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Overview of the European Upper Palaeolithic: The *Homo sapiens* bone record

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ABSTRACT

The European Upper Palaeolithic represents a period of special relevance during which anatomically modern human (*Homo sapiens*) populations arrive and radiate throughout the continent, while Neanderthals are gradually assimilated. The territorial and demographic expansion of anatomically modern humans (AMH) into new areas that took place during this period and the increase in funerary ritual resulted in a numerous collection of well-preserved human remains previously unseen in Europe. This skeletal record complements the archaeological and environmental data, and allows the development of hypotheses about biological and cultural processes in Late Pleistocene populations. We conducted an extensive compilation of most of the *Homo sapiens* fossils documented in European Upper Palaeolithic chronologies to date with the aim to explore the palaeoanthropological record and their archaeological context. The database created in this study shows a considerably extensive record of uneven quality accumulated since the mid-19th century that reveals a progressive advance and consolidation of modern human populations in western Eurasia since 45,000 BP. Our results show that the Early Upper Palaeolithic record is dominated by isolated and disarticulated remains. With the onset of the Full phase of the Upper Palaeolithic, there was a considerable increase in skeletal remains and the expansion of funerary practices throughout Europe. Despite population contractions during the Last Glacial Maximum event, the human bone record is slightly larger in the Final phase of the Upper Palaeolithic.

1. Introduction

The spread of anatomically modern humans (AMH) to western Eurasia is a major event in the Pleistocene, marking a boundary between the Middle (MP) and Upper Palaeolithic (UP). The dating of the arrival of AMH to the region is a matter of intense debate, with estimates ranging from 42,000 to 40,000 BP in Europe and the persistence of Neanderthal populations until ca. 37,500 BP in Southern and Western Iberia (Zilhão et al., 2017). The timing and spread are relevant data supported by archaeological records and genetics (Sikora et al., 2017; Yang et al., 2017; Yang and Fu, 2018; Bergström et al., 2021), as well as palaeoanthropology and chronology (Higham et al., 2014; Hublin, 2015). Although some researchers argue that AMH arrived earlier (Cortés-Sánchez et al., 2019; Hublin et al., 2020; Hublin, 2021; Slimak et al., 2022), their data is far from being confirmed.

During the Early UP, a wide range of "transitional" assemblages emerge across the continent, with key examples including Châtelperronian in France and northern and north-eastern Spain (Harrold, 1989; Pelegrin and Soressi, 2007; Soressi and Roussel, 2014; Porter et al., 2019), Uluzzian in Italy (Benazzi et al., 2011; Moroni et al., 2018; Peresani et al., 2019), Szeletian in the Czech Republic and Hungary (Zilhão, 2009; Kaminská et al., 2011; Škrdla et al., 2014), Bohunician in the Moravian region (Czech Republic) (Richter et al., 2009; Demidenko et al., 2020), and Lincombian-Ranisian-Jerzmanowician in the southern UK, Belgium, Germany and Poland (Jacobi et al., 2007; Flas, 2008, 2011). The biological authorship of these so-called "transitional" industries remains debated (Harrold, 1989; d'Errico et al., 2003; Zilhão and d'Errico, 2003; Zilhão, 2009; Flas, 2011; Soressi and Roussel, 2014; Welker et al., 2016; Rios-Garaizar et al., 2022).

Subsequently, the Early Upper Palaeolithic witnessed the spread of AMH and the assimilation of the Neanderthal population (Pinhasi et al., 2012; Villa and Roebroeks, 2014; Vaesen et al., 2021). The wide consolidation of an East European founder population in the continent around ~ 34,000 cal BP (Bennett et al., 2019; Posth et al., 2016; Sikora et al., 2017) is associated with modern behavioural patterns and a major cultural and technological shift. The Full Upper Palaeolithic gave rise to

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a continuum of highly complex archaeological cultures and industries (e.g., Aurignacian, Solutrean) including the first “vast *meta*-culture”, the Gravettian, and its several regional evolutions (Kozłowski, 2015).

The UP record provides a broad insight into past modern humans during the Late Pleistocene, mainly from extensive lithic and faunal assemblages, but also from human bones, which, as a whole, provide data about the palaeoanthropological and palaeoecological setting, subsistence strategies, dietary traits, and mortuary practices. More recently, the analysis of stable isotopes of carbon and nitrogen has made it possible to reconstruct dietary patterns, and the increase in genetic studies has allowed the identification of chromosomal sex, phylogenetic relationships, admixture events and genetic diseases. However, the palaeoanthropological record is scarce in comparison to the affluence of other archaeological materials such as lithics and faunal remains. Archaeological works and amateur reports accumulated since the mid-19th century, with a significant volume during the 20th century, constitute a considerably extensive record of uneven quality and represent an extremely relevant component of the documented material. Recent discoveries have expanded the sample of known Upper Palaeolithic fossils, which has improved our knowledge of the anatomical evolution of late Pleistocene populations. This new information is associated with a considerably extensive record accumulated over more than 150 years, with evidence of uneven quality. Incorporating the new evidence and conducting a critical review of the specimens published in previous compilations helps update the European UP fossil record and favours the development of models that seek to explain biological, technological and cultural elements involved in the dispersal and consolidation of Late Pleistocene populations in Europe. Within this context, where there is a scarcity of studies that provide an updated and unified vision of the palaeoanthropological record of the European Upper Palaeolithic, it is essential to conduct a compilation and review of the available data.

The Palaeolithic human fossil record from Europe has been intensively studied, but with a specific focus on particular topics. Thus, holistic and diachronic views of all the Upper Palaeolithic human fossils are scarce (Pettitt, 2011; Riel-Salvatore et al., 2001; Riel-Salvatore & Gravel-Miguel, 2013). Compendiums of hominin fossil remains are particularly limited in the palaeoanthropological literature. Although regional works have become more common over time. Works that provide a complete picture of the continent were developed more than 40 years ago. One of the most relevant of these catalogues to undertake a comprehensive study of the Pleistocene bone record on all five inhabited continents was a three-volume set, the second of which focuses on the European continent (Oakley et al., 1971). This compilation concisely recorded the information related to the history, context, dating, bone remains and all the bibliographical references from which the data is provided. More recently, a new compilation was published with a comparative descriptive approach to the cranial remains of late Pleistocene hominins, mainly the Neanderthals (Schwartz and Tattersall, 2002). Unlike the books by Oakley et al. (1971), this volume is more limited in terms of the number of specimens, but certainly more abundant in detail, with extensive descriptive elements and comprehensive photographs of each of the individual bones.

The evidence of the emergence of funerary practices in the hominin lineage has sparked a lively debate in palaeolithic archaeology, particularly with regard to distinguishing them from a broader set of mortuary practices. In fact, the terms ‘funerary’ and ‘mortuary’ behaviour in the palaeoanthropological literature are sometimes used synonymously, but this is incorrect. “Mortuary” refers to the response to corpses of their conspecifics and their subsequent treatment by them. Thus, mortuary behaviour is not restricted to humans; it has been observed in many animals and has been specifically studied in primates, as social species (Piel & Stewart, 2015; Pettitt, 2011). By contrast, funerary behaviour is related to the disposal of corpses, in graves, by cremation, or in sky burials, or to the perpetuation of the memory of the dead in graveyards and in the form of grave markings and grave goods (Pettitt, 2018). The earliest reliable evidence of primary burials can be traced to Skhul, Qafzeh, and Tabun in western Asia (Schick, 2002), where Neanderthals and *Homo sapiens* occupied the Levantine area in several periods between ~140-55 ka and both practised burials (Pettitt, 2011). The emergence of this tradition occurred much later than the origin of *Homo sapiens* in Africa. In fact, the early evidence of funerary practices in the continent is limited to children’s skeletons as found in Taramsa (Egypt) with a chronology around 68 ka (Vermeersch et al., 1998), Border Cave (South Africa) dated around 74 ka (D’Errico and Backwell, 2016) and Panga ya Saidi (Kenya), which records the earliest evidence of a burial, dated at 78 ka, where a deliberately excavated pit contained a skeleton in a flexed position (Martinón-Torres et al., 2021). It is significant that this practice was not observed again in modern humans for over 40,000 years.

In Europe, the debate about funerary practices during the Middle and Upper Palaeolithic also led to extensive reviews of the evidence available in the funerary record (Olària, 2008; Riel-Salvatore and Gravel-Miguel, 2013; Orschiedt, 2018). On a small-scale, a large number of regional studies have provided information for the fossil record documented in countries such as France (Henry-Gambier, 1990; Henry-Gambier, 1992; Henry-Gambier et al., 2000), Italy (Mussi, 1986; Giacobini, 2006a; Giacobini, 2006b; Fabbri & Giacobini, 2021; Alciati et al., 2005), Spain (Pérez, 2007; Cabrera et al., 2004; Arsuaga et al., 2001; de Balbín, 2015), Germany (Street et al., 2006; Bolus, 2003; Stevens et al., 2009), Slovakia (Šefčáková, 2007), and the Moravian region in the Czech Republic (Svoboda et al., 1996), among others.

The present paper aims to give an overview the palaeoanthropological record over time, integrating all existing data on *Homo sapiens* fossils including: 1) main information on localities (discovery, site location, country); 2) archaeological context (cultural attribution, period, stratigraphic context, chronometric data); 3) the anthropological description (skeletal representation, age-at-death, sex, number of bones and minimum number of individuals); and 4) mortuary behaviour (burial context, grave goods, anthropogenic modifications on bones, presence of ochre). The main objective is to explore the archaeological and palaeoanthropological record of the UP and provide an updated state of the art from the evidence. The general purpose is to evaluate the distribution of human remains across Europe and across periods, age-at-death and gender, and to explore some of the evidence of mortuary behaviour. To date, transitional horizons (e.g., Châtelperronian, Uluzzian, etc.) have not been explored in depth. To conduct this study an extensive database was created (Supplementary Table S1), containing most of the *Homo sapiens* fossil record documented in European UP archaeological contexts.

2. Methodology

2.1. Database

The creation of the database is designed to provide concise, direct information that allows rapid accessibility to the data collected. The generation of a digital database, compared to the large, printed volumes and previous compilation works, confers an advantage in terms of accessing and processing the information. The digitization of the bone record facilitates the accessibility and manipulation of the data and allows the reproducibility of the research.

The database (Supplementary Table S1) has been structured in such a way that each row contains the information of all the human remains associated with a single individual. Therefore, skeletal remains belonging to different individuals documented at the same site have been listed in different rows with the specific information related to each of them. Occasionally, large bone assemblages reveal several individuals and researchers do not establish the association of the remains for each individual. In such cases, we have indicated the minimum number of individuals (MNI) stated in the literature and a MNI of 1 individual has been designated for cases in which this information is not specified. We have unified all these individuals in the same row, except for those found in different layers, which have been separated in a row for each archaeological layer. Individuals represented by several associated bones in anatomical position have been described as "skeletons" (frequently in funerary contexts). The number of bone remains described will be indicated in each row. It should be noted that many of the bone remains discussed here were excavated over a century ago, some of them using the standard methodological approach methods prevalent at the time. Therefore, we decided to treat all the bone remains compiled in the database as a minimum number of bone remains (MNBR). Complete or incomplete bones are counted individually as 1, even though they may be fragmented into several pieces (when the bone is fragmented, it will always be indicated in the database). Some are mentioned in the bibliography with an imprecise number (e.g., various phalanges, some cranial remains) and we have considered them as a minimum number of 2 remains due to the impossibility of knowing the actual record. Indeterminate bones are counted in the total remains, but they are not taken into account within the cranial or postcranial remains. Crania are counted as a total of 28 bones (splanchnocranium: 14; neurocranium: 14), and the coxal bone as 3 (ilium, ischium and pubis).

The most relevant bibliographical references are cited for each specimen/site. Priority is not given to the first published report of the discovery, especially for older works, but rather to the most important and relevant publications that provide a broad and in-depth description of the remains, as well as genetics, palaeopathology, burial status or other relevant information. We have also cited publications in which different authors have come to different conclusions. In extensive catalogues such as Oakley et al. (1971), some of the oldest finds are only known from the original reports. In some of these cases, we have decided to reference these older works since, in many instances, they are of greater historical value. Literature that provides the direct determination of the age of the specimen itself or the geological age was also cited.

Works that carry out the best description of the stratigraphic context and the associated industry of the site are cited for the specimens that present a chronological attribution based on the archaeological context. Funerary practices during the UP can be highly variable, revealing particular features depending on the period and region observed. This generates greater complexity when it comes to understanding the forms of burial, and a challenge to determine from which aspects they are defined. Several authors have presented extensive and detailed studies on this subject (see Olària, 2008, Riel-Salvatore & Gravel-Miguel, 2013; De Balbín, 2015; Orschiedt, 2018; Fabbri & Giacobini, 2021). This work provides concise data related to the context of human remains, based on the information provided by the sources consulted. The burial status has been defined in the database as non-existent (none) and uncertain for those highly doubtful contexts. We use the broad term "mortuary activity" to describe anything related to the treatment of human corpses and death (Pettitt, 2011). For the most reliable record, the number of individuals (single, double, triple or multiple) and the type of deposition (primary or secondary) has been defined. Grave goods, the use of ochre, and anthropic modifications of human bones have also been recorded. Correspondence analysis of the mortuary treatment was performed using PAST 4.06b software (Hammer et al., 2001).

2.2. Bibliography

The database of the human compiled in this research-based work is built on the bibliography and is updated to October 2023. However, it has been necessary to revise the large volume of data carefully, especially in the older catalogues, due to the outdated nature of the information on some of the specimens. The development of accelerator mass spectrometry (AMS) over the last forty years and improvements in laboratory pre-treatment anticontamination protocols have allowed for the clarification of many chronological issues and has made it possible to provide a more reliable and precise chronological framework of the fossils. Several human remains presented in these catalogues as being from the Late Pleistocene are now known to be Mesolithic, as is the case of Combe-Chapelle, Hohlenstein-Stadel, Hahnöfersand, Veyrier, Velika Pećina, Badger Hole and Fontana Nuova, among others. Likewise, Roche Courbon, Weißenthurm and Reilingen 2 are other redated examples from the Roman age, as well as Olmo, Starosele, Paderborn-Sande, Bad Oldesloe and San Bernardino from Medieval/Modern chronology. In some cases, they have also been placed in the Middle Pleistocene/Palaeolithic due to reviews of the materials and archaeological contexts of the sites (e.g., Combe-Grenal, Swanscombe). Additionally, advances in the field of palaeoanthropology and the improvement of techniques for studying DNA preserved in skeletal remains has supplemented previous anthropological data. In summary, there are fossils which taxonomic assignment is complex due to the anatomical traits, preservation, scarce remains, fragmentary specimens or post-depositional processes (Benazzi et al., 2011; Slimak et al., 2022; Keeling et al., 2023).

The Aurignacian graves of layer 8a in Cueva Morín dated by 14C AMS at 36,590 ± 770 BP (Maíllo-Fernández et al., 2001) have not been included in this study because the bones were not preserved, but rather show a possible case of adipocere (saponification) (González and Freeman, 1973).

The criteria for inclusion and exclusion of human remains in the database have been a fundamental element in the configuration of the bone sample of this paper. The critical criteria that have been considered to summarize the *Homo sapiens* fossil record documented in European UP and the current state of palaeoanthropological research are outlined below.

2.3. Geographical and temporal criteria

Geographically, the research is restricted to eastern Eurasia, with the natural boundaries of the Caucasus, and the Dardanelles and Bosporus Straits to the south-east, and the Urals to the east. The geographical data from each site has been recorded in the database, such as the country, the region, the municipality, and latitude and longitude using the World Geodetic System (WGS) 84. We created a map using the ArcGIS Desktop 10.8 software (Esri, Redlands, California, USA) with the locations of the sites included in this study based on their geographic coordinates (Datum WGS84) (Supplementary Table S1). Several heat-maps using triangular kernel-shape by phases were generated with QGIS 3.24 software based on the number of MNI by site according to Supplementary Table S1. Likewise, the sample is temporally limited to the Upper Palaeolithic *sensu stricto*. Unlike the temporal uncertainty at the beginning of the Upper Palaeolithic, it is possible to define the end of the period precisely, as it coincides with the geological end of the Pleistocene (Marine Isotopic Stage -MIS- 2), which gives way to the Holocene (MIS 1), defined based on its clear climatic signature. The climate record observable in the Greenland ice core from the NorthGRIP project (NGRIP) provides an age of 11,700 cal BP of the Global Stratotype Section and Point (GSSP) for the base of the Holocene Epoch (Walker et al., 2009). In this way, human remains documented on archaeological levels belonging to the Upper Palaeolithic are included in the study.

The chronological approach to Upper Palaeolithic time is mainly constructed using radiocarbon dating which represents the most robust methodology, with its standard deviation of measured age at the laboratory (1 sigma) and posterior calibration at 2 sigma being a probabilistic interval shorter than other chronological approaches, such as luminescence (including Optically-Stimulated Luminescence (OSL) and thermoluminescence) and acid racemization (AAR). In Supplementary Table S1, we include all the chronological ages provided in the literature and the information corresponding to the dating technique (radiocarbon, OSL, AAR, etc.) and dated material (human bone, charcoal, fauna, shell, sediment). When provided in the literature, the taxa assignment was also indicated.

Most the radiocarbon ages of the Palaeolithic burials are obtained from the archaeological context of the inhumate, including grave goods or artifacts associated to the grave or the layer where the human bones

Table 1
Upper Palaeolithic phases used in the present work, based on Zilhão (2014).

Phase	14C BP	cal BP	Western Europe	Northern and Central Europe	Italy and SE Europe	Eastern Europe
Early	35,000	40,300	Aurignacian	Aurignacian	Aurignacian	Aurignacian
Full	30,000	34,700	Gravettian	PavlovianWillendorf-Kostenkian	Gravettian	MolodovanKostenki/Avdeevo
	21,000	25,000	Solutrean			
	19,000	22,700	Soluteogravettian, Badegoulian			
	17,000	20,200	Magdalenian	Magdalenian	Tardigravettian	Mammoth-dwellings culture
Final	12,500	14,600	Epimagdalalenian, Azilian-LaborianCreswellian	Ahrensburgian, Swiderian, Hamburgian and Federmessergruppen	Romanellian	

where recovered. One source of inaccuracy when dating in the Upper Palaeolithic context is the use of shell ornaments, as shells provide results that are biased by reservoir effects, and the thanatocoenoses of current beaches demonstrates the presence of shells over several millennia (Sivan et al., 2006). Another source of inaccuracy is the archaeological association of the radiocarbon-dated object (bone or charcoal) and the individual, as most of the archaeological sites are cave and rock-shelters often affected by post-depositional processes, or the association may be the result of palimpsests. All the samples of human bones, seashells, faunal bones and charcoal have been calibrated using IntCal20 and Marine20 curves (Heaton et al., 2020; Reimer et al., 2020) in OxCal v 4.4 (Bronk Ramsey, 2021). Marine reservoir corrections (ΔR) of local effect have not been applied.

The Upper Palaeolithic sequence was constructed over the last two centuries and was mostly based on the stratigraphies identified in localities in the French Dordogne and neighbouring areas. Lithic assemblages and typological classification of stone-tools recovered in the most well-known sites allowed us to establish the classic sequence of the UP technocomplex, using the eponymous French sites of Aurignac (Aurignacian), La Gravette (Gravettian), Le Solutré (Solutrean), La Madeleine (Magdalenian) and Mas d'Azil (Azilian) (Pettitt, 2013). Today, research conducted throughout Europe demonstrates that the UP picture is far more complex, diverse and heterogeneous. For this reason, we follow the phases proposed by Zilhão (2014), which group the UP technocomplexes into four major phases: Transitional, Early, Full and Final. The present work focuses on *Homo sapiens* fossils and ages have been clustered according to these three phases: Early, Full and Final (Table 1).

2.4. Palaeoanthropology

2.4.1. Biological ascription

The biological ascription has also been a fundamental element in the sample compilation. Bone remains have only been included in the database if they present a clear ascription to *Homo sapiens*. Findings of fragmentary bone remains or skeletal pieces with a reduced morphological variability between taxa sometimes do not allow researchers to ensure their biological affiliation. For instance, in Valdegoba Cave (Spain), some remains associated with Mousterian technology (Middle Palaeolithic) show the closest affinity with early modern humans, pending further comparative studies on Pleistocene deciduous teeth to make a taxonomic adscription (Quam et al., 2001). Furthermore, post-depositional processes, inaccuracy in the excavation methodology, and unreliable dating, which allow the intrusion of other hominin remains in recent archaeological levels, along with the existence of Neanderthal remains in Upper Palaeolithic chronologies, make it necessary to have a solid biological diagnosis of the remains.

2.4.2. Body part representation

The state of preservation of the skeletons was assessed using an Anatomical Preservation Index (API). It is an adaptation of a previous index proposed by Walker et al. (1988) and expresses the sum of the number of bones preserved for three skeletal groupings:

API1: long bones (both humeri, both radii, both ulnae, both femora, both tibia, and both fibulae) (n = 12).

API2: the long bones from API1, plus scapular and pelvic waist bones (both scapulae, both clavicles, and both coxal) (n = 18).

API3: all bones previously mentioned, plus the mandible, the splanchnocranium and the neurocranium (n = 21).

The number of bones preserved is divided by the total value of bones of the three skeletal groupings (n = 21). The preservation scores are expressed as percentages, and are divided into the following four classes:

Incomplete skeleton (<49 %).

Partial skeleton (50 %-74 %).

Almost complete skeleton (75 %-99 %).

Complete skeleton (100 %).

When it has not been possible to confirm the state of preservation of the skeletal remains, we have retained the exact statement provided by the cited author.

2.4.3. Age-at-death estimations

Physical anthropology has undergone significant developments this century, establishing new techniques and standardized processes. Traditional measurements and observations are employed in new ways to assess growth and development, sex differences, biomechanics and palaeopathology. Given the standards for data collection at the time some bone remains were found, it is likely that some of this evidence may not be accurate. This is a problem that can create a disparity with the most recent remains and disrupt analyses of the palaeoanthropological assemblage. The only real solution to this situation would be to carry out a re-examination of all the bone and skeletal remains, a task that is clearly unfeasible due to the size of the Upper Palaeolithic record. To mitigate this issue, we have confirmed the original evaluations of the fossil with the most recent morphological revisions. In some cases, the remains have not been re-examined as they have been destroyed, their whereabouts are unknown, or they have simply not yet undergone modern review. Likewise, it should be noted that most human osteologists did not use standard sexing and aging methods and terminology, which is still the case even nowadays (Falys and Lewis, 2011), making it problematic to compare age estimations with those of individuals from other geographical locations or from finds that are temporally distant. In this respect, the estimated age-at-death in particular is fairly heterogeneous in the literature. Some researchers indicate a precise age of maturation, while, in other cases, they were only able to distinguish between age categories. As far as possible, we have retained the term used by the author quoted, although we have modified some equivalent categories to adapt them to the terminology in current use (e.g., "adolescent" has been modified to "juvenile"). However, although the database may be inconsistent and yield certain disparities, in order to be able to make some observations on the bone record, we have taken precautions to control such biases in the analyses. All estimated age values have been categorized following the classifications proposed by Buikstra and Ubelaker (1994) modified with the terminology used by Olivier and Demoulin (1976): Fetal (<birth), Perinatal (±birth), Infant I (0–2), Infant II (3–11), Juvenile (12–19), Young Adult (20–34), Mature Adult (35–49) and Senile Adult (>50). Individuals with imprecise age-at-death values (e.g., ±*42*, *<13*) and large age estimates that cover more than one age class are arranged in three generic categories: Indeterminate Subadult (0–19), Indeterminate Adult (>20), and Indeterminate Adult/Subadult. Individuals with an age class already provided by the original authors have been placed within the equivalent classes established in this study. Once again, if the age class is imprecise or uncertain they are arranged in the previous generic categories. Ternary plot distribution indicating the percentage median of individuals for age categories based on data from Table 2 was performed using PAST 4.06b software (Hammer et al., 2001).

2.4.4. Sexual identification

Given its duality, the estimation of sex is less likely to be wrong, and the authors declare firmer and supported conclusions that are rarely disputed in later studies. However, in some cases, previous conclusions have been refuted by modern reanalyses. One example is the individual from "Paviland 1", found in 1823, whose discoverers identified the bones as those of a female known as the "Red Woman" or "The Witch of Paviland", but Trinkaus and Holliday (2000) later reclassified the skeleton as that of a young adult man.

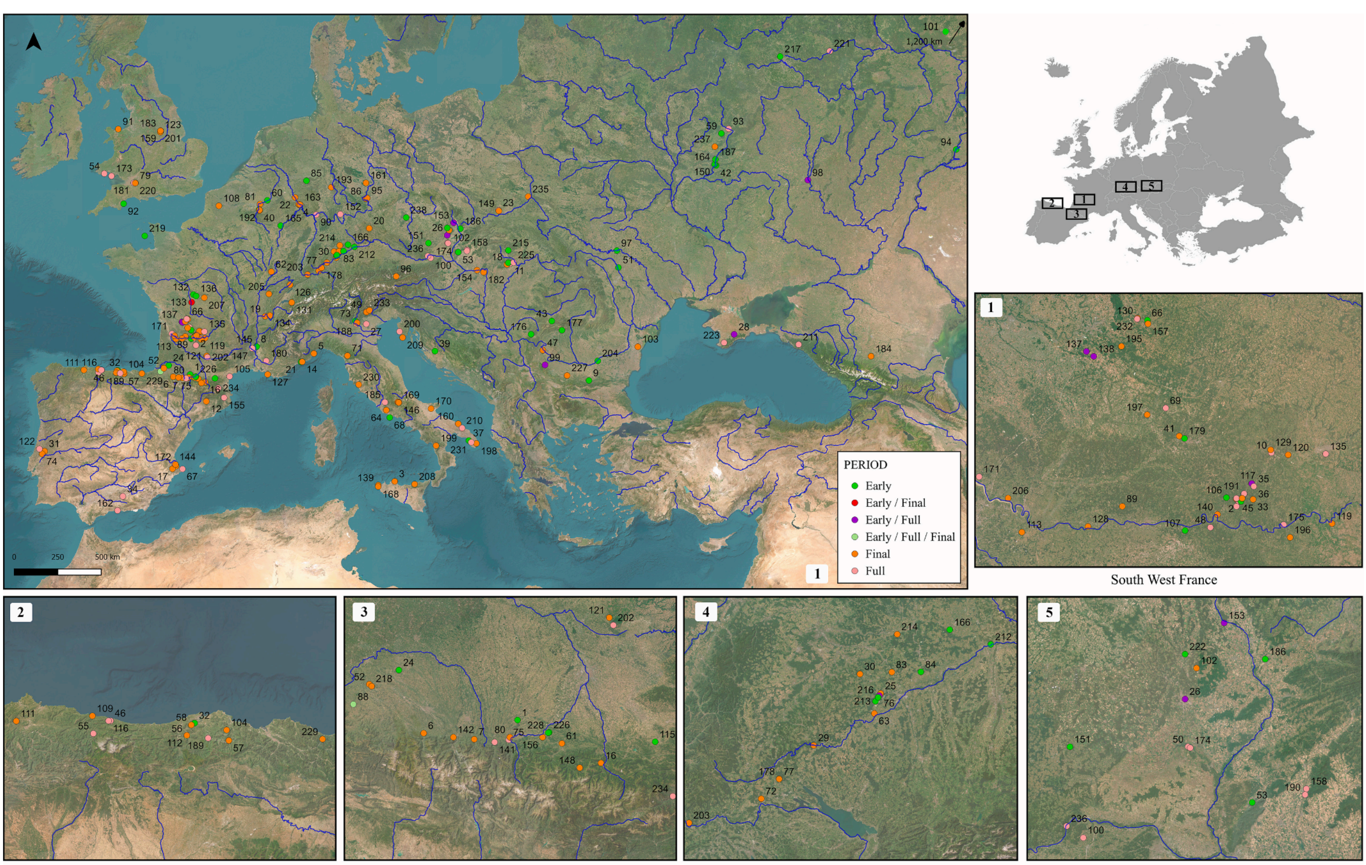

Fig. 1. Geographic distribution of the European Upper Palaeolithic sites compiled in this study that have yielded *Homo sapiens* bone remains. For site numbering, see Supplementary Material Table S2. Detailed views (1 to 5) of areas with high density of sites with human remains.

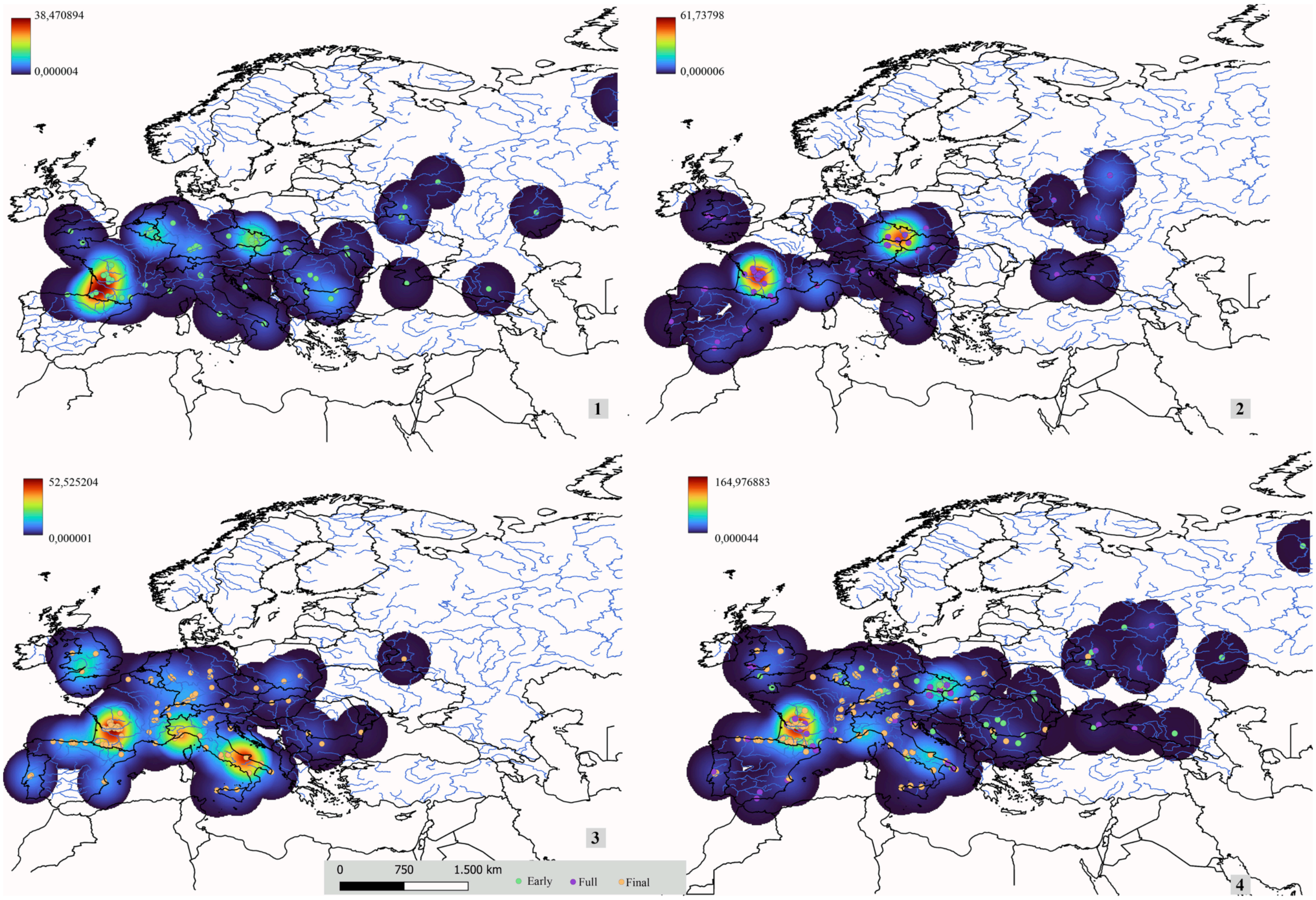

Fig. 2. Heatmap according to spatial distribution and MNI by site. Map was performed using software QGIS version 3.24 and Heatmap plugin of Early (1), Full (2), Final (3) phases and all phases (4).

3. Results

3.1. Geographical area

The present compilation of the human skeletal remains of the Upper Palaeolithic published to date reveals a palaeoanthropological record comprising 248 sites located in 20 countries (Fig. 1). The great territorial extension encompasses practically all of continental Europe and the surrounding islands (i.e. Great Britain, Sicilia, etc.), with the exception of the Scandinavian peninsula and the northern regions of present-day Germany, Poland and the Baltic countries, due to the extension of the glaciers during the entire Last Glacial Period. Human remains appear from the Iberian Peninsula in the west to the Ural Mountains in the east, and the Caucasus Mountains, and the Dardanelles and Bosporus Straits in the southeast. Although research bias may lead to an over-representation of some regions, such as south-western France region among others, a high concentration of remains have been observed in certain areas. According to the distribution of UP human remains (Fig. 1), a high density of remains can be observed following natural corridors, such as rivers (Danube, Rhine, etc.), valleys and coastal platforms that emerged during the glacial periods. The large plains are a suitable landscape for human occupancy, as evidenced by remains found in central and eastern European sites. In addition, cavities in karst terrains were optimal settings for past populations and biased the concentration of bones due to the good preservation conditions compared to open-air sites.

The geospatial distribution during the initial phase indicates a higher concentration of burials of human remains in central and western Europe, while the southern peninsulas exhibit relatively few remains, probably correlating with the migratory routes and expansion patterns of early modern humans from west to east (Fig. 2). In the Full and Final phases, an increase is observed in burials in southern regions, probably associated with the contraction of human habitation towards more temperate southern areas functioning as refugia during periods of extreme climate, such as the Last Glacial Maximum (LGM). This climatic reconfiguration, marked by cold and arid conditions in northern Europe (Banks et al., 2008, among others), led to a significant bottleneck in human genetic diversity, as evidenced in various European regions (Posth et al., 2023). It is important to emphasize that the scenario in the Iberian Peninsula appears notably more complex than in refugia in other peninsulas (Villalba-Mouco et al., 2023).

3.2. Palaeoanthropological record of the Upper Palaeolithic

The 248 archaeological sites yield a minimum of 6,604 of human bones corresponding to a minimum number of 804 individuals for the whole Upper Palaeolithic (Table 2). 66 % of the bones correspond to cranial remains and 33 % to postcranial. The remaining 1 % corresponds to the 64 bone remains for which there is no precise information on their anatomical identification, so they are not included in the cranial or postcranial categories.

Bone remains increase with a positive trend as the UP progresses. The early phase of the UP contributed the smallest number of human bones (MNBR = 877 and MNI = 147). Most of these are cranial elements, mainly teeth, and some mandibular and neurocranial fragments, while the postcranial remains are fairly residual. A significant increase is

Table 2
Summary table of the *Homo sapiens* skeletal remains from the Upper Palaeolithic. Bones that have not been identified and cannot be included in cranial or postcranial categories have only been included in the total count (MNBR = minimum number of bone remains).

MNBR	Early	Full	Final	Uncertain	TOTAL UP
Cranial	698	1728	1949	32	**4,407**
Postcranial	171	985	965	12	**2,133**
Indeterminate	8	42	14	0	**64**
Total MNBR	**877**	**2,755**	**2,928**	**44**	**6,604**
Skeletons					
Incomplete	0	8	7	0	**15**
Partial	1	12	11	0	**24**
Almost complete	0	11	25	0	**36**
Complete	0	13	7	0	**20**
Indeterminate	0	1	9	0	**10**
Total skeletons	1	45	59	0	**105**
Sex					
Male	3	40	55	0	**98**
Male?	2	0	3	0	**5**
Female	8	24	36	0	**68**
Female?	4	4	1	0	**9**
Indeterminate	130	217	269	8	**624**
Sexed individuals	17	68	95	0	**180**
Age					
Fetal	0	1	2	0	**3**
Perinatal	0	2	3	0	**5**
Infant I	0	10	12	0	**22**
Infant II	13	23	25	1	**62**
Juvenile	11	23	28	0	**62**
Young Adult	5	33	36	0	**74**
Mature Adult	3	13	32	0	**48**
Senile Adult	2	3	5	0	**10**
Indet. Subadult	23	45	34	0	**102**
Indet. Adult	45	73	133	3	**254**
Indet. Subadult / Indet. Adult	6	3	8	1	**18**
Indeterminate	39	46	46	3	**134**
Aged individuals	108	229	318	5	**660**
Total MNI	147	285	364	8	**804**

observed in the quantity of fossils preserved during the Full phase, moderate for the MNI (n = 285) but significant for the MNBR, which presents a threefold increase (n = 2,755). The number of sites falls slightly but, in contrast, the number of fossil remains and skeletal bodies rises considerably. This increase, three times greater than in the previous period, is perhaps a consequence not only of better conservation but also of a longer Full UP phase (10,000 years longer) and a growth in population density throughout Europe (Tallavaara et al., 2015). The Final phase is the largest in the entire UP (MNBR = 2,928 and MNI = 364), as the fossil sample shows a slight increase in cranial bone remains but a fall in the number of postcranial remains.

As far as skeletons are concerned, at least 105 specimens in different degrees of preservation have been recovered in the UP record (Table 1, Supplementary Table S1). In just over half of the UP skeletons (53 %) the degree of preservation is above 75 % (20 complete and 36 almost complete skeletons), followed by 24 partial and 15 incomplete bodies. As for the remaining 10 skeletons identified, the publications do not provide any records of the bones recovered and no information is

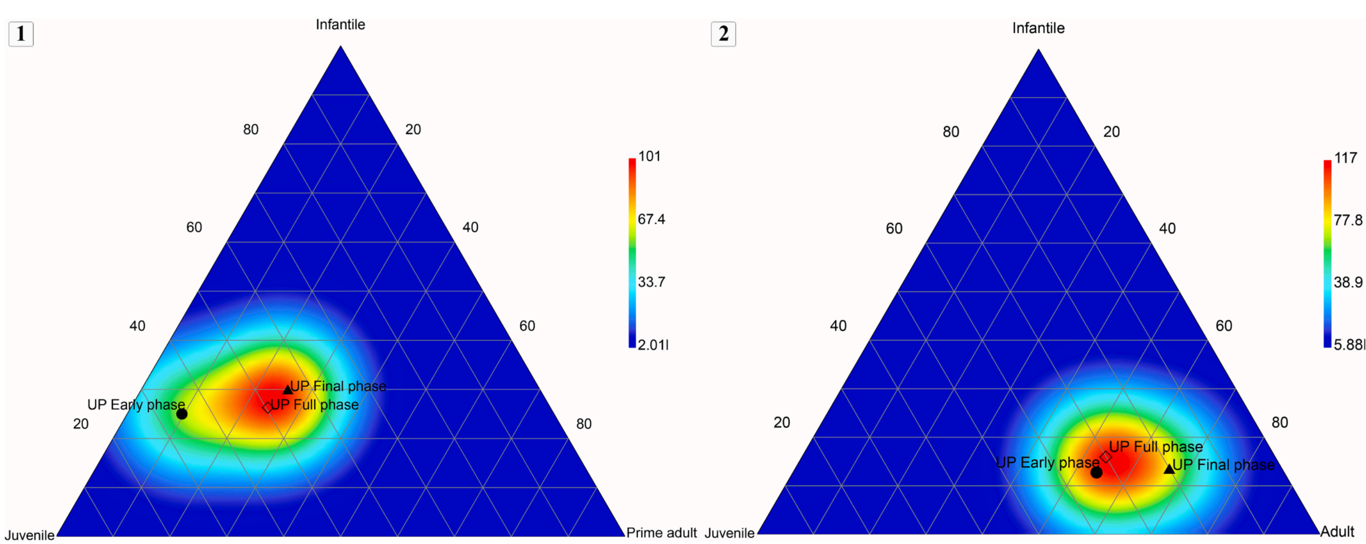

Fig. 3. Distribution of number of individuals among age groups and UP phases in two density ternary plots based on data from Table 2: 1). Infantile (Early = 13, Full = 36 and Final = 42 individuals), juvenile (Early = 34, Full = 68 and Final = 33 individuals) and prime adult (Early = 5, Full = 33 and Final = 36 individuals). 2). Infantile (same data than 1), juvenile (same data than 1) and adult, including senile individuals (Early = 55, Full = 122 and Final = 206 individuals).

Table 3
Summary of Bayesian modelling clustered by phases. Complete information of the results is provided in Supplementary Table S1. Indices: $A_{model} = 81.1/A_{overall} = 91.2$.

	Modelled (BP) 68.2 %		Modelled (BP) 95.4 %		Convergence integral %
Boundary Start Early	45,306	43,779	45,933	43,349	94.5
Boundary End Early	34,504	33,627	34,750	32,854	95.2
Boundary Start Full	34,487	33,735	34,792	33,338	96.8
Boundary End Full	20,377	20,043	20,466	19,689	98.9
Boundary Start Final	19,815	19,513	19,970	19,243	97.6
Boundary End Final	11,657	11,368	11,749	11,171	98.4

available regarding their degree of preservation (three individuals from Saint-Germain-la-Rivière, nine from Sunghir, one from Cuina Turcului, four from Kendrick's Cave, and three juveniles from Mother Grundy's Parlour).

With respect to age profiles, certain trends between UP phases can be observed when young adults, infants and juveniles are plotted (Fig. 3). Infants are represented in similar degrees in the UP phases, between 13 and 16 % of the total record of individuals. Juvenile and adult (including elderly) individuals are recorded in similar proportions for the early and full phases of the UP; juveniles account for 30–33 % (in early and full phases) but are less frequent in the final phase (20 %). Adults are also represented in similar degrees in the early and full phases (54 %) and present an upward trend tendency in the final phase (66 %). The predominance of adults can be observed in Fig. 3.2, together with the rising number of adult individuals and the falling proportion of juveniles in the final phase, which is clearly separated from the previous phases in the ternary plot. Juveniles dominate when infants, juveniles and prime adults, i.e. young adults, are plotted together (Fig. 3.1).

In terms of sexual identification, male individuals are tentatively more abundant (12.8 %) than females (9.6 %); however, a high percentage cannot be clearly classified and remain indeterminate (77.6 %), probably due to the large presence of cranial fragments, mainly teeth and fragments from the cranial vault, which complicate sex estimation based solely on a morphological study. The ratio of male to female individuals is similar in all periods except for the Early phase (three male and seven female individuals), while indeterminate individuals are clearly dominant in the UP record.

3.3. *Chronology*

Despite the relative variety of dating methods applied in archaeological contexts, in the European UP bone record, only half of the individuals in our database have been directly (N = 160; 20 %) or indirectly dated (N = 240; 30 %), as well as 4 individuals (0.5 %) without information regarding the sample.

Ages have been clustered according to three phases (Early, Full and Final) previously described in the methodology chapter. Two different command functions available in OXCAL program have been used to analyse each group and the distributions. KDE_Model was constructed using the kernel factor default values of the software itself, i.e. N(0,1) and U(0,1), as detailed in the literature (Ramsey, 2009). KDE_Model of each phase is presented separately in Fig. 2, 4.4, 4.5, 4.6 and the whole model in Fig. 3. We prefer this function rather than the SUM distribution as suggested by Ramsey (2009) for individualized analyses and density evaluation. However, the SUM function is also presented in the model Fig. 1 and Supplementary Fig. S1. The Bayesian framework is a powerful tool for constructing accurate chronological models and detecting outliers. Mainly due to the large chronological range and imprecisions of non-radiocarbon techniques, here, we only include those obtained by 14C. The analysis estimates the chronology for the beginning and end of phases (Table 3) in which radiocarbon ages have been grouped (Bronk Ramsey, 2021). The modelled results include the index of agreement (A) which gives a good measure of how well any posterior distribution agrees with the prior distribution. The index of agreement falls below 60 %. The model also includes the overall agreement (Aoverall). A Sequence function is used to constrain the dates in terms of chronological order.

We obtained good agreement ($A_{overall} = 102.9$) after considering the Sunghir 1, Sunghir 2 and Paviland dates in the Early phase of the model. However, the archaeological context of the abovementioned sites and funerary treatments (i.e. burial, ochre pigmentation, etc.) may be considered as a Full phase rather than Aurignacian as previously indicated by other authors (Pettitt, 2006), some of whom even obtained radiocarbon ages compatible with the Early phase (Jacobi and Higham, 2008). In addition, the exact location of the Cioclovina 1 skull and its relationship with lithics is unknown and the skull is even considered Aurignacian *sensu lato* (Soficaru and Trinkaus, 2020). In the case of Cussac, we do not include the radiocarbon date of locus 2, as it was considered unreliable by the radiocarbon laboratory (Aujoulat et al., 2002; Villotte et al., 2016). In Buran-Kaya III, the stratigraphic context of a human skull bone is uncertain (Péan et al., 2016; Higham et al., 2007), although it was previously attributed to the Aurignacian layer 6–4 and the date of radiocarbon (32,790 ± 280 BP, OxA-13302). Therefore, in our database (Supplementary Table S1), we prefer to consider the cultural attribution as uncertain. The other radiocarbon ages are shown in Supplementary Table S1 but, in view of the stratigraphic incongruencies reported by several authors (Péan et al., 2016; Higham et al., 2007), we excluded this site for the chronological model in Fig. 4. The neurocranium from Kelsterbach was attributed to the Early Upper Palaeolithic (Late Weichselian) based on a radiocarbon date of 31,200 ± 600 BP (Protsch and Semmel, 1978). The fossil is missing, making it impossible to resample. However, based on the large revisions conducted from the Frankfurt laboratory, the previous result is suspected to be unreliable (Street et al., 2016). For this reason, we do not include the radiocarbon date in our database and classify the cultural attribution as uncertain.

The model obtained (Supplementary Fig. S1 and Supplementary Data 1 Bayesian Model CQL code), with the mentioned samples considered in the Full phase, shows poor agreement in the case of the Cioclovina (A = 46.4) and Sunghir_669 (A = 29.4) samples, but the general model built shows good overall agreement ($A_{overall} = 91.2$ %), which indicates that ages agree with the information included in the model. The model's structure, including boundaries and SUM function, is presented in Fig. 4 and all the information is presented in the Supplementary Material (Fig. S1, Supplementary Table S3 and Supplementary Data 1), including all the ages modelled and grouped in three phases and the SUM function plotted.

Bearing in mind that funerary practices are a general trend in human behaviour and a continuous process, and that clustering sites in each phase only reflects the number of repeated times, the SUM function of the Early phase includes 38 samples, the Full, 68 samples, and the Final, 98 samples. KDE_Model analysis is shown in Fig. 4, Table S3 and the CQL in the Supplementary Data 1. The results suggest several peaks of density of dates in each phase (Fig. 3). In the detailed view, the Early phase suggests two peaks of density with high density around 40–35 ka BP, which is clearly continuous with the Full phase, whose main peaks are between 35 and 25 ka BP. The Final phase density is between 16 and 11 ka BP, indicating a gap of between 25 and 16 ka BP, which is clearly related to the Solutrean technocomplex (~24–19 ka BP) or LGM period (26.5–19) (Clark et al., 2009). Ice sheets remained in position until 19 ka

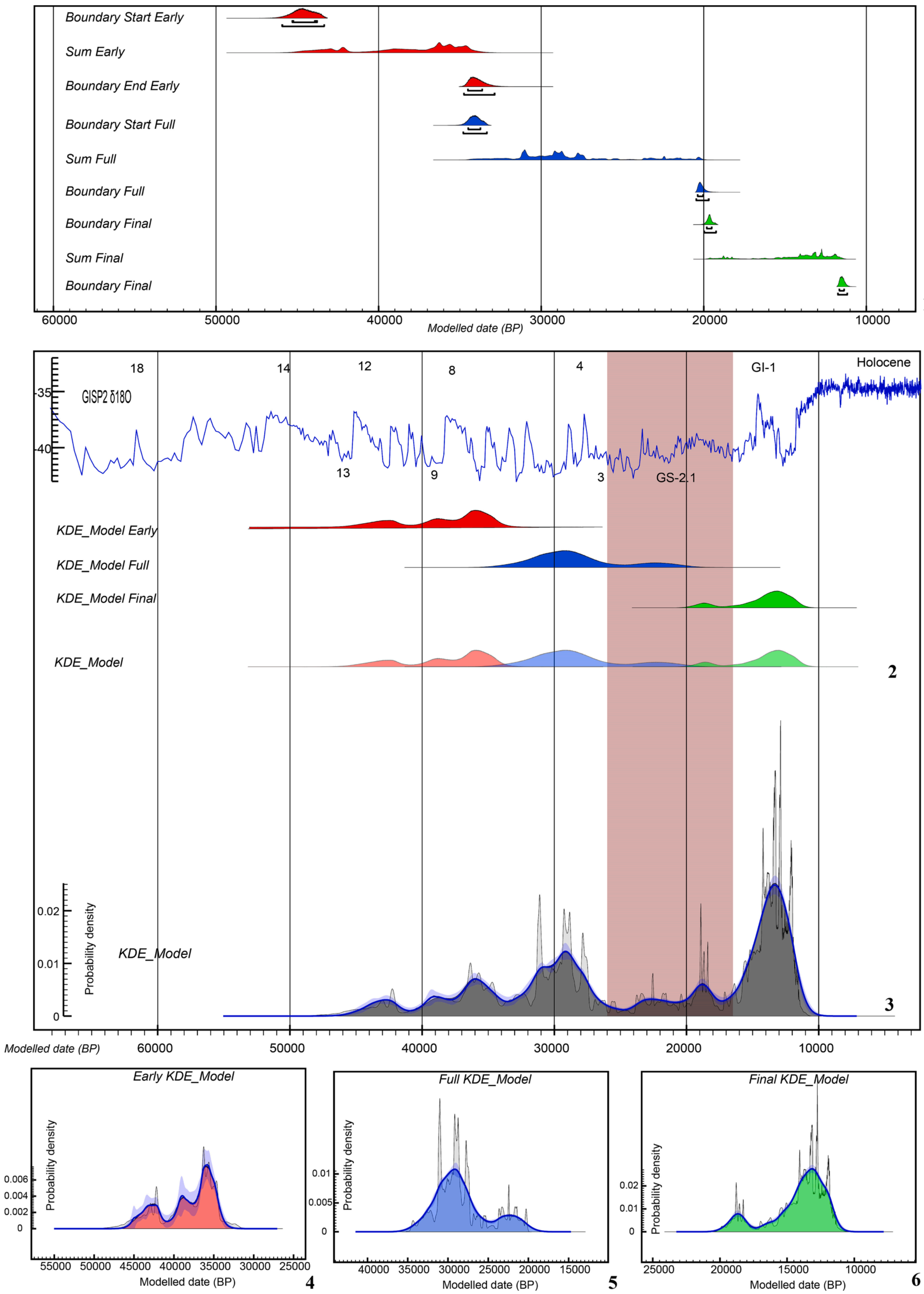

Fig. 4. Radiocarbon modelling of entire human remains. 1) Model structure including SUM function and boundaries. 2) KDE plot visualization of the overall distribution of dated sites within each phase and superposition. 3) KDE model of the overall phases signalling the variability. 4–6) Detailed KDE model of each phase (Early n = 38; Full n = 68; Final n = 98). Blue bands show the ± 1σ variability in snapshot KDE distributions. Modelled determinations were constructed using OxCal v4.4.4 Bronk Ramsey (2021) and atmospheric data from Reimer et al. (2020). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 4
Number of remains and minimum number of individuals by isolated remains, burials (primary and secondary), undefined and uncertain and UP phases.

		Primary burials															
	Isolated Remains	Single		Double		Triple		Multiple		Secondary burials		Undefined burials		Uncertain burials	Burials ∑		Total MNI
UP Phase	N	N	MNI	N	MNI	N	MNI	N	MNI	N	MNI	N	MNI	MNI	N	MNI	N
Early	146	1	1	0	0	0	0	0	0	0	0	0	0	0	1	1	147
Full	162	50	50	3	6	3	6	1	30	2	15	0	0	16	57	92	285
Final	213	58	58	7	14	0	0	1	11	1	14	1	4	50	67	87	364
Unknown	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8
Total	**529**	**109**	**109**	**10**	**20**	**2**	**6**	**2**	**41**	**3**	**29**	**1**	**4**	**66**	**125**	**180**	**804**

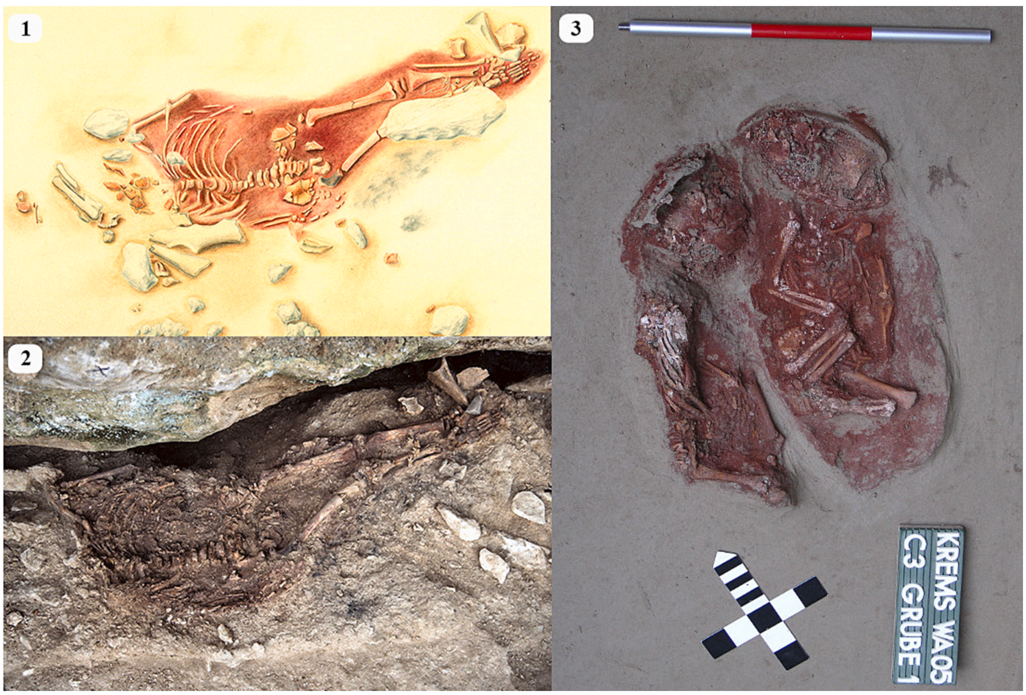

Fig. 5. 1) Composite drawing of the Lagar Velho child's burial (illustration from Guida Casella). 2) The Lagar Velho child's skeleton fully exposed (courtesy of João Zilhão) (Zilhão and Trinkaus, 2002). 3. One burial with two newborn individuals (monozygotic twins) from Krems-Wachtberg (Austria). The bodies were covered by the scapula of a mammoth, embedded in a red ochre layer and with over 50 ivory beads as grave goods (courtesy of Thomas Einwögerer, Austrian Archaeological Institute-ÖAI, Austrian Academy of Sciences-ÖAW) (Einwögerer et al., 2006). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 5
Double and triple burial combinations according to sex and age clusters. M: male. F: female.

Sex	Double	Triple
M–F	6	
M–M	1	
F-F	1	
M–Indet.	1	
Indet.-Indet.	1	
M–F–F		1
M–M–indet		1
Age	Double	Triple
Subadult - Subadult	2	
Subadult - Adult	2	
Adult - Adult	5	
Adult/Subadult - Adult/Subadult	1	
Adult-Adult-Juvenile		1
Juvenile-Juvenile-Juvenile		1

and the sea level dropped considerably (i.e. ± 100 m for the Mediterranean basin), exposing a costal platform and forcing population movements.

3.4. Mortuary activity

Burials are practically absent during the Early phase and before the onset of the Full phase cultures. The only burials or intentional depositions documented in the Early phase are two primary single burials that correspond to an adult woman found in the subsoil of Francouzská Street, Brno (Brno 3) (Svoboda et al., 1996; Schwartz and Tattersall, 2002), and a male individual about 20–25 years old (Kostenki 2) from Kostenki-XIV (Markina Gora), one of the sites that constitutes the Kostyonki-Borshchyovo archaeological complex (Oakley et al., 1971; Soffer, 1985; Alexeev, 1996; Sinitsyn, 1996). Brno 3 has been identified as a possible funerary deposition (Absolon, 1929). The geostratigraphic position of the fossil embedded in a level of sand and gravel underlying the LGM sedimentary complex (Terrace A) undoubtedly allowed researchers to establish a minimum age and frame the burial in the Early phase. In the absence of the possibility to carry out an exhaustive anthropological study and obtain radiometric dates that clarify its

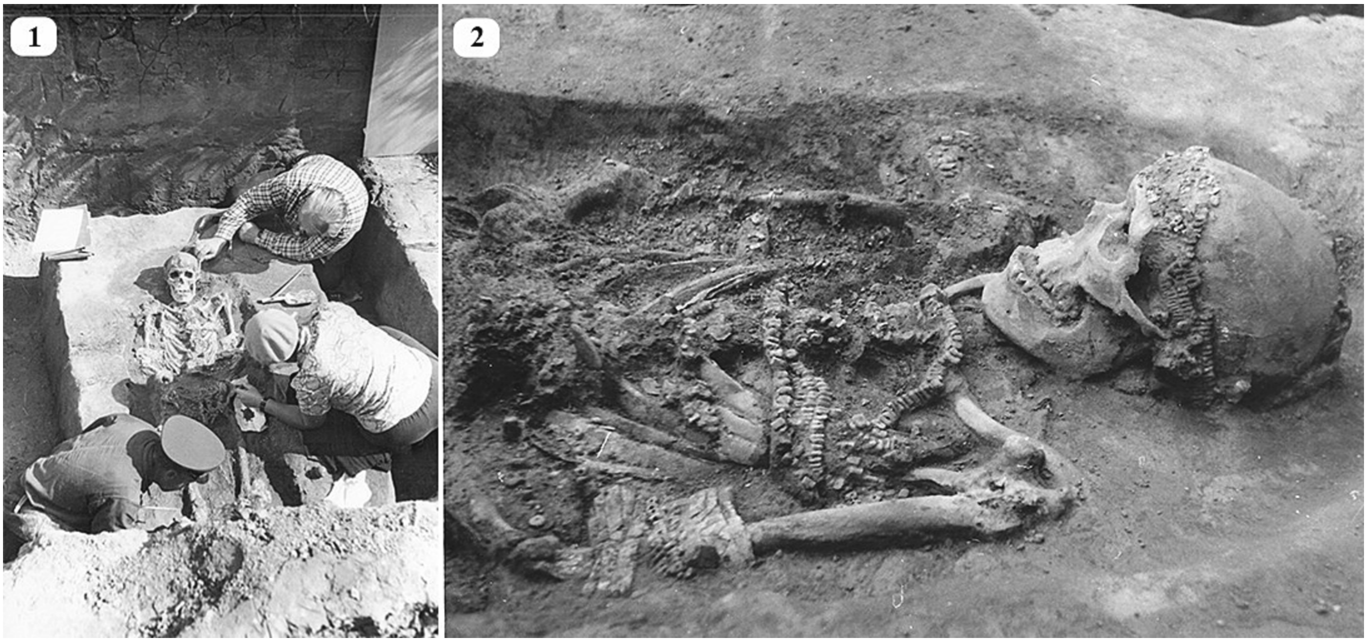

Fig. 6. Sunghir 1. 1) Excavation of the burial site in 1964 (Gavrilov, 2019). 2) *In situ* image of the head and upper thorax from the lateral view. The head and chest were decorated with many ivory beads and mammoth-ivory bracelets on his arms (Vasil'ev et al., 2021). Courtesy of Dr. Konstantin Gavrilov.

context, the destruction of Brno 3 during World War II prevents us from clarifying the reasons for the rarity of burials in this phase. In the Full and Final Phases there is a discernible pattern in the burial practices among all the hunter-gatherer territories: notably, both single and double burials present an upward trend. Statistical analysis reveals no significant differences between the occurrences of 42 and 41 single burials and 6 and 14 double burials during the Full and Final Phases respectively. In contrast, the prevalence of multiple burials fluctuates: during the Full Phase, the number rises to 30, whereas in the Final Phase, it falls steeply to 14. The number of triple burials also decreases, from nine during the Full Phase to none at all at the end of the period (Table 4).

Interestingly, the variability observed in burial practices does not appear to be directly correlated with population growth. Despite a slight increase in the number of individual burials (MNI) or elements recorded (MNBR) during the Final Phase, the frequency of multiple and triple burials diminishes. This suggests that factors beyond population dynamics may have influenced the burial patterns observed during the Full and Final Phases. For further insight, a detailed examination of contextual variables and cultural nuances within the territories studied may be warranted to elucidate the underlying reasons for these burial trends.

Funerary records also show significant differences between the sexes, with 70 male and 43 female burials. Regarding age categories, adults were buried more often than other age groups (Fig. 3), mainly young adult individuals (indeterminate adults if we consider individuals with an imprecise age category). The least represented categories in funerary depositions are fetal (n = 2) (Fig. 5.3) and perinatal individuals (n = 5). In sum, for reasons currently unknown, the burial record comprises predominantly adolescent and adult males, and relatively few females or children.

With respect to the type of burial, there is a clear preference for primary single inhumations (n = 109) (Fig. 5.1-2), compared to double (n = 10) and triple (n = 2) burials. Multiple burials (more than 3 individuals) became a widespread practice during the Gravettian, with strong continuity during the Late Upper Palaeolithic in Italy (Epigravettian). The multiple burials identified are outlined in Table 5, and exhibit a comprehensive representation of conceivable combinations of the male–female and adult-child dichotomies. Notably, the combinations observed encompass a spectrum of possibilities, and the proxy used to analyse these configurations does not reveal discernible differences that warrant particular emphasis. Two sites have provided complex funerary contexts with an unusual accumulation history: Grotta delle Arene Candide (Epigravettian) has yielded skeletal remains in a primary and secondary multiple burial (Riel-Salvatore et al., 2018; Sparacello et al., 2018; Sparacello et al., 2021); and Predmosti Ib (Pavlovian) in a primary multiple burial (Oakley et al., 1971; Ullrich, 1996; Svoboda, 2008).

Grave goods are present (19 %) in the Full and Final phases, being more frequent in the latter phase (Fig. 6). Although some of the remains require a more detailed examination, anthropogenic marks on human bones are relatively scarce (6 %), with most being identified in the Full and Final phases (Fig. 7). Traces of ochre are more abundant (18 %) in the Full and Final phases of the UP (Table 6). The correspondence analysis (Fig. 8) corroborates these data, with the scarce burials and the related traces of ochre and grave goods in the Early phase. There is an increase in burials in the Full and Final phases with the more frequent use of ochre during the Full phase and the presence of grave goods in the Final phase.

In the Full and Final Phases, ochre predominates and reaches its highest point in terms of use. The Gravettian phase stands out as the period with the highest level of ochre application, with 52 primary and secondary individuals containing ochre. The Epigravettian chronocultural phase is close behind, with 33 individuals incorporating ochre. In contrast, phases such as the Solutrean, Magdalenian, and Azilian exhibit relatively low levels of ochre use, as indicated in Table 7.

4. Discussion

4.1. Chronological framework in the European UP

The chronological approach to human remains is essential for framing the spatiotemporal processes of UP modern humans, particularly in terms of understanding the chronological framework of population movements and occupations across the European continent. Spatial-temporal determination acquires special relevance as it contributes towards establishing a chronocultural framework, an essential element for analysing the sociocultural dynamics of the UP. However,

Fig. 7. Gough's Cave (United Kingdom). 1. Human skull shaped into a cup (Bello et al., 2011). 2. Human radius showing atypical "zig-zag" incisions on the shaft (Bello et al., 2015). Scale bar = 5 cm. Courtesy of Natural History Museum (London, UK).

Table 6
Traces of ochre, anthropogenic marks on human bones and grave goods for burials observed in the European record by phases.

	Traces of ochre				Bone processing				Grave goods			
Phase	Unknown	Absence	Presence	Total	Unknown	Absence	Presence	Total	Unknown	Absence	Presence	Total
Unknown	0	4	0	4	0	4	0	4	0	4	0	4
Early	2	129	2	133	2	125	6	133	0	120	0	133
Full	7	180	58	245	16	211	18	245	13	188	44	245
Final	11	235	68	314	5	290	19	314	11	224	79	314
Total	**20**	**548**	**128**	**696**	**23**	**630**	**43**	**696**	**24**	**536**	**136**	**696**

we should bear in mind that only half of the individuals from the UP have been directly or indirectly dated. The chronological context is one of the topics that has been vigorously debated due to the inaccuracy of time ascription.

Human remains initially dated to the Palaeolithic based on the archaeological context, can now be identified as coming from later using dating methods. Several examples illustrate the problems with radiocarbon dating, such as human bones previously classified as Late Pleistocene being redated to the Mesolithic (Street et al., 2006).

The use of radiocarbon to date human remains raises two main

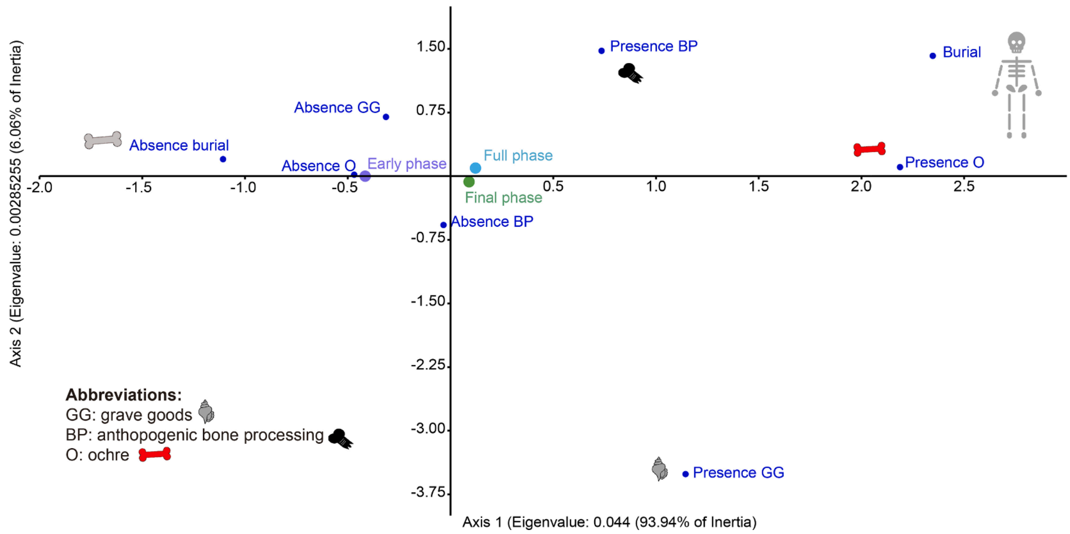

Fig. 8. Correspondence analysis of the features (in blue) according to mortuary treatment. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 7
Ochre presence of primary (P) and secondary (S) individuals according to sex and age clusters (+N individual adult/subadult).

	Individuals		Sex						Age			
			Male		Female		Indet		Adult		Sub-adult	
Phase	P	P + S	P	P + S	P	P + S	P	P + S	P	P + S	P	P + S
Full	**47**	**53**	**27**	**28**	**9**	**9**	**11**	**16**	**28**	**29**	**19**	**23 (+1)**
Gravettian-Pavlovian	46	52										
Solutrean	1	1										
Final	**35**	**45**	14	**16**	8	**8**	13	**21**	22	**27**	**13**	**18 (+2)**
Epigravettian	23	33										
Magdalenian	11	11										
Azilian	1	1										
Total	**82**	**98**	**41**	**44**	**17**	**17**	**24**	**37**	**50**	**56**	**32**	**39 (+3)**

problems. Firstly, the presence of contaminants in the samples requires several robustness pre-treatment protocols. Accordingly, standardized methods such as ABA (acid-base-acid) (Wood et al., 2012, Brock et al., 2013; 2018) are not enough to eliminate contaminants and more pre-treatments are required, such as ABox for charcoals and ultrafiltration and acid hydroxyproline (Hyp 14C) for bones. This protocol uses high-performance liquid chromatography (HPLC) to isolate single amino acids, such as hydroxyproline, an important component of bone collagen, thus effectively ensuring isolation of the collagen material only; this method was applied to four of the ten individuals from Sunghir (Sunghir 1–4) (Marom et al., 2012; Nalawade-Chavan et al., 2014). Secondly, radiocarbon is a method that allows us to date the transitional layers (Charles et al., 2003; Soficaru et al., 2006; Benazzi et al., 2011; Rachel et al., 2018; Wood et al., 2018; Hublin et al., 2020). However, the application of radiocarbon dating beyond the limit can be problematic and sensitive to small amounts of contamination (Hajdas et al., 2021; Higham, 2011). In addition, the resolution of the 14C age for the UP samples causes some imprecision intrinsic to the method, such as the fairly large confidence intervals for older samples and the lower degree of precision of the calibration curve. For this reason, the combination of several dating methods is essential to construct a robust chronology. Luminescence has become an increasingly reliable alternative for constructing quaternary chronologies when suitable organic materials are not preserved, and ages are beyond the scope of radiocarbon dating. Its application acquires great relevance in the study of the late Mousterian, Transitional and Early UP, such as Mandrin (Slimak et al., 2022), Oliveira (Zilhão et al., 2021) and St Brelade (Bates et al., 2013), among others.

Ancient DNA provides a different spatiotemporal scale related to partnership. The biological maximum date of death (DOD) separation marks the limit within which two or more dated biological relatives (parents-offspring and siblings) identified through ancient DNA analysis can be separated in time (Sedig et al., 2021).

The combination of DNA and radiocarbon highlights the complexity of dating ancient human remains, such as in case of the chronology of the Zlatý Kůň cranium. Direct radiocarbon dating placed them in the Late Upper Palaeolithic, a far later result than expected based on their anatomical characteristics, which linked them to pre-LGM populations (Rmoutilová et al., 2018). Recently, three new radiocarbon dates were performed on the same bone fragment, one of them using the ultrafiltration method. All three pushed back the previous chronology, to 19 ka cal BP in the case of the ultrafiltration method, and to 34,000 and 29,000 cal BP in the case of the standard pre-treatment process (Prüfer et al., 2021). The inconsistency between the ages obtained by different pre-treatments seems to point to high contamination of the bulk collagen. However, the mtDNA placed the female individual at ~43,000 BP. This method was also applied in the mtDNA analysis of four human remains from Bacho Kiro Cave, dating them to 43000–47000, denotating the strong potential of the method for the oldest human bones (Hublin et al., 2020).

4.2. UP population and dynamics

In recent years, palaeogenomic studies have examined the structure and dynamics of past populations, offering direct testing and complementing the archaeological inferences regarding the populations of the European UP. Ancient DNA enables us to assess human mobility in the past by comparing the genetic, spatial and temporal distance of ancient AMH. The social organization of ancient hunter-gatherer populations was similar to that currently observed, based on the reduced kinship and small effective population size of Sunghir individuals (Sikora et al., 2017). Despite their distribution throughout Europe during the Full UP, populations between 34,000 and 26,000 BP were closely related to each other (Yang & Fu, 2018), showing a remarkable correlation between biology and cultural manifestation (Gravettian). For many researchers, population growth is an event strongly linked to the cultural development of the human population (Shennan, 2001; Riede, 2009; Vaesen, 2012). An increase in technological standards and sociocultural complexity is observed with the appearance of the Gravettian (Vandiver et al., 1989; Adovasio et al., 1996; Revedin et al., 2010; Pryor et al., 2013). However, during the later phase of the Gravettian (~29,000–24,000 cal BP) some authors argue that there was potentially a decrease in the technological and typological standards (Svoboda, 2007), compared to the sophistication observed in the Early Gravettian. This pattern is also visible in the funerary behaviour, with examples dated to Early Gravettian / Gravettian including Arene Candide, Sunghir, Lagar Velho, Cro-Magnon, Krems-Wachtberg, Cussac and Paviland (Duarte et al., 1999; Aujoulat et al., 2002; Pettitt et al., 2003; Einwögerer et al., 2006; Jacobi & Higham, 2008; Dobrovolskaya et al., 2012; Marom et al., 2012; Henry-Gambier et al., 2013a; Kacki et al., 2020), while Abri Pataud, Brno-Francouzská and Předmostí Ib are the only depositions dated to the Late Gravettian / Pavlovian (Douka et al., 2020; Pettitt & Trinkaus, 2000; Svoboda, 2008). This late phase of the Gravettian seems to show the lower demographic size compared to UP levels (Maier & Zimmermann, 2017).

Within the framework of the Last Glacial Period, several abrupt climatic oscillations of irregular periodicity occurred throughout the Full UP (Marine Isotope Stage 4–2, 73,500–14,700 BP – Sanchez Goñi & Harrison, 2010). An important alteration in plant and animal populations is documented as a result of the significant cooling, drought and desertification that took place during the LGM, when the continental ice sheets reached their maximum total mass (Tallavaara et al., 2015). In this climatic process, modern human groups that had already been suffering significant population decline since the Late Gravettian were also affected, as reflected in the quantity and distribution of preserved human remains. As observed in the radiocarbon modelling conducted in our work, a gap is observed between 25 and 16 ka BP during the Solutrean technocomplex (~24–19 ka BP) or LGM period (26,5–19). Demographic simulations, based on ethnographic and palaeoclimate data, conducted by Tallavaara et al. (2015) suggest that climate was a major driver of population dynamics. According to these researchers, the population size reached about 330,000 people in 30,000 BP, an estimation in line with the extensive archaeological record of the Full UP, which shows how these populations spread and consolidated across Europe. Later, with the progressive cooling of temperatures, there was a significant drop to 130,000 people, who moved to southern latitudes and certain isolated points of central Europe. Genetic studies involving mtDNA with Y-chromosome patterns are consistent with the contraction of European populations in refuge areas and the subsequent recolonization process (Pala et al., 2012; Soares et al., 2010; Torroni et al., 2001).

The analyses indicate that only a small part of the mtDNA of modern Europeans derives from pre-LGM groups, a genetic discontinuity between pre-LGM and post-LGM groups also shown by genome-wide analysis (Fu et al., 2016). Meanwhile the second principal component of classical marker variation in Europe may have appeared from descendants of mtDNA lineages that can be traced to refuges in the Franco-Cantabrian region (haplogroups H1, H3, V, and U5b1), the Italian peninsula (U5b3) and the Eastern European plain (U4 and U5a), as a result of the great post-LGM expansion from southern and eastern European regions (Posth et al., 2023; Haak et al., 2015; Jones et al., 2015; Skoglund et al., 2014; Bramanti et al., 2009). During the end of the Final UP, there was an abrupt increase in human population movements on the continent related to the appearance of the Epipalaeolithic/Mesolithic populations (Loog et al., 2017).

4.3. The increasing occurrence of burial throughout the Full phase

In the onset of Early phase, the Aurignacian was gradually replaced by Gravettian (Kozłowski, 2015), resulting in an increase in technological and sociocultural development (Vandiver et al., 1989; Adovasio et al., 1996; Revedin et al., 2010; Pryor et al., 2013), as well as in the funerary record. There were relevant skeletal depositions from Russia (Kostenki and Sunghir) to western regions, with a significant concentration in France (Vilhonneur, Abri du Cro-Magnon, Labatut, Cussac, Fournol, Gargas Cave, Abri Pataud) and Italy (Barma Grande, Baousso da Torre, Arene Candide, Grotta delle Veneri, Santa Maria di Agnano, Paglicci, Caviglione). In Central Europe, there are only a few isolated cases of evidence (Borsuka Cave, Mittlere Klause, Geißenklösterle, Kelsterbach, Willendorf I and II), probably related to the expansion of the Alpine and Fennoscandian ice sheets that covered this area (Hughes et al., 2013). However, populations may have been linked by natural corridors, such as the Danube River (Svoboda et al., 1996), and large plains, such as the Hungarian and the Great European Plain (Strait et al., 2017).

The sites of the "Moravian cluster" are characterized by funerary practices. However, Pavlov I and Mladeč Cave have provided numerous disarticulated remains unrelated to any burial context. The partial skeleton of Pavlov 1 was documented in a primary burial dated to 25,490 ± 90 BP (Fewlass et al., 2019), supporting the cultural attribution. In contrast, direct dating at Mladeč placed the cavity in the mid-late Aurignacian (30,680 ± 380 BP and 31,190 ± 400 BP), earlier than the other Moravian deposits (Wild et al., 2005). In addition, the Pavlovian remains of a neurocranium, one mandible and several postcranial elements belonging to the individual known as "Shaman" (Brno 2) appeared under the subsoil of Brno-Francouzská Street (Pettitt and Trinkaus, 2000). The adult male was accompanied by a mammoth scapula, hundreds of tooth shells (*Dentalium*), mammal bones and movable artistic figures (Oliva, 1996).

Moreover, several human burials and numerous disarticulated bone remains were recovered from the evolved Pavlovian Dolní Věstonice (DV). A large number of disarticulated bones recovered in DVI, along with an almost complete skeleton of a young adult female, were dated to 25,950 ± 580 BP (DV 3) (Holt and Formicola, 2008). Unlike DVI, DVII yielded several postcranial pieces, along with four complete or partially complete skeletons: the primary burial of a male adult individual (DV 16) (Svoboda, 1987) and the prominent triple primary burial of juvenile individuals (DV 13, DV 14 and DV 15) (Klima, 1987). Direct bone dating provided an age between 27,220 and 26,680 BP (Fewlass et al., 2019). However, Předmostí Ib is one of the most outstanding of these sites and represents one of the largest collections of palaeolithic modern human remains, with skeletal remains of at least 30 individuals (Předmostí 1 to 30) in a large multiple primary burial (Oakley et al., 1971; Svoboda, 2008; Ullrich, 1996). The AMS dating from the lower layer provided a result of 24,340 ± 120 BP, placing the burial sector in a Pavlovian context, a local variant of the Gravettian. The absence of grave goods is a striking feature that contrasts with the high presence of large remains of mammoth, the most common fauna at the site, especially in the lower level. In some cases, the bodies were covered by mammoth scapulae as part of the funerary assemblage (Svoboda, 2008). As an exception, a polished and perforated marlstone disk was found in the vicinity of the burial. The AMS date should not be taken as conclusive due to the probably prolonged temporality of the successive burials, as well as disturbances of the sediments, the activity of carnivores, and subsequent human activities that have affected the stratigraphic reliability of the site (Svoboda, 2008). Unfortunately, all the human fossils were

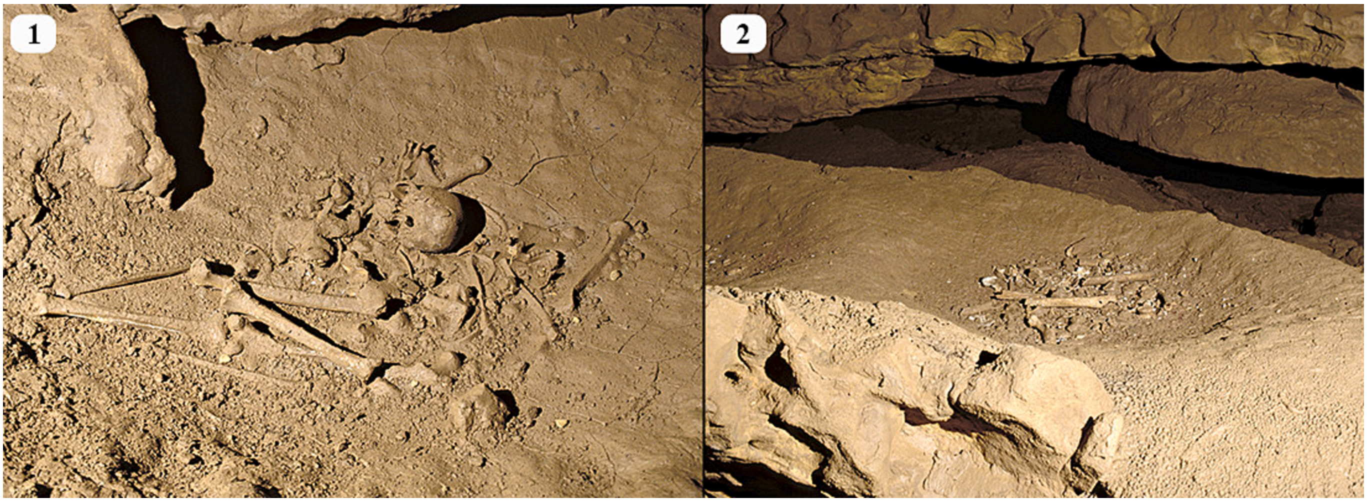

Fig. 9. Grotte de Cussac (France). The human remains occur in two areas, one of which (loci 1 and 2) is located ~150 m from the cave entrance. Remains are in and near shallow bear hibernation nests (Kacki et al., 2020). 1) Locus 2 corresponds to the largest bear nest and contains skeletal elements attributed to one adult male. 2) Locus 1 corresponds to a bear nest with remains of an adolescent and an adult. Courtesy of N. Aujoulat, France - Ministère de la Culture, CNP (Le Centre National de Préhistoire).

destroyed during World War II.

In Russia, Kostenki and Sunghir have yielded 8 almost complete Gravettian skeletons. The double child burial from Sunghir corresponds to a boy of about 12–13 years (Sunghir 2) and a girl of about 9–10 years (Sunghir 3), buried opposite each other, head-to-head, accompanied by a rich selection of grave goods including mammoth ivory ornaments and objects made of bone (Formicola and Buzhilova, 2004). Rib samples from both provided radiocarbon dates of 27,210 ± 710 BP (Sunghir 2) and 26,190 ± 640 BP (Sunghir 3), placing them between 33,000 and 29,000 cal BP (Dobrovolskaya et al., 2012), suggesting that both measurements are statistically the same radiocarbon age. Sunghir deposits also yielded a slightly earlier primary burial of a senile adult male (Sunghir 1), two possible primary burials (Sunghir 8 and Sunghir 9), and some isolated skeletal remains (Sunghir 4 to 7). Among them, a femoral diaphysis of an adult (Sunghir 4) filled with ochre has been interpreted as a human bone intentionally removed from its original pit and included among the grave goods of Grave 2 (Sunghir 2 and Sunghir 3) (Nalawade-Chavan et al., 2014). Kostyonki-Borshchyovo brought to light the burial of a senile adult male in the Kostenki II "Zamyatnin" site (Kostenki 1), one infant in Kostenki-XV "Gorodtsovskaya" (Kostenki 3) and another child in Kostenki-XVIII "Khvoikovskaia" (Kostenki 4), mainly represented by cranial elements found in burial pits containing large quantities of ochre. Direct bone dating produced a large span of more than 10,000 years, ranging between 33,400 ± 500 BP (Kostenki 2 - Anikovich, 1992) and 21,720 ± 570 BP (Kostenki 3 - Soffer, 1985).

The record of infantile individuals increases during the Gravettian, as documented in Abri de Cro-Magnon (France) with four immature individuals (CM5-1 to CM5-4) (Partiot et al., 2020), and the double burial of neonates and the single burial of an infant individual (ca. 3 months old) uncovered in Krems-Wachtberg (Fig. 5.3). Genome-wide ancient DNA revealed that the double burial contained male monozygotic twins, while the single grave contained an infant that was a 3rd-degree male relative (Teschler-Nicola et al., 2020). Individual 2 from the double burial was deposited later, which shows that the tombs were reopened to modify the content and its distribution. Bodies were covered in ochre and decorated with mammoth ivory beads, and perforated fox incisors and molluscs (Einwögerer et al., 2008). In Grotta da Baousso da Torre (Italy), the buried skeletons of two adult males (BT1 and BT2) and a boy of around 12 years old (BT3) were found inside the cavity (Villotte et al., 2016). Other Italian caves with the presence of Gravettian burials include Grotta delle Veneri (Parabita 1 and 2) (Giacobini, 2006a; Giacobini, 2006b), Barma del Caviglione (BC1) (Riviere, 1872), Barma Grande (BG1, BG5 and BG6) (Onoratini et al., 2012), Caverna delle Arene Candide (AC1) (Pettitt et al., 2003), and Grotta Paglicci (Paglicci 12 and 25) (Condemi et al., 2014). An exceptional case is documented in Santa Maria di Agnano, where a female over 20 years of age (Ostuni 1) was found placed in lateral decubitus next to the remains of her foetus (Ostuni 2), positioned in front of her pelvis (Coppola et al., 2008). Both skeletons were included in a large genetic study that involved specimens from all over Eurasia (Fu et al., 2016), but there is no detailed information regarding their relationship.

The high presence of well-preserved or partial skeletons in Central and Eastern Europe differs from the high number of isolated remains in western regions, particularly in France. Disperse human fossils characterized by cranial elements and teeth (premolars and molars) are recorded mainly in the Dordogne region, where there is a high concentration of deposits during the UP. These sites are framed in the Gravettian (Cussac, Abri Pataud, Badegoule) or the Solutrean horizon (Reignac, Fourneau du Diable, Pech de la Boissière, La Rochette, Oreille d'Enfer, Labatut, Laugerie-Haute Est). Postcranial elements are less common, only found in Grotte de Cussac (Fig. 9), Cro-Magnon, Fourneau du Diable, La Rochette, Laugerie-Haute Ouest, and a remarkable record in Abri Pataud. In the Iberian Peninsula, the record is smaller. Cova de Mollet III (Spain) yielded one neurocranium attributed to a mature female on level 4 and several bones from the lower limbs and other postcranial remains assigned to a female individual of unknown age in the Central sector (Soler et al., 2013; Rufí et al., 2018). A sample from the neurocranium was dated by 14C AMS, giving a result of 22,330 ± 90 BP. The possible existence of ochre in the archaeological sediments and the presence of ornaments associated with the fossil remains suggest that this could be interpreted as a Gravettian grave subsequently disturbed by post-depositional processes or the action of animals (Soler et al., 2013). The juvenile female cranium from Cova del Parpalló (Spain) is mentioned as a possible secondary burial (Arsuaga et al., 2001). As such, the burial context of these depositions remains uncertain. In Portugal, the complete skeleton of a ca. four years old child (LV1) was found in the Lagar Velho rock shelter. LV1 was covered with red ochre and had been buried with a perforated shell. The burial is dated to a Gravettian context, taking place at 24,660 ± 260 BP, provided from a deer pelvis sample (Duarte et al., 1999).

4.4. Final UP phase

The increase in isolated human remains during the Final phase of the UP is accompanied by the largest record of complete or partial human skeletons in the entire European UP (n = 59). The deposition of isolated and disarticulated human remains is a dominant reality in the Magdalenian context. Final UP burials are a widespread phenomenon in Europe as well, mainly in the west. Several sites yielded single, double and even triple depositions, although primary burials of more than two individuals remain unusual in accordance with previous chronologies, but do appear occasionally.

During the Epigravettian, especially in Italy, there is evidence of burial clusters, usually in cavities that act as "cemeteries", in contrast to the Magdalenian evidence (Fabbri & Giacobini, 2021). Radiocarbon determinations show that the Final phase burials discovered in Italy can mainly be classified into two groups. The first corresponds to the Epigravettian phase, framed within the Late Pleniglacial age (~28,000–13,000 BP) and includes burials from Liguria and Apulia. In Grotte des Enfants (formerly Grotta dei Fanciulli), a young adult individual and a subadult (GE1 + GE2), and a young adult female and another mature adult female (GE5 + GE6) appeared in two double burials, in addition to the single adult female (GE3) and male (GE4) burials (Formicola and Holt, 2015). In these same karst complexes and rock shelters in Balzi Rossi (Grimaldi Caves), there are three more additional sites, including another seven single burials (Grotta del Caviglione 1, Grotta da Baousso da Torre 1, 2 and 3, Barma Grande 1, 5 and 6) and one triple deposition (Barma Grande 2 + 3 + 4) (Giacobini, 2006a; Giacobini, 2006b; Villotte and Henry-Gambier, 2010). Among the Epigravettian human remains, there also appeared several isolated postcranial bones belonging to a mature adult female (Addaura 1) (Mannino et al., 2011) and, in a funerary context, the complete skeleton of a young adult female (Oriente C) (Catalano et al., 2020), and the double burial of a child (Maritza 1) and an adult male (Maritza 2), possibly disturbed by carnivores (Giacobini, 2006b). Caverna delle Arene Candide yielded 474 isolated remains (125 cranial, 345 postcranial bones and 4 indeterminate bone fragments) and 6 partial and almost complete skeletons that constitute a record revealing over 32 individuals (Arene Candide 2 to 33) deposited in a large primary and secondary multiple burial. The primary single burial of a juvenile male known as "Il Principe" (AC1) is the only burial grave framed in the Full UP phase according to a direct dating of AMS (23,440 ± 190) (Pettitt et al., 2003). Contrary to what was initially proposed, radiocarbon determinations and stratigraphic contexts point to individual and successive depositions of the bodies over a long period of time, between 12,000 and 10,000 BP (Formicola et al., 2004; Sparacello et al., 2018; Sparacello et al., 2021). Disarticulated human remains is a predominant reality in Grotta Paglicci, with 22 cranial and 52 postcranial, revealing the presence of an adult male (Paglicci 11), 14 mature adults and 8 young adults (Paglicci 43–89), and several juveniles and adults (Paglicci 1–10) (Alciati et al., 2005; Condemi et al., 2014).

More substantial, the second group is distributed across the Italian peninsula and Sicily, and dates back to the Late Epigravettian, of the Late Glacial period (~13,000–10,000 BP). The favourable conservation of complete skeletons continues during this period. Primary burials appear in sites such as Grotta delle Mura (Giacobini, 2006a; Giacobini, 2006b), Riparo Villabruna (Vercellotti et al., 2008), Riparo Tagliente (Fontana et al., 2009), and Vado all'Arancio (Giacobini, 2006a; Giacobini, 2006b). The headless skeleton of an adult male (Continenza 7) placed in prone position in the centre of a stone circle was found in Grotta Continenza (Giacobini, 2006a; Giacobini, 2006b). The observations did not allow the funerary context of the deposition to be determined, as is the case with the possible double grave attributed to an adult female (Continenza 5) and male (Continenza 6) located a few meters from Continenza 7 (Alciati et al., 2005; Serradimigni et al., 2016). One of the most remarkable sites of the Late Epigravettian is Grotta del Romito, which includes three double and three single burials. Double inhumations are represented by the skeleton of a young adult female (Romito 1) with her arm around a juvenile individual (Romito 2) suffering from a form of dwarfism, another double burial of a young adult male (Romito 3) and a juvenile female (Romito 4), and a young adult female (Romito 5) together with an adult male (Romito 6). The single burial of a male in his thirties (Romito 7), an adult male who had suffered a trauma displaying evident traces on the humerus and cranium (Romito 8), and a boy of around 11–12 years old (Romito 9) complete the record of the deposit (Fabbri & Giacobini, 2021; Giacobini, 2006; Mallegni and Fabbri, 1995; Martini et al., 2004). Stratigraphic layer A of Grotta Romanelli revealed three individual burials of an adult male and two children (Romanelli 1–3) (Fabbri, 1987), while the cranial remains of Grotta di San Teodoro are attributed to four males and three adult females (San Teodoro 1–6) (D'Amore et al., 2009). All these complex burials are framed between 12,500 and 10,300 BP. Equality in terms of the presence of buried males and females in the funerary record of the Italian Epigravettian follows the same pattern as the Final UP phase and, in general, the rest of the European UP.

The archaeological works that allowed greater insight into the French UP, and specifically the human fossils from the Magdalenian period, took place during the first half of the 20th century. The articles by Oakley et al. (1971), Henry-Gambier (1992), Henry-Gambier (1990) and Henry-Gambier et al. (2000) have made it possible to collect the limited and partial information available from those excavations. Grotte d'Isturitz yielded an astonishing assemblage of 74 neurocraniums, 14 mandibles, 18 teeth and 13 postcranial remains (Henry-Gambier et al., 2013b). In France, cranial remains define the palaeoanthropological record, while postcranial remains are minimal, and the evidence of burials is characterized by primary single graves, most commonly situated in caves and rock shelters. The infant of Abri de La Madeleine (Vanhaeren & d'Errico, 2001), the adult female and child of Abri Lafaye (Brun, 1867), the adult male from Chancelade (Testut, 1889) and the juvenile female from Roc-de-Cave (Bresson, 2000) are some examples. A particular case is observed in Le Placard, where 2 cranial vaults and several neurocranial fragments were found to display intentional cutmarks and breakage activity on the surface, interpreted by some researchers as a defleshing activity for the making skull-cups (Le Mort and Henry-Gambier, 1991). Similarly, cranial fragments displaying cut marks resulting from a human process for making containers were also found in Grotte d'Isturitz and Gough's Cave in Cheddar Gorge (Boulestin, 2012). The postcranial bones from Gough's Cave also appeared in a very fragmentary condition, arbitrarily mixed with faunal bones, showing abundant cuts, percussion marks and peeling, common signs of skinning and dismemberment activities, suggesting a possible element of ritual cannibalism (Andrews and Fernández-Jalvo, 2003).

These examples of single and double primary burials of adults and infants clearly indicate a Late Pleistocene/Late Epigravettian funerary tradition throughout Italy, differing from Epigravettian human fossils in other Eastern European countries (Temnata Dupka, Šandalja II, Cuina Turcului and Peștera La Adam), where the remains are scarce and isolated, lacking any funerary context (Strait et al., 2017; Janković et al., 2017; Cârciumaru and Nitu, 2018; Cârciumaru, 1999). A few are documented in Central Europe, exclusively in Germany (Bonn-Oberkassel, Neuwied-Irlich, Brillenhöhle) and Poland (Wilczyce). The preserved skeletons of an adult male and female were both deposited in the same burial pit in Bonn-Oberkassel. Direct dating of the remains indicates an age of 11,570 ± 100 and 12,180 ± 100 BP, respectively, suggesting a Magdalenian cultural association (Baales and Street, 1998). The evidence of Final UP burials on the Iberian Peninsula is also extremely rare. The only known examples are the single grave in El Mirón of a mature female known as the Red Lady, dating back to the Final Magdalenian (15,460 ± 40 BP) (Cabrera et al., 2004; Carretero et al., 2015), and the possible Gravettian-Solutrean secondary burial at Cova Beneito (Iturbe et al., 1993; Doménech Faus et al., 2014). El Castillo, La Lloseta, La Paseiga, Urtiaga are deposits in northern Spain that yielded several cranial and dental fragments, while, in Portugal, isolated remains were only found in the Magdalenian layer in Gruta do Caldeirão (Trinkaus et al., 2011).

4.5. General mortuary behaviour

The examination of the palaeoanthropological record across Eurasia (from the Iberian Peninsula to the Ural Mountains) over a period of 30,000 years from the early UP to the Final UP, has yielded an MNI of only 804 burials, 176 of which correspond to inhumations (109 primary burials, 20 individuals in double, six individuals in triple and 41 in multiple). A preliminary observation indicates a rise in burials during the Full and Final phases. Interestingly, single and double burials appear in equal numbers in these phases. However, a distinctive pattern emerges regarding triple and multiple burials, which are disproportionately prevalent during the Full phase, even though the Final phase exhibits a slightly larger human bone record. The question of whether these differences are linked to archaeological bias or to cultural traits remains unresolved. Nonetheless, the increasing occurrence of triple and multiple burials may potentially be associated with factors such as the expansive chronological range of this phase, spanning approximately 15,000 years, or the conditions of population concentration influenced by the changes in climate during the Last Glacial Maximum.

If burial had been a widespread practice, we would expect to find many more individuals in the record. Several hypotheses can be proposed to explain the paucity of skeletal remains, such as the low (or zero) archaeological visibility of burials, the nature of certain mortuary practices that result in the destruction of bones (i.e., the abandonment and aerial exposure of corpses), sampling biases probably related to the use of geographical settings other than caves as mortuary practices, camp sites, or rock shelters for funerary purposes (Dillehay, 2000).

Despite the scarcity of burials, and whatever the beliefs associated to them, at least two different death-related behaviours appear to have coexisted. One, seemingly more prevalent, is related to the invisibility in the archaeological record of the deceased. This may be due to a number of factors, such as a bias in the archaeological record, but also the dissolution of corpses into the environment due to the mere act of being abandoned. The other behaviour, probably more restricted, is to do with the inhumation but also with the modification of human remains in a deliberate attempt to preserve some aspect of the deceased, such as their identity, or their memory.

Barrientos (2002) modelled these two behaviours based on population density and residential mobility. Accordingly, communities with low population density and high residential mobility would probably be more likely to discard corpses, but also to practise primary burials in nonspecific locations and with minimal separation from other common areas of activity. In contrast, in high-density and semisedentary groups, more primary and secondary burials would be expected, together with the transport of the body, the marking off of burials and spatial segregation from other areas of activity, and the specific designated placement for interments.

Regarding the position of the corpses inside the tomb, the archaeological data suggest that the dominant rite positioned the skeleton in a pit in supine position with the lower limbs extended and the arms usually in partial flexion crossed over the pelvis, in a supine position and the head tilted forward (Formicola et al., 2001; Pettitt et al., 2003; Vercellotti et al., 2008; Trinkaus & Buzhilova, 2010).

The opposite situation is evident with respect to grave goods, since they are a rare and highly variable feature of UP burials, notably more frequent in the Full UP phase than in the Final phase (burials are rare in the Early phase) (Formicola, 2007; Henry-Gambier, 2008; Riel-Salvatore & Gravel-Miguel, 2013), including personal ornaments (Mussi, 1986; Onoratini et al., 2012), elements presumably related to the mortuary ritual (Zilhão & Trinkaus, 2002), and occasionally objects of prestige (Svoboda, 2008; Oliva, 1996). Usually, grave goods were exemplified by flint tools and beads (including perforated shells and other marine elements, perforated teeth, ivory, among others) (Zilhão & Trinkaus, 2002; Onoratini et al., 2012; Formicola & Holt, 2015; Vanhaeren & d'Errico, 2001). In some exceptional cases, this assemblage appears in a high quantity and rich variety, especially during the Gravettian, as in the double child burial in Sunghir, displaying a unique head to head positioning in the deposition of individuals with a prominent role within the group (Formicola & Buzhilova, 2004).

As regards distinctive features of funerary behaviour, adornments played a crucial part in differentiating ethnic groups and in fostering a sense of belonging to a specific community whose unity was shaped by the meaning and communication conveyed through these items. These artifacts stand out as significant archaeological records of vital importance for exploring the earliest expressions of symbolism. A detailed examination of these elements associated with corpses through the UP record is essential, providing geographical and chronological evidence of discontinuities that could mirror ethnic and social identities (d'Errico & Vanhaeren, 2015). As such, the variations observed in beads from Gravettian burials may indicate the presence of different ethnolinguistic groups, while the grave goods of the Magdalenian burials may reflect the social status of the deceased rather than their ethnic affiliation.

Ochre, a mineral widely used through the Palaeolithic, was implemented in artistic, ritual and domestic contexts, often concurrently manifested across both time and space (Charrié-Duhaut et al., 2013; Wolf et al., 2018). Its use spans a diverse spectrum, encompassing both direct and indirect applications (namely, in ground and pulverized forms) (Velliky et al., 2018). With its versatility, it functioned as a pigment for symbolic behaviours (Pike et al., 2012) and body ornamentation (Hoffmann et al., 2018). It also served as an adhesive (Bradtmöller et al., 2016) in a remarkably varied array of tasks, including funerary practices (Straus et al., 2015) and domestic contexts (Roper, 1992). The comprehensive nature of its use underlines its significance in diverse aspects of Palaeolithic life, contributing to both symbolic and functional dimensions within the cultural and behavioral landscape of the period. The application of ochre staining on the individual's body was a widespread practice (Fig. 4). This pigment was probably applied to the skin and clothing, and on the ground surrounding the burial pit, decorating the space occupied by grave goods, leaving detectable traces in the sediments (Zilhão & Trinkaus, 2002; Einwögerer et al., 2008; Trinkaus & Buzhilova, 2010). It is possible that, in many cases, this subtle evidence has been overlooked due to its volatility and low preservation.

5. Conclusions

Mortuary practises during the UP are diverse, with it being unfeasible to define a common funerary typology across the vast geographical and the temporal range it covers. Despite certain similarities that can be determined between burials, the spatiotemporal distribution makes it unlikely that these are the result of a common behaviour, especially if we compare populations that do not share the same cultural heritage. In the European UP, the observations of general studies on funerary behaviour are likely the reflection of several specific sites and regions of the Full and Final UP phases that have an important weight in the sample. Even though multiple burials may show the cultural patterns of specific locations in time and space, a high internal variability is observed in most funerary clusters, denoting the absence of standardized funerary practices. Considering that the archaeological record by nature is incomplete and biased, the funerary record reveals only a small fraction of the buried population and, in turn, an even smaller part of the deceased population and mortuary activities that were once in existence.

Finally, the present extensive database containing most of the AMH fossil record documented in European UP allows greater accessibility, data management and facilitates updating the information. At the same time, with this work, we have provided a wide perspective of the bone record of the entire UP. Having this body of information enables us to observe the existing problems in palaeoanthropology and helps identify which aspects require future analysis. It is an exciting time in the development of the palaeoanthropological field, with many questions to resolve and a large human fossil record brimming not only with answers but also with more questions.

CRediT authorship contribution statement

Sergio Arenas del Amo: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Software, Writing – original draft, Writing – review & editing, Supervision, Validation, Visualization. **Núria Armentano Oller:** Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Software, Supervision, Validation, Writing – original draft, Writing – review & editing. **Joan Daura:** Data curation, Formal analysis, Investigation, Methodology, Software, Writing – original draft. **Montserrat Sanz:** Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Software, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing, Resources. S.A.d.A. ellaborated the database and conceptualization under the supervision of N.A.O. All authors reviewed, commented and participated in improving the manuscript.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

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