the Uluzzian. *PLOS ONE* **13** e0196786. [PubMed: 29742147]
- Zanchetta G, Giaccio B, Bini M *et al.* 2018. Tephrostratigraphy of Grotta del Cavallo, Southern Italy: insights on the chronology of Middle to Upper Palaeolithic transition in the Mediterranean. *Quaternary Science Reviews* **182**: 65–77.