Title: New human remains from the Late Epigravettian necropolis of Arene Candide (Liguria, northwestern Italy): direct radiocarbon evidence and inferences on the funerary use of the cave during the Younger Dryas.

Authors: Vitale S. Sparacello[1,2], Irene Dori[3,4], Stefano Rossi[5], Alessandra Varalli[6], Julien Riel-Salvatore[7,] Claudine Miguel-Gravel[7,8], Alessandro Riga[4], Francesca Seghi[4], Gwenaëlle Goude[9], Sanne W.L. Palstra[10], Elisabetta Starnini[11], Vincenzo Formicola[12], Jacopo Moggi-Cecchi[4].

[1] Dipartimento di Scienze della Vita e dell'Ambiente, sezione di Neuroscienze e Antropologia, Università degli Studi di Cagliari, Cittadella Monserrato, Cagliari, Italy
[2] Univ. Bordeaux, CNRS, PACEA, UMR 5199, 33616, Pessac, France
[3] SABAP Soprintendenza Archeologia, Belle Arti e Paesaggio per le province di Verona, Rovigo e Vicenza, Verona, Italy
[4] Dipartimento di Biologia, Università Degli Studi di Firenze, Firenze, Italy
[5] Soprintendenza Archeologia, Belle Arti e Paesaggio per le province di Como, Lecco, Monza-Brianza, Pavia, Sondrio e Varese, Milano, Italy
[6] CaSEs Research Group, Department of Humanities, Universitat Pompeu Fabra, Barcelona, Spain
[7] Département d'Anthropologie, Université de Montréal, Montréal (QC), Canada
[8] Institute of Human Origins, School of Human Evolution and Social Change, Arizona State University, Tempe, AZ, USA
[9] Aix Marseille Univ, CNRS, Minist Culture, LAMPEA, Aix-en-Provence, France
[10] Centre for Isotope Research, ESRIG, University of Groningen, the Netherlands
[11] Dipartimento di Civiltà e Forme Del Sapere, Università di Pisa, Pisa, Italy
[12] Dipartimento di Biologia, Università di Pisa, Pisa, Italy

Abstract

The Arene Candide Cave is a renowned site on the northwestern Italian coast that has yielded numerous burials dating back to the terminal phases of the Pleistocene (Epigravettian culture). Thanks to the exceptional preservation of the remains, and to the information collected during the excavations conducted beginning in the 1940s, researchers were able to reconstruct a complex pattern of manipulation of older burials that consistently occurred when interring new individuals. Therefore, the Epigravettian necropolis provides a rare

glimpse into the modalities, and possibly the motives, of funerary behavior in the Late Upper Paleolithic, a period during which formal burial was highly selective. The reasons for this selection are still unclear, but it has been proposed that they may be related to "exceptional events" (violence and trauma) and "exceptional people" (disease and deformities due to congenital conditions).

This study presents an assemblage of hundreds of skeletal elements and fragments belonging to two new individuals, and to individuals of the necropolis that were already known. The remains were discovered during the reassessment of the collections kept at the Museum of Natural Sciences, Section of Anthropology and Ethnology of the University of Florence, which had never been described since their excavation in 1940-42.

The analysis extends our knowledge of the biological profile of the individuals buried at the site, which is fundamental for our understanding of Late Upper Paleolithic funerary behavior. The inclusion of two new individuals in the skeletal series, both children aged around 1-1.5 years, suggests that age may have not been a significant factor in determining funerary treatment.

New radiocarbon dates on human bone – together with the cross-referencing of the available dates with the stratigraphic relations between burials and clusters of bones in secondary deposit – suggest that the entire necropolis is bracketed within a millennium corresponding to the Younger Dryas cooling event (i.e. between ca. 12,900 and 11,600 cal BP). Arene Candide Cave was a highly-visible landmark in the landscape, and funerary gestures in the Epigravettian necropolis emphasized the ties with the ancestors. It is possible that funerary behavior at Arene Candide was a means of claiming territorial access to resources, as well as reinforcing and transmitting communal identity and values, through a period of climate-induced resource stress and competition. Isolation and small refugia during cooling events may have contributed to exacerbating genetic drift, and increased the frequency of cultural means to sanction "exceptional people and events".

Keywords: Pleistocene, Paleoanthropology, Europe, Younger Dryas, Funerary behavior.

1. Introduction

Burials provide some of the most informative data one can use to reconstruct Upper Paleolithic social norms (Pettitt 2011). However, during this period of human history, the

archaeological evidence of funerary sites is unevenly distributed in time and space. This generally makes it problematic to extrapolate past cultural conventions from burials to the Upper Paleolithic as a whole, except in rare contexts where several are found within a single region or site dating to a well-defined chronological interval (Riel-Salvatore and Gravel-Miguel 2013). Such sites offer rare, more complete glimpses into the logic of mortuary behavior and how it articulated with other facets of life in the Late Pleistocene. In particular, such clusters of burials can help highlight what made these sites particularly and recurrently important for their occupants and how this articulated with other facets of their social life, including territoriality, land-use strategies and subsistence patterns. Focusing on grave-specific features as well as with other dimensions of funerary ritual in such contexts can further help clarify elements of the belief systems that structured their use and reuse over time (Riel-Salvatore and Gravel-Miguel 2013).

The Arene Candide Cave is one place that stands out in the panorama of Upper Paleolithic funerary sites for the abundance of burials it has yielded and for the quality of their documentation, which has been supplemented by recent fieldwork and reanalysis of its mortuary record (Cardini 1980, Formicola et al. 2005, Riel-Salvatore et al. 2018, Sparacello et al. 2018). These complementary sets of data provide the resolution needed to test the idea that, at the end of the Upper Paleolithic, the site was a key location in a region characterized by bands of Final Epigravettian foragers who sought to perennialize their link to this conspicuous landmark and the surrounding resources (Riel-Salvatore and Gravel-Miguel 2013: 335-336).

Arene Candide (Italian for "White Sands") is a large cave system located in the municipality of Finale Ligure (Savona, Liguria, northwestern Italy; Figure 1), and it is one of the most important prehistoric archaeological sites in Europe due to its stratigraphy spanning from the Upper Paleolithic to the Byzantine era (Bietti and Molari, 1994; Maggi et al., 1997; Arobba et al., 2017), and to the numerous Neolithic and Upper Paleolithic burials unearthed therein since the latter part of the 19th century (Del Lucchese, 1997; Formicola et al., 2005; Sparacello et al., 2018, 2020). The investigation of the Upper Pleistocene layers began in the 1940s (Cardini, 1941, 1942, 1946, 1980) and led to the discovery of a large funerary space – apparently marked by the deposition of a complete set of elk antlers (*Alces alces*) – containing a minimum of 20 individuals in primary and secondary deposition dating to the end of the Pleistocene and attributed to the Final Epigravettian culture (Bietti and Molari, 1994; Formicola et al., 2005; Sparacello et al., 2018). A few meters below the "Epigravettian necropolis", as it became known, the famous Gravettian burial of the "Giovane Principe" was

found (i.e. the "Young Prince"; Cardini, 1942; Pettitt et al., 2003; Riel-Salvatore et al., 2017). The Epigravettian necropolis is among the largest and best-documented assemblage of Late Upper Paleolithic human remains from a single European site, and it represents an invaluable source of information for studies on the biological anthropology (e.g. Formicola and Scarsini, 1987; Formicola et al., 1990; Formicola, 1995; Holt, 2003; Formicola and Holt, 2007; Holt and Formicola, 2008; Sparacello et al., 2017; Trinkaus, 2018) and funerary behaviors (e.g. Mussi et al., 1989; Formicola et al., 2005; Formicola, 2007; Riel-Salvatore and Gravel-Miguel, 2013; Riel-Salvatore et al., 2018; Sparacello et al., 2018) of Late Pleistocene human groups.

[Figure 1 about here]

Although a large portion of the Pleistocene deposit at Arene Candide has been explored since the 1940s, the discoveries relevant to the study of funerary behaviors and human paleobiology were not evenly distributed in time and space. Virtually all burials and clusters of bones in secondary deposition belonging to the Epigravettian were unearthed during the 1940-42 excavation campaigns by Bernabò Brea and Cardini (with the contribution of Virginia Chiappella; Cardini, 1941, 1942, 1946, 1980), in an area immediately south of the main pillar of the cave (Figure 2). During the 1948-50 campaigns, the same researchers explored the easternmost portion of the cave (zones F, G, and H) and did not report the finding of Epigravettian burials (but see below). A single burial was unearthed against the southern wall during the 1970-72 excavations initiated by Cardini in zone A (Formicola and Toscani, 2014; Figure 2). Finally, excavations that took place between 2008 and 2011 under the direction of Julien Riel-Salvatore and Roberto Maggi focused mostly on zones D and F east of the 1940-42 excavations, and led to the discovery of a single human bone attributed to one of the individuals from the necropolis (Riel-Salvatore et al., 2018; Sparacello et al., 2018; Figure 2). The finding of Epigravettian human remains, and in particular of burials, is a rare occurrence at Arene Candide, as Upper Paleolithic inhumations are generally extremely rare (e.g. Riel-Salvatore and Gravel-Miguel, 2013). Therefore, each new discovery has the potential to significantly contribute to our understanding of the biology and funerary behaviors of the last Pleistocene hunter-gatherers in the northwestern Mediterranean.

[Figure 2 about here]

In this paper, we report the largest finding of Epigravettian human remains from Arene Candide since 1942. Rather than deriving from new field excavations, all the remains were

discovered in the storage facilities of the Museum of Natural Sciences, Section of Anthropology and Ethnology of the University of Florence (henceforth abbreviated to MSNF), in the context of two joint research projects (see Acknowledgements section) aimed at the systematic re-study of the composition, biology, and absolute chronology of the skeletal collections from the Finalese area in Liguria (e.g. Sparacello et al., 2019, 2020; Dori et al., 2020). All the remains belong to the Bernabò Brea – Cardini 1940-42 excavations and were left unstudied and forgotten, or, in the case of the burial, were erroneously attributed to the Neolithic (Bernabò Brea, 1956). We present here a database detailing the composition of this assemblage, the attribution of the skeletal elements and fragments to known or new individuals (cf. Sparacello et al., 2018), and new elements on the biological profile of the individuals to whom formal funerary treatment was accorded at Arene Candide. Furthermore, we performed new AMS dates directly on human bones aimed at the chronological characterization of the new material, and to a refining of the chronology of the necropolis as a whole.

1.1 Epigravettian funerary behaviors at Arene Candide and their relative and absolute chronology

The analysis of funerary behaviors in the "Epigravettian necropolis" began with Cardini (1980), who identified the primary burials and several clusters of bones using roman numerals (Figure 3). Primary inhumations contained one (II, VIII, X, XI, XV, XVI) or two individuals (Va-b and VIa-b) buried supine with extended limbs and covered with red ochre. The depositions were accompanied by abundant grave goods consisting of shell pendants, faunal remains, pierced deer canines, oblong stone pebbles, minerals, and knapped flint instruments (Cardini, 1980). In addition to a striking standardization of funerary treatment in terms of position and grave goods, Cardini also noted recurrent behaviors such as disturbing previous burials but leaving their legs in place (VIa-b and X-XI), or placing the child to the left of the adult when creating double burials (Va-b and VIa-b; Figure 3; Cardini, 1980). Single primary inhumations of children were represented by burial VIII, and two perinatal individuals (VII and IX) which were reported as lost (Cardini, 1980).

The area of the necropolis includes multiple bone clusters containing disarticulated skeletal elements, which have been the subject of different interpretations over the years. Cardini suggested that they were due to disturbances caused by subsequent interments, but that they could still be classified as burials, because they contained the bones of the same individual

deposited within depressions, which he interpreted as the original grave cuts (e.g. III, XII, XIII, XIV; Cardini, 1980). However, for two clusters (I and IV) he hypothesized "an intentional placement, almost a secondary deposition of groups of bones coming from previous disturbed inhumations" (translated from Cardini, 1980:13). In disagreement with this interpretation, secondary manipulation of burials was later proposed by Mussi et al. (1989), based on the fact that several clusters appeared to be distant from primary inhumations. This interpretation was further supported by Formicola et al. (2005) based on the radiocarbon date obtained from the cluster of disarticulated skeletal elements n° III, which at 11,830-11,330 cal BP (OxA-10998, 10,065±55 BP; Formicola et al., 2005; Table 1) was the youngest among nearby burials and appeared therefore to be a secondary deposition made in absence of subsequent interments (Formicola et al., 2005).

[Table 1 about here]

The radiocarbon determinations spearheaded by Formicola and colleagues (2005) suggested that strikingly similar funerary behaviors took place at the site in two temporal phases separated by about a millennium (Table 1; Formicola et al., 2005), indicating a remarkable continuity in the funerary program of Epigravettian hunters. However, the authors observed that additional dates were necessary, having obtained only six determinations, while four other individuals failed to produce enough collagen (Formicola et al., 2005).

The complexity of Epigravettian funerary behaviors at Arene Candide was further explored by Sparacello et al. (2018), who re-analyzed the skeletal assemblage of the bone clusters and cross-referenced the attributions to the various individuals with evidence from excavation diaries and pictures. The study concluded that clusters I and IV were indeed intentionally and neatly arranged around burial II (Figure 3), as suggested by Cardini (1980), but also that the disordered remains in cluster III contained the bones of the same two individuals present in cluster I and IV (see also Paoli et al., 1980; Formicola, 1995). This evidence is in contrast with Cardini's interpretation that bone clusters were disturbed primary burials (Cardini, 1980), but also with the more recent suggestion that cluster III was not in relation with a subsequent burial (Formicola et al., 2005; see also Mussi at al., 1989). However, it did confirm the hypothesis that the bone clusters of the Arene Candide were not linked to the simple necessity of making space for new burials, but were in fact part of a mortuary behavior involving the secondary manipulations of existing burials. Sparacello et al. (2018) assigned arabic numerals to the individuals recognized from burials and clusters (which have

roman numerals) and interpreted the above evidence in the following manner: when burying individual AC 2, a double burial, or two very close burials (individuals AC 3 and AC 4), were moved aside completely and together, resulting in the disordinate commingling of their bones into an assemblage now known as cluster III. Individual AC 2 was deposited, forming burial II, and then several skeletal elements (especially the crania) were picked from cluster III and neatly arranged in stone niches around burial II, resulting in the formation of clusters I and IV (Figure 3). Long bones were stacked in cluster IV, above which two ossa coxarum cradled the cranium of one individual (AC 4; Cardini et al., 1980:15); the cranium of the other individual (AC 3) was placed in close contact with the head of the newly inhumed, i.e. AC 2 (Sparacello et al., 2018). The authors proposed that this movement back and forth of skeletal elements from cluster III to I and IV was supported by the presence in cluster IV of some tarsals belonging to the adolescent individual from cluster XIII, which they assumed was already in place at the time of the deposition of burial II. This transportation of bones from the clusters to stone niches around new burials, also observed for burial XV, would explain the presence of clusters apparently not in direct spatial relationship with new burials, as well as the fact that these clusters do not contain complete skeletons (cf. Mussi et al., 1989, Formicola et al., 2005).

[Figure 3 about here]

Overall, the above evidence suggests that Epigravettian people at Arene Candide performed a multi-stage funerary program involving the intentional manipulation of older burials and the re-arrangement of their parts, especially crania, around new burials. This evokes a ritual connection between the bones of the ancestors, the newly-deceased, and the people performing the funerary behaviors (Sparacello et al., 2018), and echoes patterns of mortuary behaviors described in the ethnographic record as “rites of separation and incorporation” (e.g. Van Gennep, 1909; Metcalf and Huntington, 1979; Bloch and Parry, 1982; Fowler, 2004). These behaviors are typical of complex hunter-gatherer societies requiring long-term transmission of values (Woodburn, 1980), and indeed the same funerary program was repeated at Arene Candide over centuries, suggesting that it held cultural currency and meaning for a long time (Formicola et al., 2005).

However, previous work left some chronological issues open, such as undated accumulations of skeletal elements (notably the ones labeled XIII and XV), and uncertainties regarding the containment of the whole necropolis within the Pleistocene. In fact, according to the new

assessment of funerary behavior made in Sparacello et al. (2018), the last Epigravettian burial of the necropolis excavated in 1940-42 would be number II. This burial must have been emplaced after the formation of clusters I, III, and IV, and after the deposition of burial Va-b, given that this double burial is covered by cluster IV. The top of the Pleistocene sequence is dated to 12,000-11,160 cal BP (Beta-49694, 9980±140 BP; MacPhail et al., 1994; Table 1); considering the date of 11,620-11,220 cal BP obtained for Vb (Oxa-10999, 9925±50 BP; Formicola et al., 2005; Table 1), burial II and Va-b would be chronologically placed in the second half of the 12th millennium cal BP, i.e. slightly beyond the abrupt end of the Younger Dryas cooling event at 11,650-11,550 cal BP (Alley, 2000; Grachev and Severinghaus, 2005). This would indicate that the remarkable persistence of Arene Candide as a funerary space for Epigravettian groups would not only have endured several centuries, but also a major climatic shift. This chronology lends strong support to the idea that, in the specific case of the Arene Candide 'necropolis,' the recurrent use of the site as a funerary and ritual site in the terminal Pleistocene likely was a climate-mediated behavioral strategy, unlike for Upper Paleolithic burials as a whole (Riel-Salvatore and Gravel-Miguel 2013; Riel-Salvatore et al. 2018). However, a direct date on burial II would have been necessary to confirm this inference.

Sparacello and coworkers (2018) also noted that, if older bones were manipulated in the context of further depositions, the finding of human remains in any area of the cave may signal the nearby presence of additional burials. The discovery made in 2011, several meters east of the necropolis, of a bone belonging to the individual from cluster XIII (AC 13; Riel-Salvatore et al., 2018; Sparacello et al., 2018), would therefore predict that more burials could have been present in the easternmost portion of the cave. As discussed below, the materials presented in this study demonstrate that the prediction was correct.

2. Materials and Methods

The new skeletal material from the Epigravettian necropolis was contained in six cardboard and wooden boxes discovered in 2019 in the deposits of the MSNF (Moggi-Cecchi, 2014). In addition to bones, the boxes contained notes handwritten by Cardini (cf. Sparacello et al., 2018), tags written during the 1940-42 excavations at Arene Candide, and scraps of newspapers from the time. None of the tags seems to refer to the Bernabò Brea and Cardini 1948-50 excavations in the same layers. The skeletal assemblage is partially fragmentary, but can be estimated to > 150 skeletal elements, in addition to > 150 ribs and rib fragments.

As the wooden and cardboard boxes containing the assemblage were crumbling, their contents were relocated to sealed plastic bags. During this relocation, we made sure to transfer the information written in the boxes and in the excavation notes as well. Each skeletal element was identified, and, when possible, age was estimated based on dental development, epiphyseal fusion, and skeletal measurements (Schaefer et al., 2009; AlQahtani et al., 2010; Boccone et al., 2010). All the remains were photographed, and several elements were 3D scanned using the structured-light scanner DAVID SLS-3 (David Group 2007-2015, now property of HP). The 3D scans were used to virtually refit fragments, compare, and articulate elements with the skeletal material housed in other Italian museums (Museo di Archeologia Ligure, Genova and Museo Archeologico del Finale, Finale Ligure) that had been scanned in the context of previous studies (Sparacello et al., 2018) and had been uploaded in the freely-accessible (CC BY-NC) repository "The Arene Candide 3D database" https://morphosource.org/Detail/ProjectDetail/Show/project_id/206 hosted by the platform MorphoSource.org by Duke University.

In addition to virtual refitting and articulation, the skeletal elements were attributed to the known individuals from the necropolis based on their cluster/burial of provenience. This information was gained from paint dots present on some of the bones, which are color-coded based on cluster/burial (e.g. a yellow dot for burial V, an amaranth dot for cluster XIV, and two yellow and green dots for cluster I; Sparacello et al., 2018). Information from the excavation diaries and pictures (housed at the Soprintendenza Archeologia, Belle Arti e Paesaggio per le province di Imperia, e Savona) was cross-referenced with the osteological analysis, as done in previous research (Sparacello et al., 2018). The assemblage was directly compared to the skeletal collection housed in Florence and catalogued with numbers ranging from 6726 and 6731, which derive from Bernabò Brea – Cardini excavations at Arene Candide and include both Neolithic and Epigravettian remains (Moggi-Cecchi, 2014).

Once the new material was attributed to known or new individuals, we sampled several fragments of bone for AMS dating (n=20) to refine the chronology of the necropolis. Samples were collected from the rediscovered assemblage, from the Epigravettian material housed at the MSNF, and from two burials housed in the Museo Archeologico del Finale to check for consistency of our results with previous radiocarbon determinations (Formicola et al., 2005). In addition, previous dating results from the large-scale AMS dating campaign on the entirety of the historical collections from the Ligurian Neolithic (Sparacello et al., 2020) showed that one child burial previously attributed to the Neolithic (AC X, Bernabò Brea – Cardini

excavations; Bernabò Brea, 1956) was in fact Epigravettian. Finally, we also sampled the elk antlers placed near burial XV (Cardini et al., 1980), fragments of which were preserved at the above mentioned Soprintendenza.

The bone collagen was extracted at the LAMPEA Biochemistry unit (UMR 7269, Aix-en-Provence, France), according to the international laboratory standard protocols on bone chunk (adapted from Richards and Hedges 1999). Bone external cortical surfaces, and spongious parts if any, were abraded with aluminum oxide by a sandblaster and air blasted to remove the remaining dust. The collagen was then extracted by a ABA-gelatinization procedure as following: demineralization in HCl (0.05M) at 4°C for several days and rinse several times with distilled water after demineralization completed; soaking in NaOH for 20 hours to remove potential remaining contaminant and rinsed several times with distilled water; solubilization in HCl (0.01M) at 70°C for 48 hours and filtration with EzeeFilter® device. The solubilized collagen extracted was then frozen (-80°C for a few hours) and freeze-dried for 2 days. Several skeletal elements from the Epigravettian necropolis are visibly coated with a layer of consolidant originating from organic matter, which was often used not only during restoration, but also during excavation (Goude et al., 2011; Sparacello et al., 2018, 2020). It has been shown that the coating is water soluble and can be removed by pretreating with an ultrasonic bath. Although effective in most cases, this pre-treatment does not always completely avoid the effect of recent organic material on the AMS determination (Sparacello et al., 2020). This issue can be mitigated by checking for consistency in multiple dates on different skeletal elements from the same individual. However, it is important to minimize the destruction of rare skeletal material, and we could perform multi-sampling only on a few individuals at this stage of the research. After pre-treatment and collagen extraction, the preservation state of samples was first checked by using the collagen extraction yield that must be ≥ 1% (e.g. Ambrose 1990). The collagen with a correct yield was then analyzed by a Europa Scientific EA analyzer to check the quality control in preparation for carbon, nitrogen and sulphur. The stable isotope compositions of $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ were measured by a Europa Scientific 20-20 IRMS (IsoAnalytical Ltd, Crewe, UK) to investigate diet and mobility within a diachronic perspective (cf. Goude et al. 2020, and Sparacello et al. in preparation). Only the collagen samples respecting the international recommendations should be considered as reliable: C ≥ 30%, N ≥ 10% (Ambrose 1993) with C/N between 2.9 and 3.6 (DeNiro 1985). After pre-treatment and collagen extraction, ^{14}C measurements were performed at the Centre for Isotope Research (CIO) of the University of Groningen. Collagen samples were combusted to CO_2 and

graphitized to graphite (Dee et al., 2020). Graphite targets were measured on $^{14}C/^{12}C$ ratio using the MICADAS (AMS system of IonPlus developed by ETH, Synal, 2007).

3. Results

Table 2 reports a summary of the new skeletal material, of the Epigravettian material housed at the MSNF, and of the attributions to known or new individuals. The individuals are numbered based on the Arabic numeration devised in Sparacello et al. (2018). A detailed version of the table, including information by bone such as box of provenience, stratigraphic information, refitting/articulation of elements, and presence/absence of paint dots, is available as Supplementary Information 1.

[Table 2 about here]

The boxes were marked with different letters and numbers (2, VI, IX, and X), although it is uncertain whether these markings hold any stratigraphic information, given that the Roman numerals found here would have corresponded to later Holocene layers and Arabic numerals were not used in the original stratigraphy from 1940-42 (cf. Bietti and Molari, 1994). On the contrary, the notes included inside the boxes make clear reference to the Pleistocene layers identified during the excavations (e.g. Xl and Xp, above the necropolis, and Xq, the layer of the necropolis; Bietti and Molari, 1994; Supplementary Information 1). Unfortunately, several tags containing more precise information were found loose in the boxes and are no longer in association with specific bones. Still, many skeletal elements are marked with the paint dots color-coded to identify the clusters and the burials (e.g. a yellow dot for burial V, an amaranth dot for cluster XIV, and two yellow and green dots for cluster I; Supplementary Information 1; Sparacello et al., 2018); therefore, their approximate position in the necropolis can be discerned. One box contained the tag "Xd 7°", which may refer to layer Xd, i.e. the lowermost of the Holocene sequence identified by Cardini (Bietti and Molari, 1994). However, this box contains several elements marked with the paint dots, which were applied only to bones coming from specific clusters in the layer of the necropolis (Xq). This suggests that some movement of bones and tags from one box to the other occurred in the past, and that unfortunately the only reliable information regarding the spatial and stratigraphic collocation of the remains is the one deriving from the paint dots.

According to the few information that can be gathered from the documentation accompanying the skeletal material, part of the rediscovered assemblage consists of the skeletal elements found below layer Xd, in which "an almost sudden disappearance of the

ceramic" could be noticed (translated from the diaries of the II excavation campaign, 3 May 1940). In the layers from Xe to Xq, the diaries report the finding of "scattered human remains, without discernible order, belonging to individuals of various ages" (translated from the diaries of the II excavation campaign, 8-10 May 1940). The cranium we attributed to AC 24 was accompanied by a note identifying it as the "cranium of a young boy of about ten years" which was accidentally crushed during the excavation and "should be considered as lost" (translated from the diaries of the II excavation campaign, 12-17 May 1940). Unfortunately, the rediscovered assemblage does not include the mandible presumably belonging to the same individual, which appears near the crushed cranium in the photographic documentation from the same excavation campaign (cf. Supplementary Information in Sparacello et al., 2018). In the same week, the first burial (II) and the cluster of bones surrounding it (I, III, and IV) were discovered, and the excavators began to mark the remains contained in them with color-coded paint dots, which also constitute a significant portion of the rediscovered assemblage (Supplementary Information1). In addition to elements found in the layers "above the necropolis", and in clusters/burials, part of the assemblage consists of non-clustered scattered remains found in the layer of the necropolis, described as "black soil among the tombs".

Based on age, size, morphology, and articulation/refitting, the skeletal elements of the rediscovered assemblage were mostly attributed to known individuals (Figure 4; Table 2; Supplementary Information 1). Several elements belong to the adults in secondary deposit from clusters I, III, IV, XII, XIV (i.e., individuals AC 3, 4, 12, and 14), and to the adolescent in cluster XIII (i.e., AC 13) (Table 2). Another adult is represented by an almost complete mandible showing advanced wear, which we attributed to AC 31 (6726.1 in the MSNF catalogue), an individual known from a fragmentary maxilla with a similar degree of wear and numerous small fragments of cranial remains. A partial skeleton was attributed to AC 20, the child (ca. 5-7 years of age) from the double burial VIa-b, of which only the legs and feet were found in primary deposit, and are preserved at the MSNF under catalogue number 6727.1 (Table 2; Sparacello et al., 2018). The aforementioned cranium of a ca. 9-10 year old child presumably belongs to AC 24, an individual previously known only from a humerus (preserved at the Museo di Archeologia Ligure, Genoa) and an isolated ischium (MSNF 6726.6; Table 2). We attributed the skeletal elements of a ca. 6-12 month old found among the new remains, as well as the perinatal remains preserved at the MSNF under catalogue number 6726.2, to the scarce remains of two "few month-old infants" found during the 1941

campaign (VII and IX according to Cardini, 1980; 7 and 9 according to Sparacello et al., 2018). Both the 9-10 year old and the two perinatal were reported as "lost" in the excavation diaries (Sparacello et al., 2018).

In addition to adding portions of the skeleton to known individuals, including some hitherto identified based on few remains, the reassessment of the skeletal collection has yielded two new Epigravettian individuals. Both are children of about 1-1.5 years of age based on dental development and have been labeled as AC 32 and AC 33 (Table 2; Figure 4). The remains belonging to AC 32 were found in 1950, during the seventh excavation by Bernabò Brea and Cardini, in the zone "H" against the eastern wall of the cave (diaries of the VII campaign, 30 May 1950). The excavators interpreted the finding as a primary inhumation dating back to the Neolithic, based on the stratigraphy (layer Xd), and on the apparent position of the skeleton, lying on the left side with flexed limbs (Bernabò Brea, 1956). The entire skeleton, which the excavators noted lacked elements from the legs and feet, was comprised in a ca. 22 cm wide space between two rocks (diaries of the VII campaign, 30 May 1950). The remains of AC 32 were catalogued in the MSNF museum (n° 6726.1), and briefly mentioned as a Neolithic burial (Tomb X) in Bernabò Brea monography about Arene Candide of 1956. However, skeletal elements belonging to this individual were found among the rediscovered material (Table 2). Although these remains were not accompanied by reliable spatial and stratigraphic information, none of them is marked with a paint dot, suggesting that they were not found in a cluster or near/within a burial. Conversely, all the skeletal elements belonging to AC 33, the other 1-1.5 years old, were found among the rediscovered remains, and some were marked with paint dots indicating that they were found in cluster I, IV, and XII (Supplementary Information 1). Given the presence of remains of both AC 32 and 33 among the rediscovered material, certain skeletal elements could not be attributed with certainty to one of them (Table 2; Supplementary Information 1).

Table 3 summarizes the results of the AMS dating, including the known dates from previous studies (a more detailed table is available in Supplementary Information 1, including information about the fragments that were dated). All of the 20 samples treated for collagen extraction and radiocarbon dating yielded an adequate amount of collagen (>1% of the sample weight), but four had collagen that was not compatible with a reliable date based on the isotopic criteria ($C \geq 30\%$, $N \geq 10\%$, C/N between 2.9 and 3.6), including unfortunately the elk antlers. The radiocarbon determinations from these unreliable samples fall between 11,200-9,010 cal BP. Additionally, we consider the results of two individuals as incoherent.

The ca. 6-12-month-old child (AC 7 or AC 9) gave a determination well into the Holocene of 10,240 – 9,960 cal BP (GrM-22238, 8995±30 BP). While its collagen meets the criteria for a reliable date, some skeletal elements attributed to this individual are marked with a green dot, indicating that they came from cluster XII of the necropolis, while other elements have no markings, indicating that they were found scattered in the necropolis' layer. The disturbance of the skeleton must therefore have happened at the time the necropolis was forming; hence we consider this date as incoherent with the stratigraphy (see Discussion). The adult AC 31 has C and N content only slightly above the cutoff (N=11%, C=30.2%), but notes accompanying the material indicate that cranial fragments of this individual were found in the structure of Tomb XV, which is dated to 10350±45 BP (Table 3). We therefore consider the date of AC 31 (9665±35) as incoherent.

The remaining 14 samples, belonging to 10 individuals, gave dates between 12,830-12,720 cal BP (AC 16; GrM-16978, 10820±40 BP) and 12,040-11,660 cal BP (AC 32, GrM-13423 10235±30 BP), confirming the long-term use of Arene Candide for funerary purposes. Multiple coherent new dates are available for AC 33 (2), AC 12 (2), and AC 20 (3). One of the dates for AC 33 derives from an occipital condyle, which we attributed to this individual based on the fact that it was found around burial Va-b (note accompanying MSNF n° 6727.3), similarly to other elements belonging to this individual (see above); however, the attribution is not certain given that the occipital squama of both AC 32 and AC 33 were found, unmarked, among the rediscovered material. Given the similar age, size, and chronological determination of AC 32 and AC 33, we made sure to obtain an additional date from an element of AC 33 which is also present among the remains found in the (purported) primary deposition of AC 32 (right femur; Supplementary Information 1).

Thanks to the attribution and refitting of bone fragments, we were able to re-date most of the individuals from previous studies [AC 3, AC 12, AC 20 (VIb), AC 14, and AC 16; Formicola et al., 2005; Formicola and Toscani, 2014], with the exception of AC 6 (Vb) and AC 8. In addition to the new individuals, we obtained a radiocarbon determination for individuals for which the analysis failed in the past, notably AC 2, AC 13, and AC 15 (Table 3, and Supplementary Information 1).

[Table 3 about here]

Figure 5 shows the plot of the calibrated dates, with the new dates in grey and the previously published dates in black; determinations for samples with low-quality collagen, or with

incoherent results, are reported in the table but not in the figure. The results of this study are consistent with previous dates for AC 20 (VIb) when dating the same fragment used in Formicola et al. (2005) (indicated with an asterisk in Figure 5) and when dating rediscovered fragments attributed to this individual. Dates that are consistent with previous determinations are given by individuals AC 14 and AC 16. For AC 12, our two dates on different fragments from the rediscovered remains are virtually identical, while the extraction made on the cranium attributed to the same individual yielded collagen of poor quality. The previous date obtained for AC 12 (indicated by a circle in Figure 5) is slightly older, showing a 95% confidence interval that does not overlap with the new ones (X-square test), but is compatible with the dates (published and new) obtained for AC 14, and it may in fact belong to this individual (see Discussion). A more significant discrepancy is observable for AC 3: the new date is significantly older than the previously published one (X-square test), and – more coherently with funerary behavior (Sparacello et al., 2018; see introduction) – overlaps with the new date obtained for AC 2 (Table 3, Figure 5).

[Figure 5 about here]

4. Discussion

The reassessment of the skeletal collections from Liguria preserved at the MSNF led to the discovery of a large assemblage of Epigravettian human remains from Arene Candide that had been lost to science for almost 80 years. Although part of the information collected by the excavators was lost, the cross-referencing of this rediscovered assemblage with the rest of the known collection, excavation diaries, and pictures, yielded new data on the biological composition of this extremely important Epigravettian necropolis. The integration of information derived from the rediscovered skeletal material with new radiocarbon dates on human remains complemented and refined the previous chronology of the necropolis (Formicola et al., 2005), and provided further insights into the complexity of Epigravettian funerary behavior at the site.

The rediscovered assemblage appears to derive exclusively from the excavations by Bernabò Brea and Cardini in 1940-42 (I-IV campaigns) and does not include notes making reference to the different layers and areas explored during 1948-50 excavations (V-VII campaigns). The remains can be therefore attributed to the general area of the 1940-42 excavations, i.e. immediately south of the main pillar of the eastern wing of the cave (Figure 2a). It is difficult to reconstruct the events that led to the neglect of these remains, but we present here a

possible scenario. We know that the skeletal elements belonging to the Arene Candide burials and clusters were cleaned and restored at the Istituto Italiano di Paleontologia Umana in Florence by R. Parenti and P. Cassoli, and that several of those burials were reconstructed for the exhibitions in the museums of Finale Ligure and Genova (Bernabò Brea, 1956). The skeletal elements described in this paper do not appear in the first list of human remains made by Cardini in 1954 after the restoration, nor are they mentioned in the monograph published in 1980, ten years after Cardini's demise (Cardini, 1980; Paoli, 1980; Sparacello et al., 2018). It is possible that, being mostly composed of elements found outside clusters, the remains discussed here were considered secondary. Due to that lesser status, they would have not been restored, and would have been eventually forgotten when Bernabò Brea was transferred away from Liguria and Cardini passed away. The following generations of anthropologists, more interested in reconstructing taphonomic changes and funerary gestures at the site (Formicola et al., 2005; Sparacello et al., 2018), puzzled over the eventual destiny of these skeletal elements, which were reported in the excavation diaries and visible in pictures, but had been irretrievable for decades.

For the most part, the remains studied here include elements belonging to already known adults, children, and one adolescent found in secondary deposition (clusters I, III, IV, XII, XIII, and XIV). The rediscovery of these elements gave the opportunity to date fragments belonging to known individuals without damaging their intact bones. In addition, the joint assessment of the new material with the collections housed in the MSNF led to the identification of the two lost infants (one perinatal and one aged ca. 6-12 months) labeled as VII and IX by Cardini (1980). Furthermore, two new individuals, aged between 1 and 1.5, could be added to the Epigravettian skeletal series. On the other end of the age spectrum, the rediscovered material includes an almost complete mandible of an adult with the most advanced degree of wear observed in the skeletal series, which is compatible with the few maxillary remains of AC 31 (MSNF n° 6728.2). Several scholars suggest that Late Upper Paleolithic funerary behavior may have been highly selective (particularly Gravettian and Epigravettian), and formal burial may have been accorded to exceptional people and exceptional events (Pettitt, 2011; Formicola, 2007; Sparacello et al., 2018). Exceptional factors may have included violence and disease, especially congenital, whose skeletal traces are found with extremely high frequency in Upper Paleolithic burials (Formicola, 1995; Formicola et al., 1990; Trinkaus, 2018; see below). The present analysis suggests that age may have not been a significant factor in determining funerary treatment at Arene Candide,

given that all age classes are represented. Given the high-mortality rates of infants and children among hunter-gatherers (e.g., Volk and Atkinson, 2013), it may be suggested that reasons other than "exceptionality" could have determined the funerary treatment in these cases. However, one possible link between age and a specific funerary behavior at Arene Candide can be hypothesized based on the presence of children placed on the left of the adult in the two double burials of the site (Va-b and VIa-b; Figures 2 and 3), or in the clear connection between the manipulation of burial X (adult) and the deposition of burial XI (child). Children may have been therefore connected to multiple burials, which may be related to an exceptional simultaneous death, an accident, or even human sacrifice (Formicola, 2007). Unfortunately, it is not possible to precisely reconstruct the depositional context of the two new children, and whether they could have been associated to another burial. In addition, more high-quality funerary data is necessary to further elaborate on issues of meaning, and especially on possible "accompanying deaths".

At this stage, we can infer that all elements belonging to AC 33 were found either within clusters of secondary depositions or scattered in the layers of the necropolis and above. Regarding AC 32, it was identified as a Neolithic primary burial during the 1950 excavation (VII campaign; Bernabò Brea, 1956). However, despite the claim made by the excavators that the skeleton was lying crouched on the left side, the only available picture suggests that the remains were not in clear anatomical connection (Tav. VI in Bernabò Brea, 1956), and the diaries state that they had been disturbed during excavation (diaries of the VII campaign, 30 May 1950). Furthermore, the partial skeleton was enclosed in a small space (ca. 22 cm) between two stones and lacked any element from the knee down. Given the recurrent funerary behavior described at Arene Candide of moving aside previous burials leaving in place legs and feet (VIa-B, and X-XI), and depositing disturbed bones within stone niches, the evidence described may represent a secondary deposition. Further investigations of this area of the cave (zone H) may find new elements to support this hypothesis, and possibly discover an associated primary deposition.

For the moment, the evidence provided by AC 32 confirms that funerary/mortuary behaviors occurred in the easternmost portion of the cave, as hypothesized based on the finding of the human talus belonging to AC 13 in zone F (Riel-Salvatore et al., 2018; Sparacello et al., 2018). A connection between the east portion of the cave and the area of the necropolis excavated in 1940-42 consists also in the finding of few remains belonging to AC 32 among the rediscovered skeletal assemblage. Overall, these findings suggest that further evidence of

funerary activities are likely to be found in future excavations in the unexplored Pleistocene deposit of Arene Candide cave.

Further insights into the funerary use of the cave are derived from the new set of radiocarbon dates on human bone. Unfortunately, as happened in previous studies, some of the extractions yielded collagen of low quality. Analyzing low-quality collagen increases the risk that the obtained ^{14}C age has been affected by foreign carbon sources, resulting in deviations compared to the true ^{14}C age. Indeed, these unreliable collagen samples gave determinations that are too young and are not coherent with other dates for the same individual (AC 12) or with the stratigraphic relations between burials and clusters (e.g., AC 4 must necessarily be older than AC 2). A possible foreign carbon source can have been the consolidant (animal glue) that was profusely applied to bones during excavation, as mentioned in the excavation diaries especially in reference to the set of elk antlers (diaries of the IV campaign, 7 April 1942). Combined with the relatively low collagen amount that was left in the bone materials, these foreign carbon sources could have affected the dating results, if they permeated the bone in a manner that could not be removed during pretreatment and collagen extraction (Devièse et al., 2019).

However, in one case (a 6-12-month-old child belonging to either AC 7 or AC 9) the radiocarbon determination is clearly too recent despite the sample passing the requirements for good-quality collagen. Two of the five bones attributed to this individual are marked with the paint dots indicating that they belonged to one of the clusters of the necropolis (Supplementary Information 1), yet its calibrated date falls in the 9th millennium BCE. The small fragment that was dated (proximal ulna) did not bear a paint dot; therefore, it could belong to a different individual who died around the same age, was deposited in the layers above the necropolis in the Early Holocene, and was brought to a lower stratigraphic level via animal burrowing. Certainly, it is not an intrusive Mesolithic burial, given that the few remains attributed to this individual are scattered in Pleistocene layers (Supplementary Information 1). However, we believe that it is more likely that this date is unreliable due to contamination (see below), and nevertheless should not be used to chronologically frame the necropolis. In fact, a hiatus in the stratigraphy is reported at Arene Candide between the top of the Pleistocene sequence and the earliest Neolithic layers (6880±60 uncal BP; Beta-66553; Maggi, 1997a, b), probably due to intensive erosive phenomena associated to the 8,200 BP climatic event (Kobashi et al., 2007). Similarly, we consider incoherent the date of AC 31, despite being only slightly younger than the other dates we obtained (9665±35 BP). In this

case, the CN criteria are just above the threshold, but the radiocarbon determination is incoherent with the information available on the deposition of this fragmentary individual. In fact, according to original accompanying notes, the cranial fragments of AC 31 were found, together with the more complete cranium of AC 12, in niches within the funerary structure of AC 15 (burial XV), which is dated to 10325±30 BP (Table 3). Incoherent dates from different skeletal elements of the same individual, both yielding good-quality collagen according to laboratory standards, were also observed during the large-scale dating of the Neolithic skeletal series from Arene Candide and nearby caves (Sparacello et al., 2020), and were attributed to consolidant and plaster contamination which could not be removed by pretreatment.

The possibility that samples passing the requirements for good-quality collagen may nevertheless yield a date biased by exogenous carbon sources is further suggested by the discrepancies between the dates in Formicola et al. (2005) and the ones obtained in this study. Our results suggest that the dates previously obtained for both AC 3 and AC 6 are slightly too young, and significantly different than our date for AC 3. In fact, the primary burial of AC 6 (Va-b) must be older than AC 2 and AC 3, given that it is covered by the primary burial of AC 2 and the organized cluster of bones IV, where elements belonging to AC 3 were retrieved (Sparacello et al., 2018; see also Introduction). Another slight discrepancy regards the two dates we obtained for AC 12, with ours being slightly younger than the one previously published (Formicola et al., 2005). Clusters XII, XIV, and III, were originally recognized as a single cluster given their proximity (this cluster was labeled III* in the notes accompanying the material; see also Formicola et al., 2005). Based on the list of bones attributed to each cluster signed by Cardini in 1954 (Sparacello et al., 2018) and on the tags accompanying the rediscovered material, it appears that some elements later attributed to XII (based on the green paint dot) may in fact belong to the larger cluster III*. It is therefore possible that the fragment of rib attributed to AC 12, which was dated in Formicola et al. (2005), belonged in fact to AC 14, as the dates seem to suggest. Alternatively, discrepancies could be attributed to different pretreatment protocols used in Formicola et al. (2005).

We propose a new chronological assessment of the necropolis, based on the new AMS dates (multiple dates from the same individual were combined), the stratigraphic/funerary relationship among burials, and the above discussion (Figure 6). The earliest directly-dated individuals were buried around 12,800-12,500 cal BP (AC 16, AC 14 in cluster XIV, AC 8/burial VIII, AC 20 in the double burial Via-b, and probably AC 12 in cluster XII, which

falls in a period in which the calibration curve has multiple peaks; Figure 6). It is not possible at this stage to assess the chronological placement of the sequential burial AC 10-11, given the high error present in the only date available for that burial (GX-16960-A, 11605±445 BP). The last burials were emplaced around 12,100-11,800 cal BP (the two infants AC 32 and 33, AC 2/burial II, and AC 3 in clusters I-III-IV; funerary associations and stratigraphic relationships between clusters and burials suggest also that AC 4 in clusters III-IV and AC 5 and 6 or burial Va-b are contemporaneous). In between these two phases fall the dates of two individuals (AC 13 in cluster XIII, and AC15/burial XV), whose calibrated range is unfortunately ample due to a plateau in the calibration curve.

[Figure 6 about here]

Overall, the new dates place the Epigravettian necropolis more firmly within the boundaries of the Younger Dryas cooling event, with the earliest burials dating to its onset, and the latest around its end, i.e. between ca. 12,900 and 11,600 cal BP (Alley, 2000). In addition, the new dates obtained for AC 12, 13, and 15 fall between the "two phases" of funerary use of Arene Candide proposed by Formicola et al. (2005; see also Introduction), suggesting that the cave was used to bury the dead more continuously, albeit rarely, during the latest cooling climatic event. Interestingly, no evidence of funerary use of the cave, and indeed very little human presence, is detectable in the layers below the Epigravettian necropolis until ca. 27,879-27,292 cal BP (Pettitt et al., 2003), with the burial of the Gravettian "Principe" during another cooling period (Rellini et al., 2013; Riel-Salvatore et al., 2018). It is possible that the use of Arene Candide as a funerary site during the Younger Dryas was a cultural response to climate-induced social dynamics (Cashdan et al., 1983; Blockley and Gamble, 2012; see discussion in Meltzer and Bar-Yosef, 2012; cf. Crombé, 2019); funerary practices may have reinforced communal identity (Bloch and Parry, 1982; e.g. Grosman and Munro, 2016) and transmitted values over time (Woodburn, 1980; Bell, 1992, 1997) during a period of increased resource stress and competition. Indeed, as argued elsewhere, the use of the site as a long-term cemetery may well have represented an effort to materially invest in making the site a natural *and cultural* landmark to ensure a specific group's privileged access to the surrounding territory and its resources under conditions of greater ecological unpredictability (Riel-Salvatore and Gravel-Miguel 2013). It should also be noted that the cave had a strategic placement in the context of the Ligurian-Provençal arc, given that it overlooked a narrowing of the coastal plain (ca. 1 km of width during the Younger Dryas; see bathymetric profiles at https://portal.emodnet-bathymetry.eu/; Smith et al., 2011) connecting the ample lowlands of

the river Rhône basin in southern France and of the river Arno basin in Italy, areas which show evidence of raw material exchanges (Tomasso and Porraz, 2016). Moreover, relatively low mountain passes (less than 500 m a.s.l.) are present nearby (e.g. Bocchetta di Altare and Colle di Santa Libera), which - considering the high precipitation and low altitude of glaciers during the Younger Dryas in the Maritime Alps (Ivy-Ochs et al., 2009; Spagnolo and Ribolini, 2019; Rea, 2020) – would most likely have been the first passages allowing access to the Po plain for anyone coming from the west. Arene Candide was therefore at the crossroad between the glacial refugia of hunter-gatherers of western and southern Europe (Djindjian, 2015; Tallavaara et al., 2015). The site was also a highly-visible landmark on the landscape, due to the aeolian white sand dune that raised up to its entrance at 90 m a.s.l. (Figure 7). It may therefore have been an ideal location for a corporate group to place a permanent and specialized funerary site, in order to claim control over a territory through direct ties with ancestors (Goldstein, 1976, 1981, 1995; Kelly, 2001, 2007; Walker, 2019). Indeed, an emphasis on the connection between the newly deceased, the funerary rite, and the ancestors is evoked by the secondary manipulation of burials (Sparacello et al., 2018) and other ritual behaviors at the site, like the intentional breaking of pebbles (Gravel-Miguel et al., 2017; Riel-Salvatore et al., 2018). However, at this stage little is known about the residential and logistic mobility, territorial behavior, and social organization of Epigravettian hunter-gatherers in western Liguria, and what might have been the predictable and localized resources that were defended (Charles and Buikstra, 1983; Walker, 2019). Future research will explore the role of Arene Candide within the Ligurian Tardiglacial hunter-gatherer network of resource procurement, especially during times of climatic change and sea-level variation. Furthermore, the excavation of the remaining Epigravettian layers at Arene Candide may shed further light into the frequency and continuity of use of the site over generations of hunter-gatherers.

[Figure 7 about here]

Another possibility, which does not exclude the ones formulated above, is that the worsening climatic conditions of the younger Dryas may have further reduced the genetic exchange among Epigravettian communities, thus indirectly influencing funerary behavior. Genetic analyses suggest that earlier Upper Paleolithic people had larger mating networks to limit the levels of inbreeding (Sikora et al., 2017), and yet an overabundance of developmental anomalies is present in the Pleistocene skeletal series (Trinkaus, 2018). This is possibly in part due to the aforementioned selection of "exceptional individuals and events" (Formicola,

2007; Pettitt, 2011), for which we have evidence at Arene Candide both in the Gravettian burial of "Il Principe" (Cardini, 1942; Pettitt et al., 2003) and in the Epigravettian necropolis (Formicola et al., 1990; Formicola, 1995; Sparacello et al., 2018). Individuals from the necropolis appear to have a surprising frequency of deformities that may be linked to recessive (Formicola et al., 1990; Formicola, 1995) and even dominant (Sparacello et al., 2019, and forthcoming) mutations in the X chromosome, and two of these individuals are ritually connected through funerary behavior (AC 2 and AC 3). However, even if the sample is biased by an intentional selection, the presence of a type of special funerary behavior suggests that Gravettian and Epigravettian people recognized these conditions as something to be ritually contained and sanctioned (Pettitt, 2011). Greater isolation of Epigravettian communities may have exacerbated inbreeding, leading to an increase of these "exceptional events", and contributing to the formation of the necropolis. New paleopathological and genetic studies on the remains of the necropolis, including the differential diagnosis of conditions observed in the rediscovered material, will further investigate this intriguing theory.

5. Conclusions

For the number of well-preserved burials, and the details on funerary gestures that can be reconstructed from the available documentation, the Arene Candide Cave and its Epigravettian necropolis represents a unique site in the European panorama, and a rare glimpse into the modalities, and possibly the motives, of Late Upper Paleolithic funerary behaviors. While extrapolating from a single site is usually not advisable, the inferences made at Arene Candide may assume a universal dimension, at least in the world of Late Glacial hunters, given the ties that seem to link Epigravettian and Gravettian sites in time and space, in terms of culture, genetic makeup, and funerary gestures. The finding of new remains from such a site is therefore of relevance, especially when, as in this case, the skeletal material did not emerge from new excavations – a process that is always partially destructive – but from misplaced and long-forgotten museal collections.

The skeletal material rediscovered at the MSNF improves our knowledge of the biological composition of the necropolis dating back to the Epigravettian, a period during which, similarly to the Gravettian, formal burials are rare, and were accorded to selected individuals, possibly on the basis of biological factors (disease, especially congenital) and "exceptional events" (trauma and violence). Two new individuals were recognized among the new skeletal

remains, both around 1-1.5 years of age, and numerous skeletal elements were attributed to already known individuals. Since all age classes are now represented in the assemblage, age at death seems not to be a significant factor in the determination of funerary treatment.

This study proposed a new chronological framework of the necropolis, based on new AMS dates on human bone, and on the cross-referencing of the available dates with the stratigraphic relations between burials and secondary depositions. Based on this analysis, it appears clear that Epigravettian funerary behavior at Arene Candide, and the complex practices of manipulating older burials when burying new inhumations, are bracketed within the Younger Dryas cooling event. It is possible that funerary behavior at Arene Candide, a site that was strategically placed and highly-visible in the landscape, was a way of claiming territorial access to resources, as well as reinforcing and transmitting communal identity and values, through a period of climate-induced resource stress and competition. It can also be hypothesized that isolation and reduced genetic exchange, due to the moving into small refugia during cooling events, may have contributed to the exacerbation of genetic drift, making certain negative "exceptional events" more common, and indirectly contributing to the formation of the necropolis.

Acknowledgements

The authors would like to acknowledge the past work of Virginia "Ginetta" Chiappella, a woman archaeologist whose fundamental contribution to archaeological research in Liguria during the 20th century, and especially at Arene Candide, was often overlooked.

We are grateful to the directors and curators of the museums where the skeletal collections are preserved, for continuous assistance during the data collection: Monica Zavattaro and Fabio di Vincenzo (Museo di Storia Naturale – Sezione di Antropologia e Etnologia, Università degli Studi di Firenze), Patrizia Garibaldi, Guido Rossi, Irene Molinari (Museo di Archeologia Ligure, Genova), Daniele Arobba and Andrea De Pascale (Museo Archeologico del Finale, Finale Ligure).

Thanks to the Soprintendenza Archeologia, Belle Arti e Paesaggio per le provincie di Imperia e Savona, for granting access to the skeletal collections, especially the Superintendent and the Officers Nico Radi, Marta Conventi, and Stefano Costa. We are grateful to Roberto Maggi, Chiara Panelli, Gabriele Martino, Giuseppe "Cisque" Vicino, Maria Tagliafico, Giovanni

Murialdo, Elisa Bianchi, Simona Mordeglia, Walter Siciliano, David Caramelli, Giovanna Stefania, Luca Bachechi, Chiara Bullo, Brunetto Chiarelli, Sébastien Villotte, Christopher Knüsel, Erik Trinkaus, and Fabio Negrino for assistance during data collection and for useful discussions.

VSS thanks archaeologist David Warneke, primatologist Matt Stewart, and Jess "Bop" Perkins for helping this study to Do Go On during the data analysis.

For the Arene Candide 3D surface scans: Soprintendenza Archeologia, Belle Arti e Paesaggio per la città metropolitana di Genova e le province di Imperia, La Spezia e Savona provided access to these data originally appearing in Sparacello et al., (2018), the collection of which was funded by Marie Skłodowska-Curie European Union COFUND/Durham Junior Research Fellowship [under EU grant agreement number 267209], and by the Wolfson Institute for Health and Wellbeing, Durham,UK. The files were downloaded from www.MorphoSource.org, Duke University.

The project BUR.P.P.H: Burial practices at the Pleistocene - Holocene transition: the changing role of pathology, violence, and "exceptional events" (VSS) has received financial support from the French State in the framework of the "Investments for the future" Program, IdEx Bordeaux, reference ANR-10-IDEX-03-02. The project DEN.P.H.: Dental anthropology at the Pleistocene-Holocene transition – insights on lifestyle and funerary behaviour from Neolithic Liguria (Italy) (ID) is funded by the European Union's Horizon 2020 research and innovation programme under the Marie Skłodowska-Curie grant agreement No 752626.

Funding for the 2008-13 excavations at Caverna delle Arene Candide and the subsequent analyses was provided by Freddy S.p.A., the Social Sciences and Humanities Research Council of Canada, Université de Montréal, Arizona State University and the University of Colorado Denver.

Thanks to the Editor and two Reviewers for their useful comments.

Literature Cited

Alley, R. B., 2000. The Younger Dryas cold interval as viewed from central Greenland. Quat. Sci. Rev. 19, 213–226.

AlQahtani, S.J., Hector, M.P., Liversidge, H.M., 2010. The London atlas of human tooth and eruption. Am. J. Phys. Anthropol. 142, 481–490.

Ambrose, S.H., 1990. Preparation and characterisation of bone and tooth collagen for isotopic analysis. J. Archaeol. Sci. 17, 431-451.

Ambrose, S.H., 1993. Isotopic analysis of paleodiets: methodological and interpretative considerations, in: Sandford, M.K., (Ed.), Investigations of ancient human tissue Chemical analyses in Anthropology. Gordon and Breach Science Publishers, Langhorne, pp. 59-130.

Arobba, D., Panelli, C., Caramiello, R., Gabriele, M., Maggi, R., 2017. Cereal remains, plant impressions and 14C direct dating from the Neolithic pottery of Arene Candide Cave (Finale Ligure, NW Italy). J. Archaeol. Sci. Rep. 12, 395-404.
https://doi.org/10.1016/j.jasrep.2017.02.015

Bell, C., 1992. Ritual theory, ritual practice. Oxford University Press, Oxford.

Bell, C., 1997. Ritual: perspectives and dimensions. Oxford University Press, Oxford.

Bernabò Brea, L., 1956. Gli scavi nella Caverna delle Arene Candide (Finale Ligure). Parte Prima: gli strati con ceramiche, Campagne di scavo 1948–50. Collezione di Monografie Preistoriche ed Archeologiche. Istituto Internazionale di Studi Liguri, Bordighera.

Bietti, A., 1987. Some remarks on the new radiocarbon dates from Arene Candide cave (Savona, Italy). Hum. Evol. 2, 185-190.

Bietti, A., Molari, C., 1994. The Upper Pleistocene deposit of the Arene Candide cave (Savona, Italy): general introduction and stratigraphy. Quat. Nova 4, 9-27.

M. Bloch, M., J. Parry, J., 1982. Death and the Regeneration of Life. Cambridge University Press, Cambridge.

Blockley, S.M., Gamble, C.S., 2012. Europe in the Younger Dryas: animal resources, settlement, and funerary behavior, in: Eren, M.I. (Ed.), Hunter-gatherer behavior: human response during the Younger Dryas. Left Coast Press, Walnut Creek, pp. 179-194.

Boccone, S., Micheletti Cremasco, M., Bortoluzzi, S., Moggi-Cecchi, J., Rabino Massa, E., 2010. Age estimation in subadults Egyptioan remains. J. Comp. Hum. Biol. 61, 337–358.

Cardini, L., 1941. Ricerche paletnologiche nella Caverna delle Arene Candide. Arch. Antropol. Etnol. 70, 110-119.

Cardini, L., 1942. Nuovi documenti sull'antichità dell'uomo in Italia: reperto umano del Paleolitico superiore della Grotta delle Arene Candide. Raz. Civil. 3, 5-25.

Cardini, L., 1946. Gli strati mesolitici e paleolitici della caverna delle Arene Candide. Riv. Stud. Lig. 12, 29-37.

Cardini, L., 1980. La necropoli mesolitica delle Arene Candide. Mem. Ist. It. Paleont. Um. 3, 9-31.

Charles, D.K., Buikstra, J.E., 1983. Archaic mortuary sites in the Central Mississippi drainage: distribution, structure, and behavioral implications, in: Phillips, J.L., Brown, J.A., (Eds.), Archaic hunters and gatherers in the American Midwest. Academic Press, New York, pp. 117-144.

Dee, M.W., Palstra, S.W.L., Aerts-Bijma, A.Th., Bleeker, M., De Bruijn, S., Ghebru, F., Jansen H.G., Kuitems M., Paul D., Richie R.R., Spriensma J.J., Scifo A., van Zonneveld D., Verstappen-Dumoulin B.M.A.A., Wietzes-Land P., Meijer, H.A.J., 2020. Radiocarbon Dating at Groningen: New and Updated Chemical Pretreatment Procedures. Radiocarbon 62(1), 63-74. doi:10.1017/RDC.2019.101

Del Lucchese, A., 1997. The Neolithic burials from Arene Candide: the Bernabò Brea-Cardini excavation, in: Maggi, R. (Ed.), Arene Candide: a Functional and Environmental Assessment of the Holocene Sequence (Excavations Bernabò Brea - Cardini 1940-50), Memorie dell'Istituto Italiano di Paleontologia Umana, n.s., 5. Il Calamo, Rome, pp. 605–609.

DeNiro, MJ., 1985. Post-mortem preservation and alteration of in vivo bone collagen isotope ratios on relation to palaeodietary reconstruction. Nature 317(6032), 806-809.

DjinDjian, F., 2015. Territories and economies of hunter-gatherer groups during the last glacial maximum in Europe. Quat. Int. 412, 37-43.

Dori, I., Varalli, A., Seghi, F., Moggi-Cecchi, J., Sparacello, V.S., 2020. Environmental correlates of growth patterns in Neolithic Liguria (northwestern Italy). Int. J. Paleopath. 28, 112-122.

Formicola, V., 1995. X-linked hypophosphatemic rickets: a probable Upper Paleolithic case. Am. J. Phys. Anthropol. 98, 403–409.

Formicola, V., 2007. From the Sunghir children to the Romito dwarf: aspects of the Upper Paleolithic funerary landscape. Curr. Anthropol. 48, 446-453.

Formicola, V., Frayer, D.W., Heller, J.A., 1990. Bilateral absence of the lesser trochanter in a Late Epigravettian skeleton from Arene Candide. Am. J. Phys. Anthropol. 83, 425-437.

Formicola, V., Scarsini, C., 1987. Contribution to the knowledge of the late Epigravettian human remains from Arene Candide cave (Liguria, Italy): a peculiar-shaped skull. J. Comp. Hum. Biol. 38,160-170.

Formicola, V., Pettitt, P.B., Maggi, R., Hedges, R., 2005. Tempo and mode of formation of the Late Epigravettian necropolis of Arene Candide cave (Italy): direct radiocarbon evidence. J. Archaeol. Sci. 32, 1598-1602.

Formicola, V., Holt, M.B., 2007. Resource availability and stature decrease in Upper Paleolithic Europe. A microevolutionary adaptive model. J. Anthropol. Sci. 85, 153–164.

Formicola, V., Toscani, F., 2014. A Late Epigravettian skeleton of an adolescent from Arene Candide Cave (Excavations 1970-1971). Bull. Mus. Anthropol. Préhist. Monaco 54, 131-138.

Fowler, C., 2004. The Archaeology of Personhood: An Anthropological Approach. Routledge, Abingdon.

Goldstein, Lynne G., 1976. Spatial Structure and Spatial Organization: Regional Manifestations of Mississippian Society. Unpublished Ph.D dissertation, Department of Anthropology, Northwestern University, Evanston.

Goldstein, Lynne G., 1981. One-dimensional archaeology and multi-dimensional people: Spatial organization and mortuary analysis, in: Chapman, R., (Ed.), The Archaeology of Death. Cambridge University Press, Cambridge, pp. 53-69.

Goldstein, Lynne G., 1995. Landscapes and Mortuary Practices, in: Beck, L.A., (Ed.), Regional Approaches to Mortuary Analysis. Plenum Press, New York, pp. 101-121.

Goude, G., Müller, K., Buscaglia, F., Reiche, I., 2011. Détermination de l'état de conservation, du consolidant et dosages isotopiques (δ13C, δ15N) d'ossements d'anciennes collections anthropologiques Le cas de la grotte La Pollera (Ligurie, Italie). ArchéoSciences 35, 223–233.

Goude, G., Dori, I., Sparacello, V.S., Starnini, E., and Varalli, A., 2020. Multi-proxy stable isotope analyses of dentine microsections reveal diachronic changes in life history adaptations, mobility, and tuberculosis-induced wasting in prehistoric Liguria (Finale Ligure, Italy, northwestern Mediterranean). Int. J. Paleopath. 28, 99-111.

Grachev, A. M., Severinghaus, J. P., 2005. A revised +10±4°C magnitude of the abrupt change in Greenland temperature at the Younger Dryas termination using published GISP2 gas isotope data and air thermal diffusion constants. Quat. Sci. Rev. 24(5-6), 513–519. doi:10.1016/j.quascirev.2004.10.016

Gravel-Miguel, C., Riel-Salvatore, J., Maggi, R., Martino, G., Barton, C., 2017. The Breaking of Ochred Pebble Tools as Part of Funerary Ritual in the Arene Candide Epigravettian Cemetery. Camb. Archaeol. J. 27(2), 331-350. doi:10.1017/S0959774316000640

Grosman, L., Munro, N.D., 2016. A Natufian ritual event. Curr. Anthropol. 57, 311-331.

Holt, B.M., 2003. Mobility in Upper Paleolithic and Mesolithic Europe: evidence from the lower limb. Am. J. Phys. Anthropol. 122, 200-215.

Holt, B.M., Formicola, V., 2008. Hunters of the Ice Age: the biology of Upper Paleolithic people. Yrbk. Phys. Anthropol. 51, 70–99.

Ivy-Ochs, S., Kerschner, H., Maisch, M., Christl, M., Kubik, P.W., Schlüchter, C., 2009. Latest Pleistocene and Holocene glacier variations in the European Alps. Quat. Sci. Rev. 28, 2137-2149. https://doi.org/10.1016/j.quascirev.2009.03.009

Jones, J.R., Marín-Arroyo, A.B., Straus, L.G., Richards, M.P., 2020. Adaptability, resilience and environmental buffering in European Refugia during the Late Pleistocene: Insights from La Riera Cave (Asturias, Cantabria, Spain). Sci. Rep. 10, 1217(2020). https://doi.org/10.1038/s41598-020-57715-2

Kelly, R.L., 2001. Prehistory of the Carson Desert and Stillwater Mountains: Environment, Mobility, and Subsistence in a Great Basin Wetland. Anthropological Papers, Vol. 123. University of Utah Press, Salt Lake City.

Kelly, R.L., 2007. The Foraging Spectrum: Diversity in Hunter-Gatherer Lifeways. Smithsonian Institution Press, Washington.

Kobashi, T., Severinghaus, J.P., Brook, E.J., Barnola, J.-M., Grachev, A.M., 2007. Precise timing and characterization of abrupt climate change 8200 years ago from air trapped in polar ice. Quat. Sci. Rev. 26, 1212-1222.

MacPhail, R.I., Hater, J., Hillson, S., Maggi, R., 1994. The Upper Pleistocene deposits at Arene Candide: soil micromorphology of some samples from the Cardini 1940-42 excavations. Quat. Nova. 4, 79-100.

Maggi, R., 1997a. The radiocarbon chronology, in: Maggi, R. (Ed.), Arene Candide: a Functional and Environmental Assessment of the Holocene Sequence (Excavations Bernabò Brea - Cardini 1940-50), Memorie dell'Istituto Italiano di Paleontologia Umana, n.s., 5. Il Calamo, Rome, pp. 31–52.

Maggi, R., 1997b. Summary: a modern excavation carried out fifty years ago, in: Maggi, R. (Ed.), Arene Candide: a Functional and Environmental Assessment of the Holocene Sequence (Excavations Bernabò Brea - Cardini 1940-50), Memorie dell'Istituto Italiano di Paleontologia Umana, n.s., 5. Il Calamo, Rome, pp. 635–642.

Meltzer, D.J., Bar-Yosef, O., 2012. Looking for the Younger Dryas, in: Eren, M.I., (Ed.), Hunter-gatherer behavior: human response during the Younger Dryas. Left Coast Press, Walnut Creek, pp. 249-269.

Metcalf, P., Huntington, R., 1979. Celebrations of Death. Cambridge University Press, Cambridge.

Moggi Cecchi, J., 2014. Le collezioni antropologiche, in: Moggi Cecchi, J., Stanyon, R., (Eds.), Il Museo di Storia Naturale dell'Università degli Studi di Firenze – le collezioni antropologiche ed etnologiche. Firenze University Press, Florence, pp. 183-197.

Mussi, M., Frayer, D.W., Macchiarelli, R., 1989. Les vivants et les morts. Les sepultures du Paléolithique supérieur en Italie et leur interpretation. BAR Int. Ser. 508, 435-458.

Paoli, G., Parenti, R., Sergi, S., 1980. Gli scheletri mesolitici della caverna delle Arene Candide (Liguria). Mem. Ist. It. Paleont. Um. 3, 31-154.

Pettitt, P.B., 2011. The Palaeolithic origin of human burial. Routledge, London.

Pettitt, P.B., Richards, M., Maggi, R., Formicola, V., 2003. The Gravettian burial known as the Prince ("Il Principe"): new evidence for his age and diet. Antiquity 77, 15–19.

Rea, B.R., Pellitero, R., Spagnolo, M., Hughes, P., Ivy-Ochs, S-, Renssen, H., Ribolini, A., Bakke, J., Lukas, S., Braithwaite, R.J. 2020. Atmospheric circulation over Europe during the Younger Dryas. Sci. Adv. 6(50), eaba4844.

Rellini, I., Firpo, M., Martino, G., Riel-Salvatore, J., Maggi, R., 2013. Climate and environmental changes recognized by micromorphology in Paleolithic deposits at Arene Candide (Liguria, Italy). Quat. Int. 315, 42-55.

Richards, M.P., Hedges, R., 1999. Stable isotope evidence for similarities in the types marine food used by late mesolithic humans at sites along the Atlantic coast of Europe. J. Archaeol. Sci. 26, 712-722.

Riel-Salvatore, J., Gravel-Miguel, C., 2013. Upper Paleolithic mortuary practices in Eurasia: a critical look at the burial record, in: Tarlow, S., Nilsson Stutz, L. (Eds.), The Oxford Handbook of the Archaeology of Death and Burial. Oxford University Press, Oxford, pp. 303- 346.

Riel-Salvatore, J., Gravel-Miguel, C., Maggi, R., Martino, G., Rossi, S., Sparacello, V.S., 2018. Recent excavations and new insights into Epigravettian funerary ritual at Caverna delle Arene Candide, in: Cristiani, E., Borgia, V., (Eds), Palaeolithic Italy: Advanced studies on early human adaptations in the Apennine Peninsula. Sidestone Press, Leiden, pp. 335-355.

Schaefer, M., Black, S., Scheuer, L. 2009. Juvenile osteology – a laboratory and field manual. Academic Press, New York.

Sikora, M., Seguin-Orlando, A., Sousa, V.C., Albrechtsen, A., Kornelliussen, T., 2017. Ancient genomes shown social and reproductive behavior of early Upper Paleolithic foragers. Science 358, 659-662.

Smith D.E., Harrison S., Firth C.R., Jordan J.T., 2011. The early Holocene sea level rise. Quat. Sci. Rev. 30, 1846-1860.

Spagnolo, M., Ribolini, A., 2019. Glacier extent and climate in the Maritime Alps during the Younger Dryas. Palaeogeogr. Palaeocl. 536, 109400. https://doi.org/10.1016/j.palaeo.2019.109400

Sparacello, V.S., Villotte, S., Shackelford, L.L., Erik Trinkaus E., 2017. Patterns of Humeral Asymmetry among Late Pleistocene Humans. C. R. Palevol. 16(5-6), 680-689.

Sparacello, V.S., Rossi, S., Pettitt, P., Roberts, C.A., Riel-Salvatore, J., Formicola, V., 2018. New insights on Final Epigravettian funerary behavior at Arene Candide Cave (Western Liguria, Italy). J. Anthropol. Sci. 96, 161-184.

Sparacello, V.S., Dori, I., Rossi, S., Varalli, A., Moggi Cecchi, J., Riel-Salvatore, J., Formicola, V., 2019. Further insights on Late Upper Paleolithic (Epigravettian) funerary use of Arene Candide Cave (Liguria, Italy). New AMS dates and paleopathology Am. J. Phys. Anthropol. [Suppl] 68, 234.

Sparacello, V.S., Varalli, A., Rossi, S., Panelli, C., Goude, G., Palstra, S.W.L., Conventi, M., Del Lucchese, A., Arobba, D., De Pascale, A., Zavattaro, M., Garibaldi, P., Rossi, G., Molinari, I., Maggi, R., Moggi-Cecchi, J., Starnini, E., Biagi, P., Dori, I., 2020. Dating the funerary use of caves in Liguria (northwestern Italy) from the Neolithic to historic times: results from a large-scale AMS campaign on human skeletal series. Quat. Int. 536,30-44. doi.org/10.1016/j.quaint.2019.11.034.

Sparacello, V.S., Panelli, C., Rossi, S., Dori, I., Varalli, A., Goude, G., Starnini, E., Biagi, P., 2019. The re-discovery of Arma dell'Aquila (Finale Ligure, Italy): New insights on Neolithic funerary behavior from the sixth millennium BCE in the north-western Mediterranean. Quat. Int. 512, 67-81.

Synal, H-A., Stocker, M., Suter, M., 2007. MICADAS: A new compact radiocarbon AMS system. Nucl. Instrum. Meth. B 259, 7-13.

Tallavaaraa, M., Luotob, M., Korhonenc, N., Järvinend, H., Seppä, H., 2015. Human population dynamics in Europe over the Last Glacial Maximum. PNAS 112, 8232-8237.

Tomasso, A., Porraz, G., 2016. Hunter-gatherers' mobility and embedded raw material procurement strategies: a critical view from the Mediterranean Upper Paleolithic, Evol. Anthropol. 25(3), 164-174.

Trinkaus, E., 2018. An abundance of developmental anomalies and abnormalities in Pleistocene people. PNAS 115, 11941-11946

Van Gennep, A., 1909. Les Rites de passage. Étude systématique des rites. Picard, Paris.

Volk, A.A., Atkinson, J.A., 2013. Infant and child death in the human environment of evolutionary adaptation. Evol. Hum. Biol. 34, 182-192.

Walker, S., 2019. The persistence of place: Hunter-gatherer mortuary practices and land-use in the Trent Valley, Ontario. J. Anthropol. Archaeol. 54, 133-148.

Woodburn, J. C., 1980. Hunters and gatherers today and reconstruction of the past, in: Gellner, E., (Ed.), Soviet and Western Anthropology. Duckworth, London, pp. 95–117.

Figure 1

Click here to access/download;Figure;Figure1 mod.tif

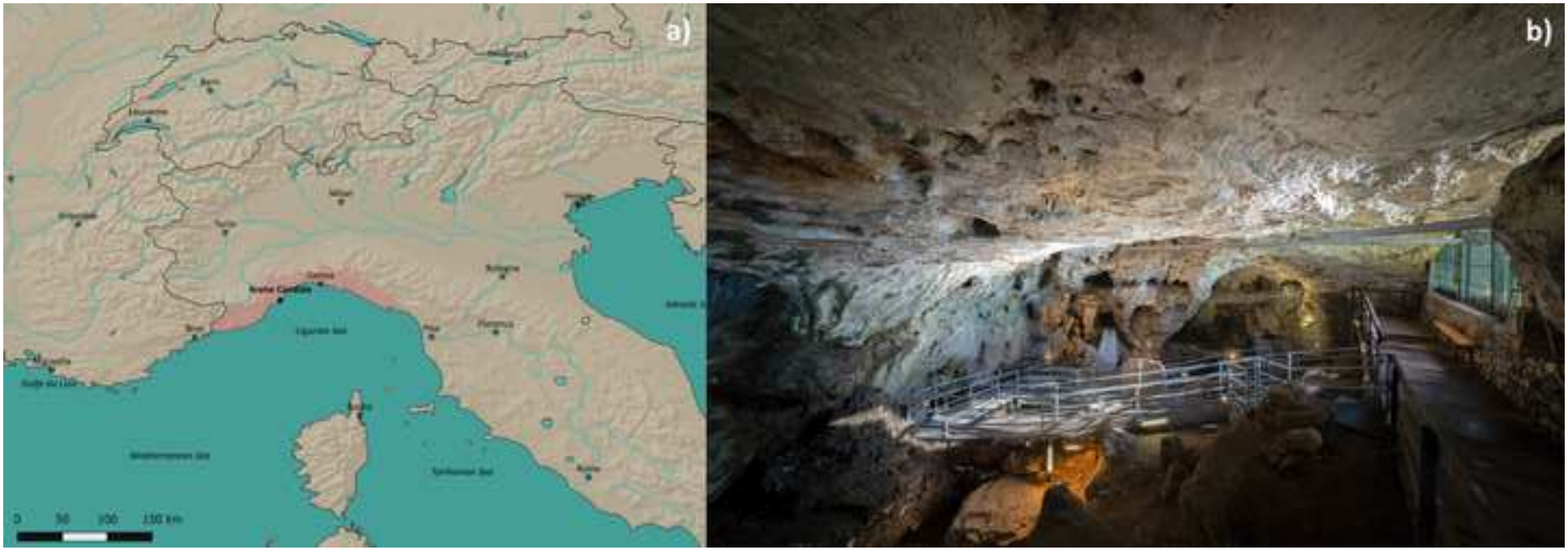


Figure 2

Click here to access/download;Figure;Fig2_mod VSS.tif

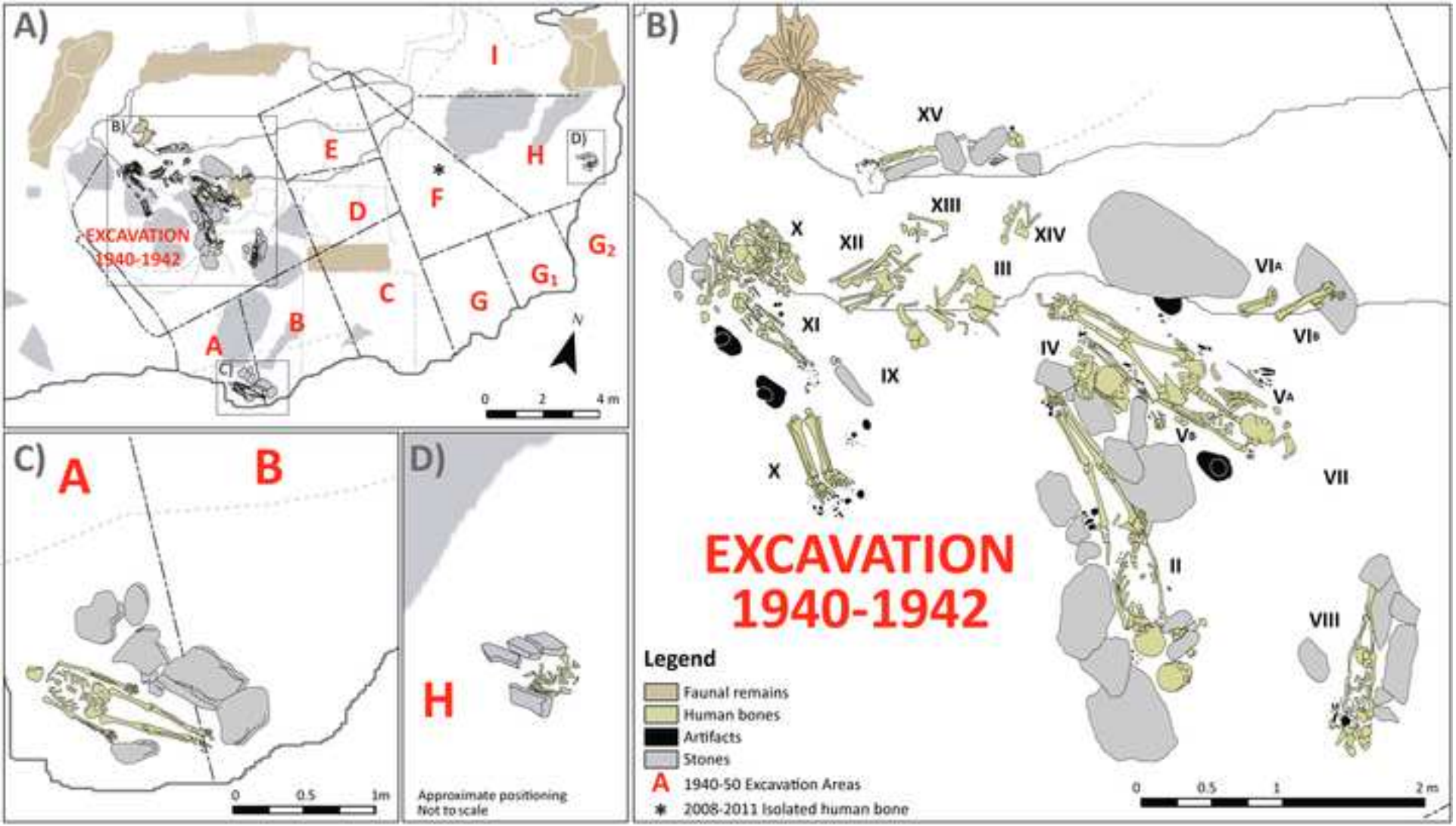


Figure 3

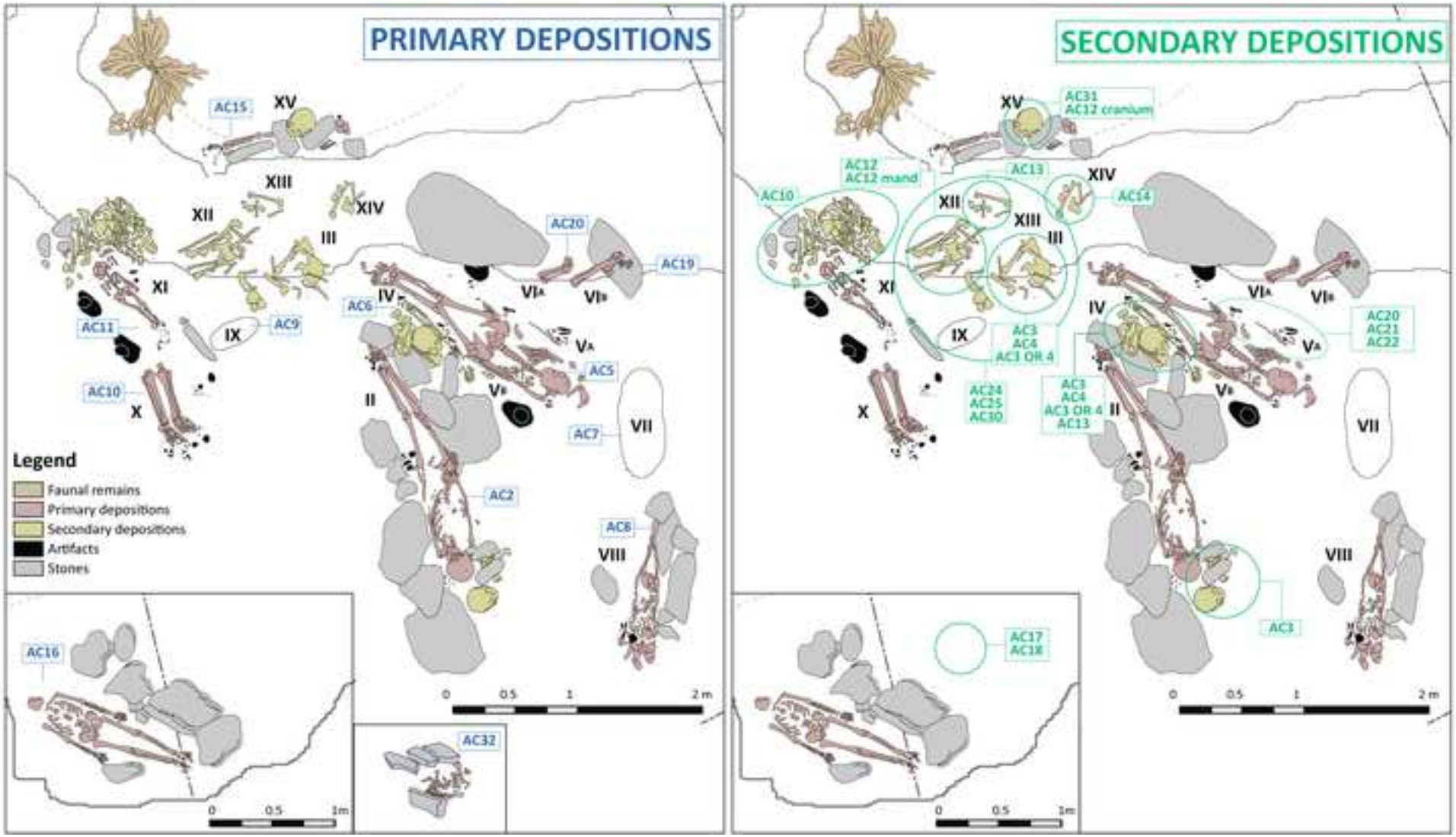


Figure 5

Click here to access/download;Figure;Figure 5_mod.tif

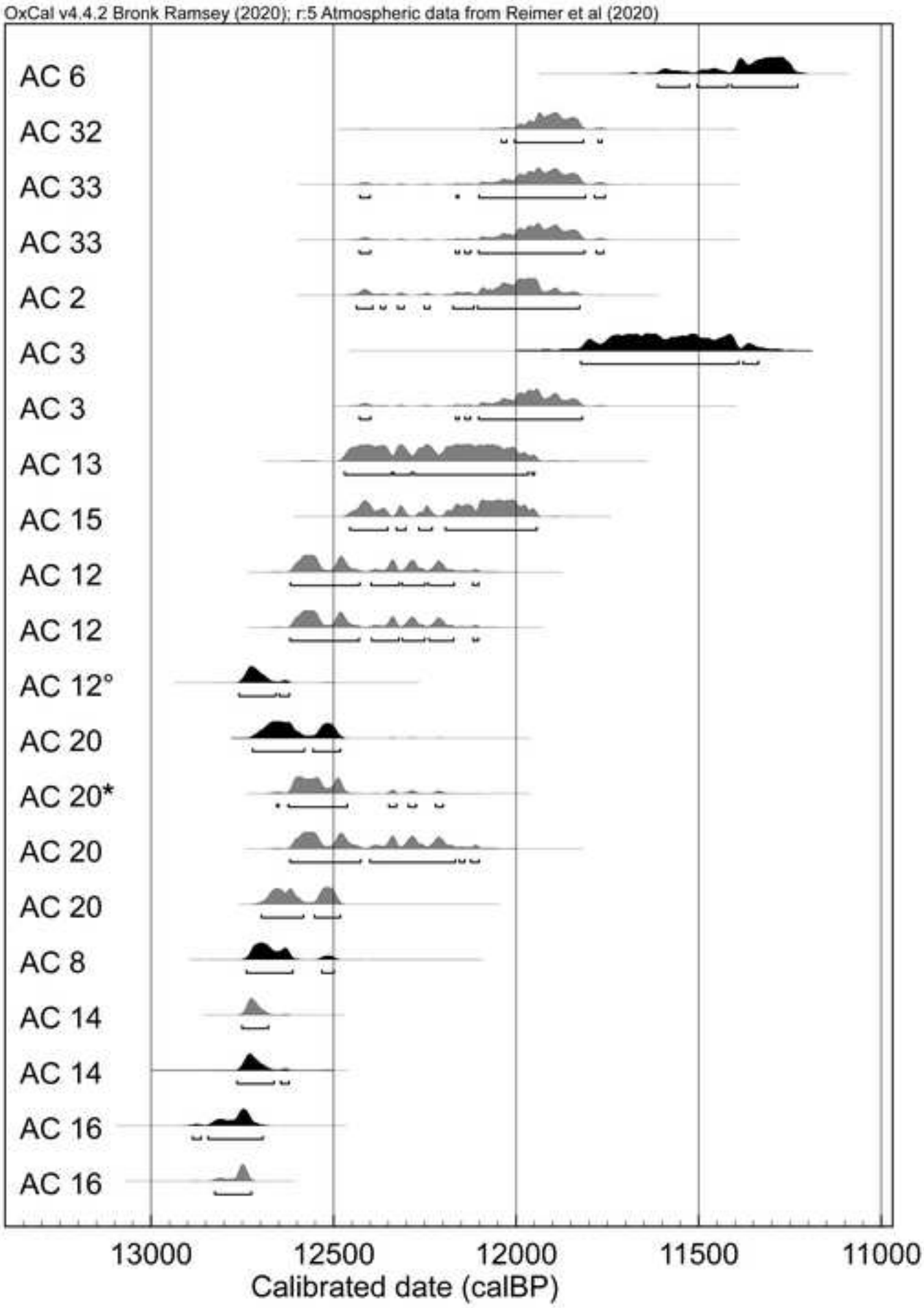


Figure 6

Click here to access/download;Figure;Figure 6.tif

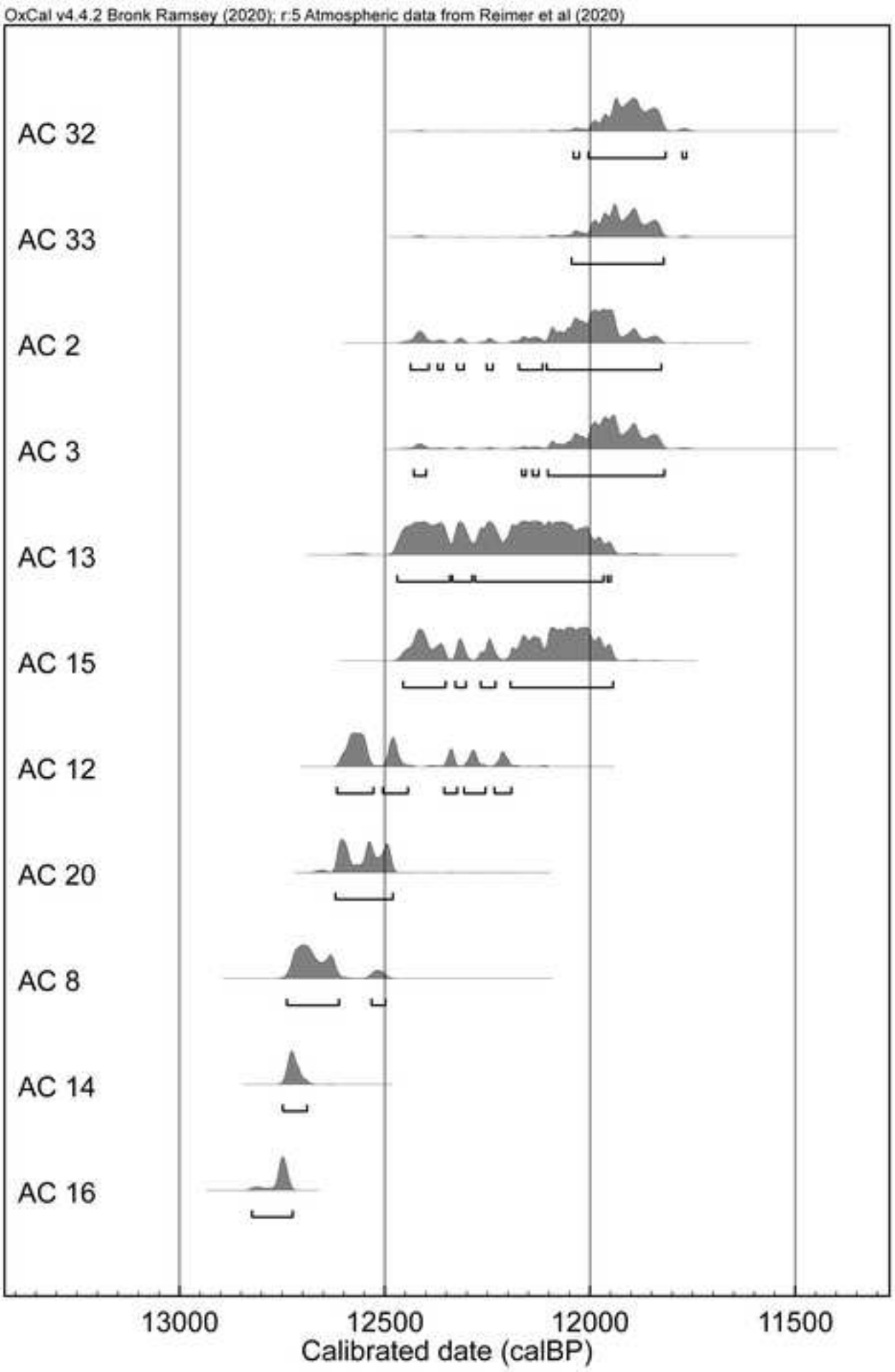


Figure 7

Click here to access/download;Figure;Figure 7 - Dune or is it June.tif

Figure 1 – A) The geographical location of the Arene Candide Cave in the northwestern Mediterranean (made with Natural Earth. Free vector and raster map data). B) A view of the main hall in the eastern part of the cave (photo from Archivio Museo Archeologico del Finale / MUDIF).

Figure 2 – A) General map of the eastern part of the Arene Candide Cave, indicating the quadrant in which it was divided by Bernabò Brea's and Cardini's excavations. The position of the human talus found in 2011 and belonging to AC 13 is indicated by an asterisk. B) Detail of the area with the main concentration of burials belonging to the Epigravettian necropolis, showing the disposition of the primary depositions and of the clusters of secondary depositions. The Roman numerals derive from Bernabò Brea – Cardini numeration. C) Detail of the burial of AC 16, discovered during the 1970-72 campaign. D) Detail of the burial of AC 32, discovered during the 1950 campaign, and previously attributed to the Neolithic (approximate position, image not to scale). Modified from Figure 2 in Sparacello et al., 2018.

Figure 3 – Numeration of the burials, individuals, and clusters of secondary deposits of human remains of the Epigravettian necropolis. Left: the Roman numerals derive from Bernabò Brea – Cardini numeration, and the numeration from Sparacello et al., 2018 for primary depositions. Right: Roman numerals derive from Bernabò Brea – Cardini numeration, and the numeration from Sparacello et al., 2018 for the individuals in secondary deposition.

Figure 4 – On the left, some examples of the attribution of new material to known individuals using virtual anthropology methods. A) Fragments of pubic bones from the new materials used in the virtual reconstruction of the os coxa of Arene Candide 4 (left, 3D model OCX_L_OORG; https://doi.org/10.17602/M2/M10678) and Arene Candide 3 (right, 3D model OCX_R_OR6; https://doi.org/10.17602/M2/M10678); B) a right scapula reconstructed from fragments, which is contralateral to the left scapula of Arene Candide 12; C) a fragmentary sacrum articulating with the right os coxa of AC 12 (3D model OCX_R_OG; https://doi.org/10.17602/M2/M10690); left tarsals bones contralateral to the corresponding elements belonging to Arene Candide 4 (3D model TAL_R_OR23, https://doi.org/10.17602/M2/M10744; NAV_R_OR23, https://doi.org/10.17602/M2/M10682). Right, the skeletal element belonging to AC 32 (6726.1 of the MSNF catalogue), previously attributed to the Neolithic and denominated AC X BB following the Neolithic numeration of Bernabò Brea – Cardini excavation at Arene Candide (1940-50). The asterisks indicate elements that were attributed to this individual from the rediscovered materials in secondary deposition.

Figure 5 – AMS dates on human remains from the Epigravettian necropolis, calibrated using OxCal 4.4 (https://c14.arch.ox.ac.uk/oxcal/OxCal.html), on human remains from Formicola et al., 2005, and this study. ° This fragment attributed to AC 12 may in fact belong to AC 14 (see text). * We re-dated the same fragment dated by Formicola et al., 2005.

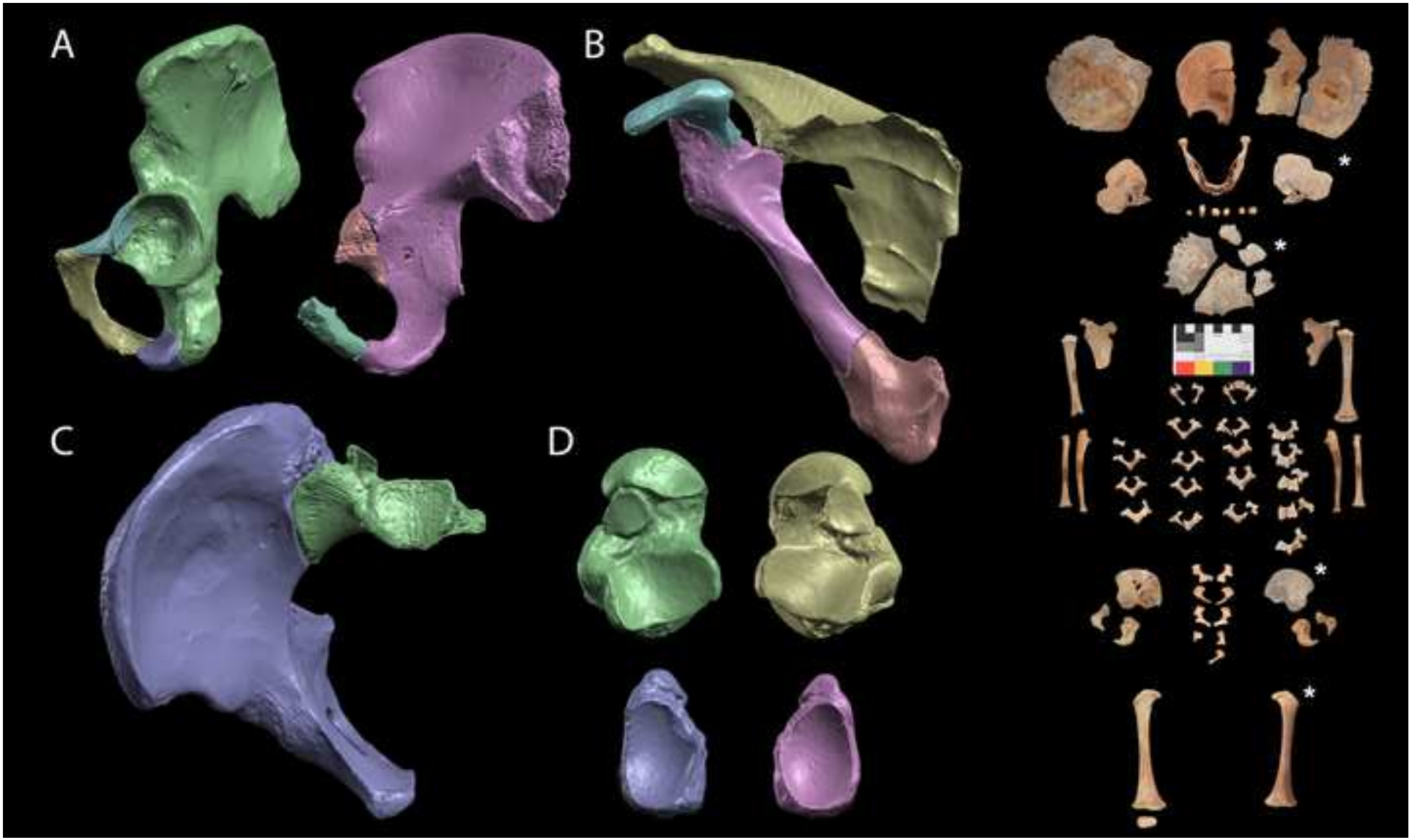
Figure 6 – The new chronological assessment of the Epigravettian necropolis based on selected and combined calibrated dates (using the function R-Combine in OxCal 4.4; https://c14.arch.ox.ac.uk/oxcal/OxCal.html), from this study and Formicola et al., 2005.

AC 32: GrM-13423; AC 33: combined GrM-22252 and GrM-16989; AC 2: GrM-15920; AC 3: GrM-22474; AC 13: GrM-22397; AC 15: GrM-13678; AC 12: combined GrM-22237 and GrM-22396, OxA-11002 non used because it could belong to AC 14; AC 20: combined OxA-11000, GrM-14525, GrM-22399, and GrM-22251; AC 8: OxA-11001; AC 14: combined GrM-22250 and OxA-11003; AC 16: combined OxA-11949 and GrM-16978.

Figure 7 – The white sand dune rising to the entrance of the Arene Candide Cave, before being quarried away in the first half of the twentieth century (photo from Archivio Museo Archeologico del Finale / MUDIF).

Figure 4

Click here to access/download;Figure;Figure 4.tif



Layer or cluster/burial	Corresponding layer from II Campaign	Individual (Sparacello et al., 2018)	Material	Lab. Code	14C Age (yr BP)	Reference
M1	Xe, Xf	-	bone (fauna)	Beta-49694	9980±140	MacPhail et al., 1994
M1-2	Xe-Xi	-	charcoal	Beta-53091	10740±90	MacPhail et al., 1994
M1-2	Xe-Xi	-	charcoal	R-740	10910±90	Bietti, 1987
M3-4	Xo-Xq	-	charcoal	R-743	11750±95	Bietti, 1987
III		AC 3	bone (human)	OxA-10998	10065±55	Formicola et al., 2005
Vb		AC 6	bone (human)	OxA-10999	9925±50	Formicola et al., 2005
VIb		AC 20	bone (human)	OxA-11000	10585±55	Formicola et al., 2005
VIII		AC 8	bone (human)	OxA-11001	10655±55	Formicola et al., 2005
XII		AC 12	bone (human)	OxA-11002	10720±55	Formicola et al., 2005
XIV		AC 14	bone (human)	OxA-11003	10735±55	Formicola et al., 2005
XVI		AC 16	bone (human)	OxA-11949	10810±65	Formicola and Toscani, 2014

Table 1 – Published radiometric dates for the Epigravettian necropolis at the time of this study. Determinations with several hundred years of error have not been reported (see Table 2 in Formicola et al., 2005).

New skeletal remains from the Epigravettian necropolis				
Individual[1]	**Burial/cluster Cardini, 1980**	**Skeletal elements and conditions**	**Dental remains**	**Age**
AC 3	I, III, IV	cervical vert. (3i, 2d); lumbar vert. (3d); os coxae (ff/ff); tentatively attributed: thoracic vert. (1i, 2d, 4f-ff)		Adult
AC 4	III, IV	cervical vert. (1i); thoracic vert. (1i); os coxae (ff/-); talus (i/-); navicular (i/-)	URI1	Adult
AC 6	Va/Vb	thoracic vert. (f)		ca. 3
AC 7 or 9	Could be one of the "perinatals" from tomb VII and IX considered as "lost" by Cardini	frontal (ff); parietals (ff); temporal (ff); humerus (-/i); ulna (-/ff); cervical vert. (1f); sacrum (1f); tibia (f/d); fibula (ff)		ca. 6-12 months
AC 12	XII	scapula (d/d); radius (f/-); sacrum (f); fibula (-/f)		Adult
AC 13	XIII	scapula (5ff); ulna (-/f); MC (2i/-); hand phalanx (5i); lumbar vert. (1i); os coxae (f/-); femur (ff/-); fibula (f/-); MT (1i/1i); foot phalanx (2i); ribs (1i)		ca. 15-16
AC 14	XIV	scapula (d/-); cervical vert. (3i, 1d); thoracic vert. (1i, 4d, 6f); ribs (24 i, f, ff)		Adult
AC 20		parietal (-/17ff); temporal (-/3f); clavicle (i/i); scapula (i/i); humerus (i/2f); radius (i/i); MC (i); cervical vert. (2f); thoracic vert (4f); sacrum (6f); femur (-/i); tentatively attributed: MC (1i)	LC, LM	ca. 5-7
AC 24		frontal (9f); zygomatic (i/i); parietals (>10f); temporal (i/i); occipital (5f); maxilla (i); >20ff; ilium (i/d); ischium (-/i); pubis (-/i); sternum (1f)	URdm2, URI1, URI2, URP1, URM1, URM2 (R1/2) URM3 (Crc)– URI2, ULC, ULP2, ULM1, ULM3	9-10
AC 31		mandible (d)	LRP2, LLP2, LRM1, LLM1, LRM2, LLM2, LRM3	Adult
AC 32		temporal (i/-); occipital (5f); ilium (i/-); femur (i/-)		ca. 1-1.5
AC 33		parietal (11f); zygomatic (i/-); occipital (d)[2]; mandible (d); scapula (f/-); humerus (d/-); thoracic vert (3f); lumbar vert (2 elements); ilium (i/-); pubis (i/-); femur (-/d);	LRdc (Ri), LRdm1, LRdm2 (R1/4) – LLdc, LLdm1 URM1 (Cr ½)	ca. 1-1.5
AC 32 or AC 33		clavicle (i/-); scapula (1f); MC (1i); hand phalanx (1i); tibia (i/-); fibula (i/-); MT (1i); rib (1ff)		ca. 1-1.5
AC 3 or AC 4		foot phalanx (1i)		Adult
AC 3 or AC 12 or AC 14		navicular (-/i)		Adult
Non attributed		carpals (9i); MC (10i, 1f); hand phalanges (17i); coccyx (2f); MT (3i); foot phal (2i); sesamoid (1i)		Adult
Ribs		>100 (i, d, f, ff)		Children and adults

Table 2 – Summary database of the new skeletal elements belonging to the Epigravettian necropolis and their attribution to known individuals. A more detailed version of the database, by bone and by individual, is available in Supplementary Information 1. Side of the element is indicated based on the position with respect to the slash, i.e. (left/right) when appropriate; preservation is indicated by: i (intact or minimally damaged); d (damaged); f (fragment); ff (small fragment).

[1] Numeration devised in Sparacello et al., 2018 up to number 31

[2] attributed to AC 33 rather than 32 because it was found in the area of Tomb V. More remains of AC 33 seem to be in the proximity of Tomb V, where an occipital squama (new materials) is present.

Skeletal remains from the Epigravettian necropolis catalogued at the MNSF					
Individual[1]	**Burial/cluster Cardini, 1980**	**Skeletal elements and conditions**	**Dental remains**	**Age**	**Note**
AC 6	Vb	temporal (-/i); ribs (2f); fragments		ca. 3	MSNF n° 6727.2
AC 7 or AC 9	Could be one of the "perinatals" from tomb VII and IX considered as "lost" by Cardini	frontal (ff); parietal (ff); tibia (ff/i); fibula (ff/i)		perinatal	MSNF n° 6726.2; different individual than the ca. 6-12 months-old in new materials
AC 12	placed above Tomb XV	frontal (f); parietal (f/f); temporal (d/d); sphenoid (ff); zygomatic (i/i); maxilla (i); mandible (i)	URI2, URC, URP1, URP2, URM1, URM2, URM3 - ULI1, ULI2, ULC, ULP1, ULP2, ULM1, ULM2, ULM3 - LRI1, LRI2, LRC, LRP1, LRP2, LRM1, LRM2, LRM3 LLI1, LLI2, LLC, LLP1, LLP2, LLM1, LLM2, LLM3	Adult	also known as AC 19 MSNF n° 6725
AC 15	XV	zygomatic (i/-); mandible (3f); clavicle (f/-); scapula (ff); ulna (f/f); carpals (1i); MC (1i); hand phalanges (3i); vertebrae (>30ff); os coxae (2ff); tibia (d/f); fibula (d/d); MT (1i) foot phalanges (12i); epiphyses (10i); ribs (>10ff); >50 ff	URI1, ULI1, ULI2, URC, ULC, URP1, URM1, ULM1, URM3, ULM3, LRI1, LRI2, LLI2, LRC, LLC, LRP1, LLM1, LRM2, LLM2, LRM3, LLM3	ca. 12-13	MSNF n° 6728.1
AC 20	VIb	parietal (3f/-); clavicle (-/i); cervical vert. (1f); tibia (i/i); fibula (f/i); tarsals (6i); MT (5i); foot phalanges (9i); epiphyses (2i); tentatively attributed: cervical vert. (1d,1f), rib (1i), sacrum (1 element)		ca. 5-7	MSNF n° 6727.1; remains tentatively attributed are 6726.3
AC 24		ischium (i/-)		ca. 9-10	MSNF n° 6726.6
AC 31	note says "adult of the burial of the Antlers" [Tomb XV]	cranial fragments (>50ff); maxilla (f)	"URI2, URP1, URP2 (only root) - ULP1, ULP2, ULM1, ULM2"	Adult	MSNF n° 6728.2
AC 32	Tomb X of the Neolithic numeration	frontal (f); parietal (d/d); temporal (-/i); mandible (i); scapula (d/d); humerus (i/d); radius (i/i); ulna (i/i); MC (1i); phalanges (4i); thoracic vert. (19f); cervical vert. (3f); lumbar vert. (9f); sacrum (>10 f); ilium (-/i); ischium (i/i); pubis (i/i); femur (-/i); ribs (>50ff)	dULI1, LLI1, LRI2; dLC, dLRC, dLRM1, dLM1, dLRM2, dLLM2, LRM1, LLM1	ca. 1-1.5	MSNF n° 6726.1
AC 33		occipital base (ff)		ca. 1-1.5	MSNF n° 6727.3[2]

Table 3 – Summary database of the skeletal elements belonging to the Epigravettian necropolis catalogued at the Museo di Storia Naturale dell'Università di Firenze, sezione di Antropologia ed Etnologia, and their attribution to known individuals. A more detailed version of the database, by catalogue number, is available in Supplementary Information 1. Side of the element is indicated based on the position with respect to the slash, i.e. (left/right) when appropriate; preservation is indicated by: i (intact or minimally damaged); d (damaged); f (fragment); ff (small fragment).

[1] Numeration devised in Sparacello et al., 2018 up to number 31

[2] attributed to AC 33 rather than 32 because it was found in the area of Tomb V. More remains of AC 33 seem to be in the proximity of Tomb V, where an occipital squama (new materials) is present.

Lab. Code	Individual	MSNF catalogue	Individual Sparacello et al., 2018	Bernabò Brea - Cardini	Other denominations	Age	Sex	Museum	14C Age (yr BP)	Note[1]
Measured by CIO	AC 24	-	24			ca. 9-10	U	MSNF	*8180±30 (unreliable)*	*CN criteria not met N<10% C<30%*
Measured by CIO	AC 4	-	4	IV		Adult	M	MSNF	*8555±30 (unreliable)*	*CN criteria not met N=10% C<30%*
Measured by CIO	AC 12	6725	12	XII	19 (Scarsini, 1987)	Adult	M	MSNF	*8630±30 (unreliable)*	*CN criteria not met N<10% C<30% C/N=4.0*
GrM-22238	AC 7/9	-	7, 9	VII, IX		ca. 6-12 mo	U	MSNF	*8995±30*	*Criteria met but result incoherent with stratigraphy*
Measured by CIO	Elk Antlers	-						MAF	*9600±30 (unreliable)*	*CN criteria not met C/N=4.6*
GrM-22400	AC 31	-				Adult	U	MSNF	*9665±35*	*CN criteria borderline N=11%, C=30.2%; incoherent date*
GrM-13423	AC 32	6726		X (Neolithic)		ca. 1-1.5	U	MSNF	10235±30	
GrM-22252	AC 33	-				ca. 1-1.5	U	MSNF	10245±40	
GrM-16989	AC 33	6727				ca. 1-1.5	U	MSNF	10250±40	
GrM-15920	AC 2	-	2	II		Adult	M	MAF	10280±35	
OxA-10998	AC 3	-	3	III		Adult	M	MAL	10065±55	
GrM-22474	AC 3	-	3	III		Adult	M	MSNF	10260±35	
GrM-22397	AC 13	-	13	XIII		ca. 15-16	U	MSNF	10350±45	
GrM-13678	AC 15	6728	15	XV	13 (Alciati et al., 2005)	ca. 12-13	U	MSNF	10325±30	
GrM-22237	AC 12	-	12	XII		Adult	M	MSNF	10460±40	
GrM-22396	AC 12	-	12	XII		Adult	M	MSNF	10465±40	
GrM-14525	AC 20[2]	6727	20	VIb	15 (Alciati et al., 2005)	ca. 5-7	U	MSNF	10495±35	
GrM-22399	AC 20	-	20	VIb	15 (Alciati et al., 2005)	ca. 5-7	U	MSNF	10460±45	
GrM-22251	AC 20	-	20	VIb	15 (Alciati et al., 2005)	ca. 5-7	U	MSNF	10565±40	
GrM-22250	AC 14	-	14	XIV		Adult	U	MSNF	10720±40	
GrM-16978	AC 16	-	16	XVI	17 (Paoli et al., 1980)	ca. 13-14	U	MAF	10820±40	

Table 3 – New AMS dates performed for this study. A more detailed version of the table, including sample type, nitrogen and carbon content, and calibration details is available in Supplementary Information 1.

[1] Details in Supplementary Information.

[2] Same fragment used in Formicola et al., 2005.

Author Contributions

Vitale Sparacello: conceptualization, investigation, methodology, writing – original draft, funding acquisition, project administration.

Irene Dori: methodology, investigation, funding acquisition.

Stefano Rossi: visualization, data curation.

Julien Riel-Salvatore, Claudine Miguel-Gravel: investigation, writing – original draft, funding acquisition.

Alessandra Varalli, Alessandro Riga, Francesca Seghi: investigation, methodology.

Gwenaëlle Goude, Sanne WL Palstra: methodology, formal analysis, resources.

Elisabetta Starnini: supervision, investigation, resources.

Vincenzo Formicola, Jacopo Moggi-Cecchi: conceptualization, supervision, resources.

All authors: writing – review and editing.

Supplementary Information

Click here to access/download

e-Component/Supplementary data

Suppl Info_PaperAC_bis.xlsx