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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

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**A B S T R A C T**

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 that began 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, which had never been described since their excavation in 1940-42, were discovered during the reassessment of the collections kept at the Museum of Natural History, Section of Anthropology and Ethnology of the University of Florence.

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
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 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 aspects of their social life, including territoriality, land-use strategies and subsistence patterns. Focusing on grave-specific features as well as 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 inhabited 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; Fig. 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, 1997a,b; Arroba 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, 1948, 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., 2018). The Epigravettian necropolis is among the largest and best-documented assemblages 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.

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 (Fig. 2). During the 1948–50 campaigns, the same researchers explored the eastern-most 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, Fig. 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, Fig. 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.

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 History, 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., 2019a, 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 one 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 (Fig. 3). Primary inhumations contained one (II, VIII, X, XI, XV, XVI) or two individuals (Va-b and Vla-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 (Vla-b and X-XI), or placing the child to the left of the adult when creating double 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

Fig. 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 Fig. 2 in Sparacello et al. (2018).
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 No. 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).

The radiocarbon determinations spearheaded by Formicola et al. (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 reanalyzed 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 (Fig. 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 et 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

![Fig. 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.](image)

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).

<table>
<thead>
<tr>
<th>Layer or cluster/ burial</th>
<th>Corresponding layer from II Campaign</th>
<th>Individual (Sparacello et al., 2018)</th>
<th>Material</th>
<th>Lab. Code</th>
<th>14C Age (yr BP)</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>M1</td>
<td>Xe, XF</td>
<td>–</td>
<td>bone (fauna)</td>
<td>Beta-49694</td>
<td>9980 ± 140</td>
<td>MacPhail et al. (1994)</td>
</tr>
<tr>
<td>M1-2</td>
<td>Xe-Xi</td>
<td>–</td>
<td>charcoal</td>
<td>Beta-53091</td>
<td>10,740 ± 90</td>
<td>MacPhail et al. (1994)</td>
</tr>
<tr>
<td>M3-4</td>
<td>Xo-Xq</td>
<td>–</td>
<td>charcoal</td>
<td>R-743</td>
<td>11,750 ± 95</td>
<td>Bietti (1987)</td>
</tr>
<tr>
<td>III</td>
<td>AC 3</td>
<td>bone (human)</td>
<td>OxA-10998</td>
<td>10,065 ± 55</td>
<td>Formicola et al. (2005)</td>
<td></td>
</tr>
<tr>
<td>Vb</td>
<td>AC 6</td>
<td>bone (human)</td>
<td>OxA-10999</td>
<td>9925 ± 50</td>
<td>Formicola et al. (2005)</td>
<td></td>
</tr>
<tr>
<td>Vlb</td>
<td>AC 20</td>
<td>bone (human)</td>
<td>OxA-11000</td>
<td>10,585 ± 55</td>
<td>Formicola et al. (2005)</td>
<td></td>
</tr>
<tr>
<td>VIII</td>
<td>AC 8</td>
<td>bone (human)</td>
<td>OxA-11001</td>
<td>10,655 ± 55</td>
<td>Formicola et al. (2005)</td>
<td></td>
</tr>
<tr>
<td>XII</td>
<td>AC 12</td>
<td>bone (human)</td>
<td>OxA-11002</td>
<td>10,720 ± 55</td>
<td>Formicola et al. (2005)</td>
<td></td>
</tr>
<tr>
<td>XIV</td>
<td>AC 14</td>
<td>bone (human)</td>
<td>OxA-11003</td>
<td>10,735 ± 55</td>
<td>Formicola et al. (2005)</td>
<td></td>
</tr>
<tr>
<td>XVI</td>
<td>AC 16</td>
<td>bone (human)</td>
<td>OxA-11949</td>
<td>10,810 ± 65</td>
<td>Formicola and Toscani (2014)</td>
<td></td>
</tr>
</tbody>
</table>
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 (Fig. 3). Long bones were stacked in cluster IV, above which two ossa coxarum cradled the cranium of one individual (AC 4; Cardini, 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).

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 rearrangement of their parts, especially crania, around new burials. This makes 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 ± 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 occurrence.

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 (Schafer 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 to 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
Graphite targets were measured on 14C/12C ratio using the MICA-3. Results found here would have corresponded to later Holocene layers and Supplementary Information 1. Presence/absence of paint dots, is available as box of provenience, stratigraphic information, redacted version of the table, including information by bone such as 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 δ13C, δ15N and δ34S 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, 14C measurements were performed at the Centre for Isotope Research (CIO) of the University of Groningen. Collagen samples were combusted to CO2 and graphitized to graphite (Dee et al., 2020). Graphite targets were measured on 14C/13C ratio using the MICA-DAS (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.

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 to 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. XI 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 lowestern 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, May 3, 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 accidently 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 Information 1). 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 (Fig. 4; Tables 2 and 3; 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; Tables 2 and 3), 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 Vla-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 and 3; 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 6726.2; Table 2 and 3). 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 (Table 3), to the scarce remains of AC 32 and 33 among the rediscovered material, and some 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 seem to be in the proximity of Tomb V, where an occipital squama (new materials) is present.

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 1.5 years old, found during the 1941 campaign (VII and IX according to Cardini, in the zone “H” against the eastern wall of the cave (diaries of the VII campaign, May 30, 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, May 30, 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 4 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/N between 2.9 and 3.6), including unfortunately the elk antlers. The radiocarbon determinations from these unreliable samples fall between 11,200–9010 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 ± 9960 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 10,350 ± 45 BP (Table 4). 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, 10,820 ± 40 BP) and 12,040–11,660 cal BP (AC 32, GrM-13423 10,235 ± 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° 67273), 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).

Fig. 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 Fig. 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 Fig. 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). It is possible that, being mostly composed of elements described in this paper do not appear in the first list of human remains found outside clusters, the remains discussed here were tentatively attributed: cervical vert. (1d,1f), rib (11), sacrum (1 element) ischiium (1-); cranial fragments (>50ff); maxilla (f)

4. Discussion

The reassessment of the skeletal collections 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 Bernabo 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 (Fig. 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 remains 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. Cassidy, and that several of those burials were reconstructed for the exhibitions in the museums of Finale Ligure and Genova (Bernabo Brea, 1956). The skeletal elements described in this paper do not appear in the first list of human remains found 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 et al., 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 Epi-Gravettian skeletal series. On the other end of the age spectrum, the individuals, aged between 1 and 1.5, could be added to the Epi-Gra

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* Details in Supplementary Information. 
* Same fragment used in Formicola et al. (2005).
Among the rediscovered skeletal assemblage. Overall, these creases the risk that the obtained $^{14}$C age has been affected by foreign carbon sources, which can influence the radiocarbon dating results. Furthermore, the possibility that samples passing the requirements for good-quality collagen may not accurately reflect the true age of the bone due to contamination or other factors.

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 from our date for AC 3. In the case of AC 6, the primary burial date is slightly younger than the dates we obtained, which could be due to contamination or other factors. In fact, the primary burial of AC 6 (Va-b) is dated to 10,325 ± 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.

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, April 7, 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 (Deviése 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. However, it is not an intrusive Mesolithic burial, given that the few remains attributed to this individual are scattered in Pleistocene layers (Supplementary Information 1).

Of the few remains belonging to AC 32, 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 10,325 ± 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.

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).

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 rediscovred 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, April 7, 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 (Deviése et al., 2019).

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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 8200 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 10,325 ± 30 BP (Table 3).

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(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 (Fig. 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; Fig. 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, 11,605 ± 445 BP). The last burials were dated 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 AC 4 in clusters III-IV and AC 5 or 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.

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 Arne Candide proposed by Formicola et al. (2005; see also Introduction), suggesting that the cave was used to bury the dead more continuously, albeit barely, 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 Arne Candide as a funerary site during the Younger Dryas was a cultural response to climate-induced social dynamics (Cashdan, 1983; Blockley and Gamble, 2012; see discussion in Meltzer and Bar-Yosef, 2012; cf. Crembé, 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 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 Arne 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 Arne Candide may shed further light into the frequency and continuity of use of the site over generations of hunter-gatherers.

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 Arne 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 surprisingly high frequency of deformities that may be linked to recessive (Formicola et al., 1990; Formicola, 1995) and even dominant (Sparacello et al., 2019b, 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
Fig. 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.
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.

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 Gravel-Miguel, investigation, writing — original draft, funding acquisition. Alessandra Varalli, Alessandro Riga, Francesca Seghi: investigation, methodology. Gwenâelle Goude, Sanne WL Palstra, methodology, formal analysis, resources. Elisabetta Starinni, supervision, investigation, resources. Vincenzo Formicola, Jacopo Moggi-Cecchi, conceptualization, supervision, resources. All authors, writing — review and editing.

Declaration of competing interest

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Appendix A. Supplementary data

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