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Invited review

The modern human colonization of western Eurasia: when and where?

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ABSTRACT

Dating the timing of the replacement of local Neandertal populations by modern humans in western Eurasia at the dawn of the Upper Palaeolithic remains challenging due to the scarcity of the palaeontological evidence and to the complexity of the archaeological record. Furthermore, key specimens have been discovered in the course of excavations that unfortunately did not meet today's archaeological standards. The importance of site-formation processes in the considered time period makes it sometimes difficult to precisely assign fragmentary remains *a posteriori* to distinct techno-complexes. The improvements in dating methods have however allowed for the clarification of many chronological issues in the past decade. Archaeological and palaeontological evidence strongly suggest that the initial modern colonization of eastern Europe and central Asia should be related to the spread of techno-complexes assigned to the Initial Upper Palaeolithic. This first expansion may have started as early as 48 ka cal BP. The earliest phases of the Aurignacian complex (Protoaurignacian and Early Aurignacian) seem to represent another modern wave of migrations, starting in the Levant area. The expansion of this techno-complex throughout Europe completed the modern colonization of the continent. The interpretation of a third group of industries referred to as "transitional assemblages" in western and central Europe is much debated. At least in part, these assemblages might have been produced by Neandertal groups that may have survived until c. 41 ka cal BP, according to the directly dated Neandertal specimens of Saint-Césaire (France) and Spy (Belgium).

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1. Introduction

The arrival of so-called "modern humans" in western Eurasia more than 40,000 years ago is a major event in the history of the Pleistocene colonizations of the continent. After a long-separated evolution that may have lasted more than 400,000 years (Hublin, 2009), the descendants of a western Eurasian clade, represented in Europe by the Neandertals, was again in contact with the descendants of its African sister group, ancestral to all extant humans. The definition of what should be called "modern humans" and the age of the oldest representatives of this clade have been much debated. However, there is little discussion regarding the anatomical distinction between local Neandertals and the late members of our species at the limit between the Middle and Upper Palaeolithic (MP and UP), which witnessed the replacement of one group by the other.

For this key period, the archaeological and palaeontological records of Europe are by any standard much richer and better studied than those of any other region of the Old World. Nevertheless, many questions surround the precise process of this population change. The notion that modern humans could have directly emerged from local European archaic forms is no longer supported by the vast majority of scholars. Still, the fossil evidence has raised the question of possible interbreeding between the two groups (eg. Trinkaus et al., 2003; Rougier et al., 2007) and this issue has been readdressed by recent advances in palaeogenetics (Green et al., 2010; Prüfer et al., 2014). The amount of gene flow from Neandertals into western Eurasian extant populations is today only detectable at a low level (<2%), but it might have been higher in some regions at the beginning of the Upper Palaeolithic and later reduced by selection and/or population replacements. Similar questions have arisen in the field of prehistory regarding possible cultural interactions between local populations, who were the makers of MP assemblages, and immigrants, bringing new behaviours and techniques into the region. Some support the view that

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cultural changes observed among the last European Neandertals are endogenous (d'Errico, 2003) and represent an independent transition toward “cultural modernity”, experienced by the Neandertals. Others relate at least a portion of these changes to the effect on local populations of the settlements of modern immigrants in a more or less distant geographical range (Hublin et al., 1996; Hublin, 2012; Rousset, 2013; Soressi and Rousset, 2014). Central to all of these debates is the question of the possible chronological overlap between the two groups of populations on a continental scale, the duration of this overlap and the nature of their interactions. In the complex transition that took place in Europe between 50 and 35 ka cal BP,¹ it is essential to precisely recognize the occurrences of the earliest modern humans and latest Neandertals. Establishing a chronology for these occurrences has long been primarily dependent on the analysis of stratigraphic relationships between archaeological assemblages, which may or may not yield human remains. Although stratigraphy remains an essential way to reconstruct palaeolithic chronologies, it also presents major limitations. On a large geographical scale, geological or geophysical markers are reliably used as isochrones, but cultural markers can only be used to establish coarse-grain chronologies. On a fine chronological scale, cultural horizons are generally time transgressive. Therefore, and specifically when dealing with issues such as possible chronological overlap between various techno-complexes, it is essential to rely on accurately established calendar dates.

Unfortunately, for a long time the dating tools needed to establish such a fine chronology have been missing. The main available technique—radiocarbon dating—was notoriously imprecise at the limits of its range of applicability. Although a large number of dates have been produced for various late Middle Palaeolithic or early Upper Palaeolithic layers, minor contaminations by modern carbon could produce incoherent results (Higham et al., 2009). In many cases, radiocarbon dating has been revealed to be misleading, to a large extent due to contamination issues and the lack of a precise calibration curve.

However, in the course of the past two decades, spectacular progress in the implementation of the radiocarbon method has greatly improved our ability to resolve chronological issues. The use of AMS dating has resulted in the reduction in the size of required samples and in the possibility to directly date precious specimens, such as artefacts and fossil hominins. Pre-treatment methods have also improved the reliability of the results by reducing and ideally eliminating contamination. In the case of charcoal samples, ABOx treatment has been proposed to replace older ABA treatments (Wood et al., 2012). In the case of the dating of bones, the ultra-filtration has been improved (Brown et al., 1988; Brock et al., 2007; Talamo and Richards, 2011) to selectively extract collagen. The dating of shells has also been significantly improved (Russo et al., 2010). All of this progress has resulted in new attempts at dating sites in a time window that long remained unreachable for radiometric dating. The establishment of a calibration curve extending back in time to 50 ka BP has finally allowed the elaboration of a reliable calendar chronology back until the late Middle Palaeolithic (Reimer et al., 2013).

One should also mention significant advancements obtained with luminescence methods (TL, OSL). Although these methods are not always applicable in the context of archaeological cave sites and do produce dates that are generally impeded by larger uncertainties than the radiometric dates, they nevertheless provide an additional source of information in the reconstruction of the

chronology and remain the primary resource for sites lying beyond the limits of the radiocarbon method. The OSL method is increasingly being used to establish chronologies of sediment deposits present at almost all archaeological sites – as opposed to organic material providing radiocarbon dates or speleothems allowing the use of U-series methods. It should, however, be established whether those sediments were exposed to sufficient sunlight prior to burial/deposition at the site. The development of the single grain dating technique (Jacobs and Roberts, 2007; Thomsen et al., 2007; Duller, 2008) has allowed for a better understanding of the different sources of variability in the doses recorded (bleaching effects, heterogeneities in beta dose rate).

The goal of this paper is to briefly review the current evidence regarding the direct or indirect dating of human remains discovered in archaeological or geological layers assigned to the time period of the replacement. It will also discuss the chronology of assemblages that have not yielded human remains but that have been tentatively assigned to the first modern humans in Europe, based on cultural arguments. The various controversies surrounding these issues will also be briefly outlined.

In the concerned time period, three groups of assemblages have been assigned to the earliest modern peopling of Eurasia. They cover different windows of time between 50 and 35 ka cal BP and their direct association with anatomically modern human remains is variably substantiated. “Initial Upper Palaeolithic” (IUP), “transitional assemblages” (TA) and Aurignacian assemblages will be considered separately hereunder.

2. Initial Upper Palaeolithic

The first known occurrence of modern humans out of Africa and into the Levant is well documented by fossil remains at Qafzeh and Skhul (Israel) between 119 ± 18 ka and 81 ± 13 ka BP (Shea, 2008). However, a long discussed question relates to the fact that the MP assemblages associated with these early modern humans (Tabun type C) display limited differences with those associated with later Neandertals in the same area (Tabun type D) (Bar-Yosef, 1998). The Levantine MP assemblages are quite distinctive from those produced in Africa in the same time period, a puzzling observation considering the widely accepted African origin for modern humans. The picture is, however, different further south in the Arabian Peninsula, where an early penetration and possibly a persistence of MP modern populations, already in the first half of the MIS 5, has also been claimed. There, no human remains have been found but African-looking MP assemblages – including some that are reminiscent of the Nubian assemblages of Egypt, Sudan and the Horn of Africa – have been described (Armitage et al., 2011; Rose et al., 2011).

Whatever the exact distribution and posterity of these MIS 5 modern peoplings in southwest Asia were, there is to date no compelling evidence that they expanded much further north than the Mount Carmel region in Israel. The colonization of the middle latitudes of Eurasia is thus generally related to a later migratory movement between 60 and 50 ka BP and the archaeological landmarks of this exodus have naturally been sought out in southwest Asia. The Emirian industry was often regarded as being intermediate between the MP and UP, and could be considered to be a proxy marking the start of this later wave of migrations. From a typological point of view, Emirian assemblages are characterized by the “Emireh points” described in various sites of the Levant including: Boker Tachtit, Ksar Akil, Umm el Tlel, Emireh Cave, Wadi Antelias and Wadi Aghar. Technologically, all of these assemblages also share specific methods and techniques for the production of elongated blanks that have sometimes been described as retaining reminiscences from the MP Levallois technology or at least typologically looking like elongated Levallois points.

¹ Calibrated dates in this paper are generated using the InCal09 and OxCal4.1 programs (Bronk Ramsey, 2009; Reimer et al., 2009).

Boker Tachtit, in the Negev desert, stands as the site where the transition toward the UP has been best investigated via the analysis of 4 successive layers (Marks, 1983). At Boker Tachtit, elongated blanks were initially produced by bi-polar debitage and display faceted platforms. In the overlying layers, the *débitage* evolves toward a more UP-style unipolar production, which allowed Marks (1983) to propose a first definition of the IUP. UP tools such as endscrapers and burins are found in all layers. The dating of Boker Tachtit obviously needs to be re-investigated, but the lowermost layer of the site (Layer 1) has yielded two radiocarbon dates c. 47 ¹⁴C ka BP with a very large sigma (SMU-259: 46,930 ± 2420 BP and SMU-580: 47,280 ± 9050 BP) (Marks, 1983). These age ranges open the possibility that the Emirian dates to beyond 50 ka in calibrated chronology.

Further north, another important site is Üçağızlı 1 Cave, where similar industries have been discovered (Kuhn et al., 2009). It is primarily from the description of the material of this site that S. Kuhn (Kuhn, 2003) attempted to provide a broader definition of the IUP. Although originally the two terms are not exclusive, the designation IUP of this kind of assemblages was then generally preferred to that of “transitional”, because it did not imply a genetic relationship with the local Middle Palaeolithic, and because IUP industries, although they retain some MP-like features, show virtually all characteristics considered typical of the Upper Palaeolithic *sensu lato*. In particular, at Üçağızlı, the IUP layers have yielded shell beads and bone artefacts (Kuhn et al., 2009) that are reminiscent of the fully developed Upper Palaeolithic of western Eurasia. The IUP layers (I,H,G,F,E) of Üçağızlı have provided radiocarbon ages noticeably younger than the dates of Boker Tachtit, ranging between 41,400 ± 1100 ¹⁴C BP and 34 ka ± 690 ¹⁴C BP, which would correspond to a range between c. 45 and 39 ka cal BP (Kuhn et al., 2009). It should be noted, however, that these dates show little consistency with their stratigraphic distribution and might well represent only minimum ages. Using Bayesian modelling, Douka et al. (2013) proposed an inception for of the IUP at Üçağızlı between 44.3 and 43.5 ka cal BP (68.2% probability). At

Ksar Akil, relatively young ages have also been obtained from radiocarbon dating of shells. There, the end of the Mousterian has been modelled at 43.2–42.4 ka cal BP (68.2% probability) and is followed by the IUP (Douka et al., 2013).

There is a growing trend to group assemblages sharing specific techno-typological attributes under the denomination “IUP” rather than to simply lump together all of those belonging to a time period predating the European UP (Kuhn and Zwyns, 2014). Beyond the Levant area, this definition of the IUP seems to be applicable to a series of industries covering a wide geographical domain (Fig. 1). Tsanova and Bordes (2003), Tsanova (2008) and Teyssandier (2008) have identified similar techniques for blank production in sites from eastern Europe, among which one should mention Temnata and Bacho Kiro (Layer 11) in Bulgaria, as well as the sites yielding Bohunician in Moravia (Škrdlá, 2003). In all of these sites, one finds a combination of techniques aiming at the production of elongated products using the narrow side of large cores by bipolar or unipolar debitage. Here again the products look like elongated Levallois points. The similarities in knapping techniques between the Bohunician and the Levantine Emirian assemblages has also been pointed out by Bar-Yosef (2003, 2007), Tostevin (2003), Škrdlá (2003) and Hoffecker (2009), who highlight the lack of continuity between the local Middle Palaeolithic traditions from central Europe and these IUP assemblages. Much further east, the Kara-Bom (Siberia) assemblages (layers 5 and 6) have also been identified as a north Asian variant of IUP in the Altai region where Zwyns et al. (2012) described the burin-core technology as one of its specific technological markers (Fig. 2). These assemblages already yield ornamental items (perforated teeth) at around 43 ka ¹⁴C BP (Zwyns et al., 2012).

It has been proposed (Müller et al., 2011) that the IUP documented in southwest Asia, eastern and central Europe, and further east in central Asia, represents a first expansion of modern humans into Eurasia that may have been partly unsuccessful and that in any case did not make it to western Europe. This first colonization of the middle latitudes by modern humans would have taken place

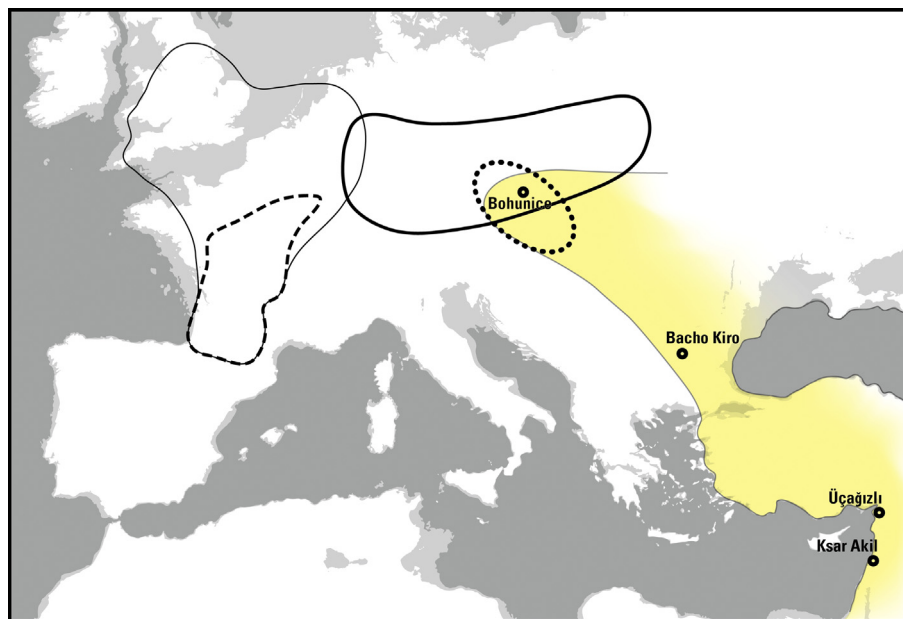


Fig. 1. Geographical distributions of the lithic assemblages, discussed in the text, for the time period between 50 and 45 ka cal BP. Note that the other late MP assemblages present in Europe at this time period (e.g. Discoidal-Denticulate Mousterian in France, late Mousterian in Spain, Italy and Belgium) are not represented on this map. Coloured areas represent assemblages tentatively assigned to modern humans and areas limited by black lines are tentatively assigned to late Neandertals. ■ Initial Upper Palaeolithic (Emirian/Bachokirian/Bohunician), ●●●● Szeletian, - - - - “Classic MTA” (Soressi and Rousset, 2014), ——— “Extended MTA” (Ruebens, 2013), ——— Keilmessergruppen and Blattspitzengruppe.

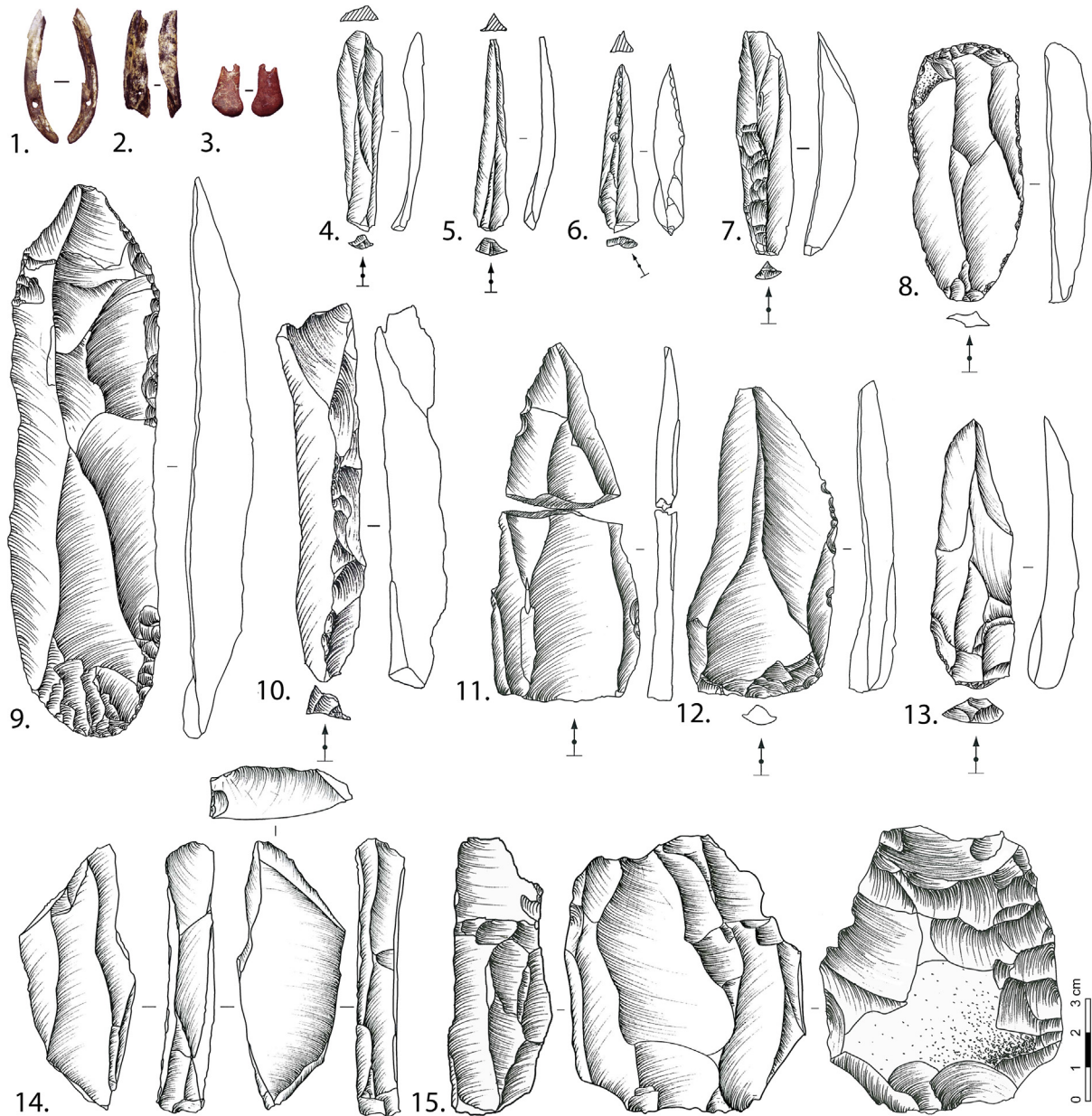


Fig. 2. Initial Upper Palaeolithic from Kara-Bom (Altai), horizons 6–4 (Zwyns, 2012): 1) Perforated ungulate tooth (fragmented), 2–3) perforated bone pendants 4–6) small blades/bladelets 7, 10) neocrested blade, 8) endscraper on blade, 9) large blade, 11–13) convergent blanks, 14) burin-core 15) sub-volumetric blade core.

during the mild conditions of the GIS 14–13. TL dates in Bohunice (Richter et al., 2009) providing a weighted age of 48.2 ± 1.9 ka BP suggests that the Bohunician was produced before GIS 12. A similar situation is observed in northern Asia where the IUP is documented at 47 ka cal BP and would have therefore appeared in the Altai during GIS 12 (Zwyns et al., 2012). According to the model proposed by Müller et al. (2011), this earliest modern peopling of Eurasia could have been facilitated by a major demographic depletion of the Neandertal populations in eastern Europe, resulting from the Heinrich event H5 a major climatic deterioration c. 49–48 ka ago, comparable in its intensity to the glacial maximum of the MIS 4.

In terms of human remains, the IUP is to date quite poor. One human maxilla has been discovered in the Layer XXV at Ksar Akil (Ksar Akil 2, nicknamed “Ethelruda”). The specimen lacks all dental crowns and was initially assigned by Ewing (1963) to a “Neanderthaloid”. This identification is however questionable and Metni

(1999) underlined that all of the published measurements of this specimen are within the range of variation of modern humans. It has therefore been proposed (Copeland and Yazbeck, 2002; Yazbeck, 2004) that this specimen could represent an anatomically modern human. A series of teeth of modern morphology has also been discovered in the IUP layers of Üçağızlı Cave (Kuhn et al., 2009). The layer of Ethelruda has been modelled between 42.4 – 41.7 ka cal BP (68.2% probability), in the context of a rather recent set of dates for the IUP of Ksar Akil (Douka et al., 2013). Layer 11 from Bacho Kiro has yielded a fragment of the left side of the mandibular corpus, bearing a first deciduous molar (Gleń and Kaczanowski, 1982). The top of layer 11 provided a conventional radiocarbon date >43 ka ^{14}C BP (Mook, 1982) but also more recent AMS dates of ca 39–38 ka ^{14}C BP (43.2–42.4 ka cal BP) (Hedges et al., 1994). The analysis of the lithics from this level does not suggest any admixture (Tsanova and Bordes, 2003), one can rather

suspect an unsuccessful pretreatment of the ^{14}C samples. Unfortunately, the hominin specimen has since been lost. Finally, one should mention the newly discovered femur of Ust-Ishchim (Omsk, Russian Federation) directly dated at 45 ka cal BP (Gibbons, 2014). This specimen displays a fully modern morphology and has yielded a high-resolution genetic sequence, indisputably relating it to an early wave of modern migration into central Asia. Although it has been found out of any archaeological context, its age closely coincides with that of the IUP development in central and northern Asia.

3. “Transitional assemblages”

In Europe, the “transitional assemblages” represent a group of industries chronologically overlapping with the IUP and the beginning of the Aurignacian complex. Although IUP assemblages were initially incorporated into the TA, there is a growing tendency to separate the two. Similarly, on techno-typological grounds, it is difficult to connect most of the TA assemblages to those belonging to the Early Ahmarian-Protoaurignacian group. The very term ‘TA’ originally expressed the notion that these industries display some Middle Palaeolithic reminiscence with a variable proportion of UP technical features. However, although the IUP of eastern Europe does not seem to be rooted in the local MP assemblages and is likely intrusive in this region, it is generally assumed that the TA resulted from a local evolution of the late MP groups. This continuity is variably supported by techno-typological and/or geographical arguments. It also seems consistent with the direct association of Neandertal human remains with one of the transitional assemblages, the Châtelperronian. According to this understanding, the TA group encompasses the Szeletian, the Lincombian-Ranisian-Jerzmanowician (LRJ), the Châtelperronian and the Uluzzian. Geographically, this group is primarily represented in western Europe, with the Châtelperronian, the LRJ and the Uluzzian, but it also extends into central Europe with the Szeletian and the LRJ and marginally into the Balkans and Greece with the Uluzzian.

3.1. Szeletian

The Szeletian is primarily represented in the Czech Republic and Hungary (Fig. 1) and might represent the oldest TA industry. It is characterized by the occurrence of foliate points that seem to have been inherited from the late MP tradition of the *Blattspitzen* of central Europe and displays *chaîne opératoire* also reminiscent of the local MP. Based on luminescence dates and various stratigraphic arguments, the Szeletian is mostly assigned to the GIS 12, roughly between 48 and 44 ka cal BP and would therefore be contemporaneous with IUP industries such as the Bachokirian and the Bohunician of eastern Europe (Allsworth-Jones, 1990; Nigst, 2012).

There are very few human remains that can be associated with the Szeletian and they are all questionable. At the upper Remete cave near Mária Remete (Hungary), three worn teeth (Right inferior I1, I2 and C1), probably from the same individual, have been assigned to the so-called “Trans-Danubian Szeletian” or Jankovichian (Gábori-Csánk, 1983). The identification of the Jankovichian industry is quite debated (Svoboda and Siman, 1989) and it has been argued that the Remete cave likely represents a late Micoquian with some foliate elements (Gábori-Csánk, 1983; Allsworth-Jones, 1990). On the basis of metric arguments, these teeth have been assigned to a Neandertal (Kretzoi in Gabori Csank, 1983). Another possible Szeletian hominin is represented by a lower right M2 (although a lower M1 cannot be discounted) found in Slovakia at Dzeravá Skala (Kaminská et al., 2004). The specimen comes from a layer predating 34 ka ^{14}C BP (c. 39 ka cal BP). As this layer has

yielded some foliate elements, it has sometimes been identified as Szeletian (Churchill and Smith, 2000). The specimen was initially described by Hillebrand (1914) as Neandertal. However, both the Szeletian association and the Neandertal nature of the tooth are questionable. The stratigraphy of the site has been profoundly disturbed by cryoturbation and mechanical processes (Kaminská et al., 2004) and the layer also yielded material assigned to the Early Aurignacian. Furthermore, the morphology of the tooth is quite modern. It displays a simple four-cusp pattern and lacks a mid-trigonid crest.

3.2. Lincombian-Ranisian-Jerzmanowician

The term “Lincombian-Ranisian-Jerzmanowician” (LRJ) was proposed by Desbrosse and Koslowski (1988) in a slightly different formulation than that of Koslowski (1983). It encompasses industries initially assigned to the Lincombian from the southern UK and Belgium, to the Ranisian or Altmühlian from Germany and to the Jerzmanowician of Poland, primarily described from the material from the Nietoperzowa cave (see review in Flas, 2006, 2011). The LRJ is therefore distributed on a very broad geographical range, extending west to east over approximately 1500 km, but covering a rather narrow latitudinal band between 50 and 55° north (Fig. 3).

The chronological extension of the LRJ is difficult to establish precisely, mostly due to the perturbation of layers in many sites and to poor excavation methods in sites excavated in the past. It seems to have lasted for a relatively short period. The oldest occurrence of the LRJ is dated c. 38 ka ^{14}C BP (43 ka cal BP) at Nietoperzowa cave (layer 6): GrN-2181: 38,160 ± 1250 BP on charcoal and Gd-10569: 37,600 ± 1300 BP on bone (Koslowski, 2002) and between 44.3 and 42.5 ka cal BP at Glaston, UK (Cooper et al., 2012). In his critical examination of the available dates, Flas (2011) concludes that the LRJ ended c. 35 ka ^{14}C BP (c. 40 ka cal BP).

The lithic assemblage consistently yields foliate points displaying a partial bifacial retouch (Jerzmanowice points) and also bifacial leaf points (Fig. 4). It is a blade industry implementing the debitage of the blanks from two striking platforms and displays some UP elements. Most authors have connected the production of bifacial points in the LRJ with the local tradition of *Blattspitzen* in the late MP of Central Europe as well as possibly with the bifacial tradition of the late Mousterian of western Europe, characterized by small handaxes (Ruebens, 2013). The LRJ assemblages have also been sometimes grouped with the Szeletian of central Europe, but the two assemblages seem to belong to two different windows of time.

From a palaeontological point of view there is no indisputable association of human remains with LRJ assemblages and the current evidence is rather contradictory. A large series of Neandertal remains from the cave of Spy, Belgium, has been directly dated to c. 36 ka ^{14}C BP (c. 41 ka cal BP) (Semal et al., 2009) (Fig. 5). This age clearly fits the chronological span of the LRJ represented in the stratigraphy of the cave. Until these dates were obtained, the two Neandertal skeletons from Spy cave, unearthed in 1885–1886, have been traditionally associated with the uppermost Mousterian layers of the site (e.g. Zeuner, 1940). However, the poorly recorded circumstances of the discovery of these remains make it difficult to precisely assign them to a specific archaeological horizon of the site, which yielded Mousterian, LRJ and Aurignacian assemblages. These individuals could very well have been buried by the LRJ makers in the underlying Mousterian layers. The fact is that none of the Mousterian assemblages of this region match the dates directly obtained on the Spy Neandertal remains (Semal et al., 2009). The latest known Belgian Mousterian assemblages from Scladina Cave and Wallou pre-date the Neandertals from Spy (Pirson et al., 2012).

On the other side of the channel, the site of Kent’s Cavern (UK) has yielded conflicting evidence. There, a fragmentary maxilla

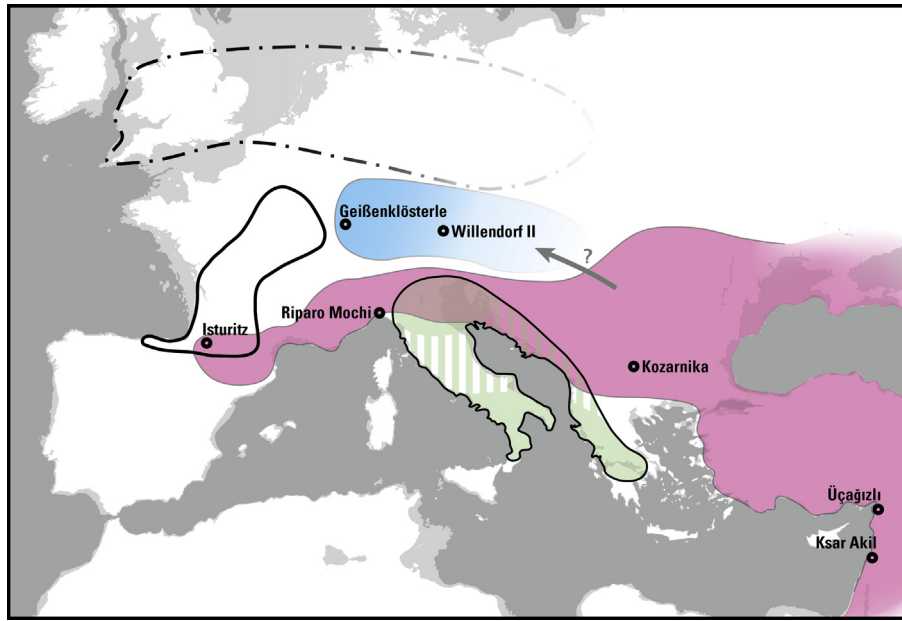


Fig. 3. Geographical distributions of the main transitional assemblages of western Eurasia and of the earliest extension of the Aurignacian complex c. 42 ka cal BP. Coloured areas represent assemblages tentatively assigned to modern humans and areas limited by black lines are tentatively assigned to late Neanderthals. ■ Early Ahmarian/Kozarnikian/Protoaurignacian, ■ Early Aurignacian, ■ Uluzzian, Châtelperronian, LRJ.

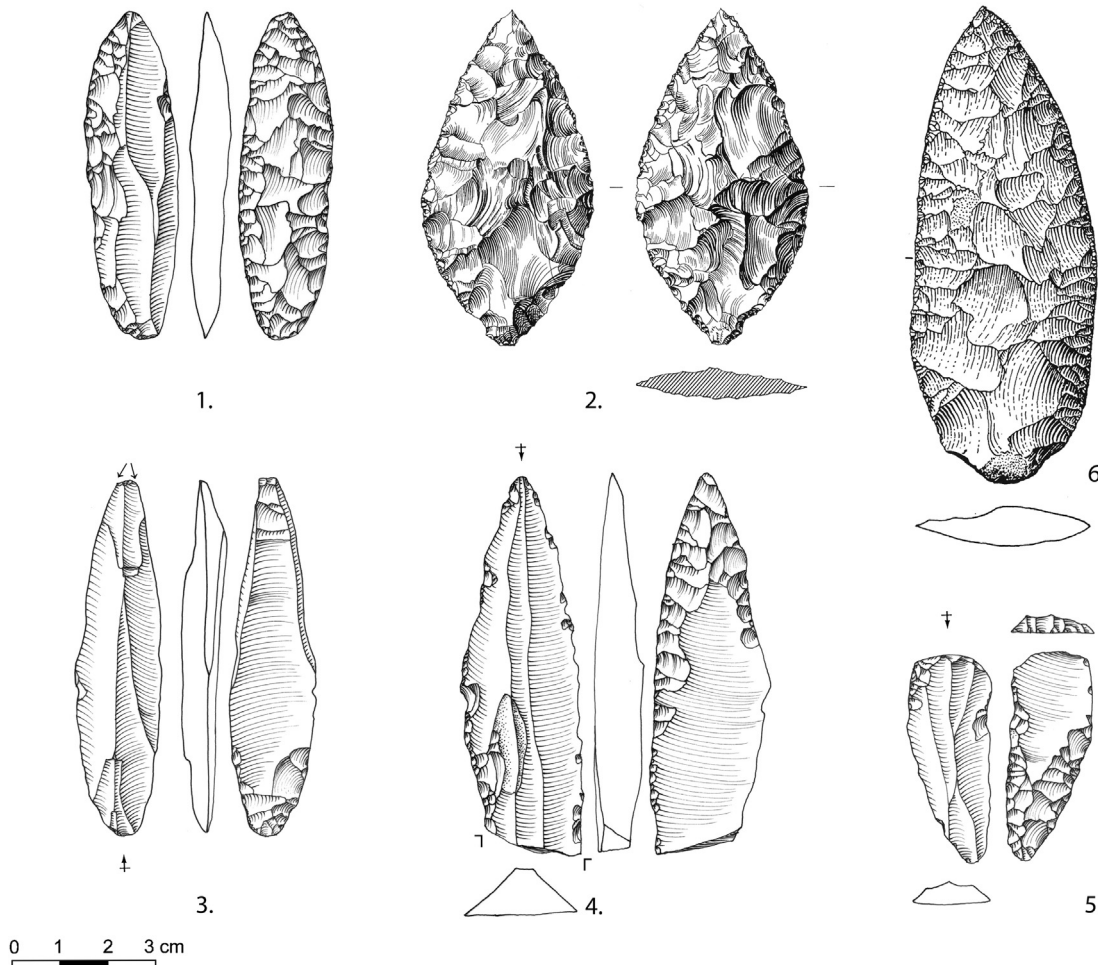


Fig. 4. LRJ lithics (1–5) (after [Flas, 2006](#)): 1) Jertzmanowice point from Robin Hood Cave (UK), 2) bifacial point from Ranis 2 (Germany), 3) burin from Robin Hood Cave (UK), 4) Jertzmanowice point from Spy (Belgium), 5) endscraper from Goyet Cave (Belgium). Late MP (Keilmessergruppen): 6) foliate point from Königsau (Germany) (after [Mania and Toepfer, 1973](#)).



Fig. 5. Neandertal skeletal elements from the Spy 1 and 2 skeletons (Lohest Collection, 1886), tentatively assigned to the LRJ from the Spy Cave (Belgium) by Semal et al. (2009). Photo: Patrick Semal, Copyright: RBINS.

(Kc4) is tentatively assigned to a Lincombian layer underlying a speleothem, which is itself overlaid by an Aurignacian layer. This fragmentary specimen has been directly dated at $30,900 \pm 900$ ^{14}C BP (36.4–34.7 ka cal BP) (Hedges et al., 1989) and has been recently identified as most likely modern (Higham et al., 2011b). Recently, the dating of faunal elements from the sector from which the specimen comes has led to the proposal that the direct date obtained on the specimen is underestimated and Kc4 has been re-assigned to a period between 44.2 and 41.5 ka cal BP (Higham et al., 2011b). This dating has, however, been much debated. White and Pettitt (2012), in particular, have questioned the integrity of the stratigraphic section in this part of Kent's Cavern as well as the condition of excavation and the recording of the material at the time of its discovery in 1927. On-going work to date additional samples from the sequence has also shown the situation to be more complex than previously understood (Proctor et al., 2013). Taking into account the Spy evidence and until a new direct dating of the Kc4 specimen is performed, the claim for the modern nature of the LRJ makers in the British Islands at 44 ka cal BP relies on rather weak evidence.

3.3. The Châtelperronian

The Châtelperronian has often been presented as being the most iconic of the transitional assemblages, although it generally displays little evidence of MP components in its lithic production. It is known from the Pyrenees region and the Spanish Basque country to southwest and central France (Fig. 3). To date, it has not been identified east of the Rhône valley and its northernmost extension has been recently recognized at the site of Ormesson in the Paris basin (Bodu et al., 2014). In a recent review, Soressi and Rousset (2014) have identified a little over 40 Châtelperronian sites, but many of them represent rather ephemeral occupations and few have yielded multiple Châtelperronian layers. Among them, the Grotte du Renne at Arcy-sur-Cure stands out due to its very rich archaeological material represented by several hundred thousand faunal elements and artefacts.

The Châtelperronian assemblage is characterized by a high frequency of Châtelperron points or knives. These artefacts are backed

blades, produced with a specific *chaîne opératoire* on cores at the intersection of a narrow and wide surface (Pelegriin, 1995; Rousset, 2013). The assemblage displays Upper Palaeolithic tools, in particular endscrapers. It should be noted that bladelet production has been identified, in particular in the site of Quinçay (Rousset, 2011). Although the bladelet production is independent from blade production, it is done with a similar method, which contrasts with the Protoaurignacian bladelet production. In addition, the UP flavour of the Châtelperronian has been reinforced by the discovery of body ornaments and bone tools at the Grotte du Renne. The occurrence of ivory and bone waste in the Châtelperronian layers strongly suggests that these objects have been locally produced (d'Errico et al., 1998). Six pierced teeth have also been identified at the site of Quinçay (Granger and Lévêque, 1997).

The rooting of the Châtelperronian in the local Mousterian of Acheulean Tradition and therefore its “transitional” nature is primarily based on the following arguments listed by Soressi and Rousset (2014): a) both industries share the same interest for backing tools and for un-retouched backed blanks, b) they display a rather high frequency of elongated backed artefacts, c) In both industries the production of blanks is guided by the need to obtain backed artefacts (retouched and un-retouched), and d) the geographic distribution of both assemblages coincides (but see Ruebens, 2013). Although it has sometimes been claimed that the Châtelperronian displays a certain MP style component (Connet, 2002), this issue is today much disputed (Soressi and Rousset, 2014). There is however the possibility that when the MP component of an assemblage is high, it would be systematically considered “admixed” or re-assigned to a Mousterian techno-complex. In Saint-Césaire side-scrapers represent about half of the retouched tools from the Châtelperronian Ejob SUP layer. This component is associated with a typical Châtelperronian blank production. The occurrence of Mousterian-like *débitage* and tools in a Châtelperronian layer might either result from MP persistence into the CP or from a post-depositional admixture of Mousterian objects into a CP assemblage. However, according to Soressi (2011), the surface states of the artefacts do not separate these two components.

Many of the radiocarbon dates that have been obtained from Châtelperronian layers since the 1960's were implemented without

pre-treatment to resolve contamination issues and should likely be simply discarded. AMS ^{14}C dates based on ultrafiltered samples have however been produced in the past few years, notably at the sites of Les Cottés (Talamo et al., 2012), Grotte du Renne (Hublin et al., 2012a) and Saint-Césaire. According to these recent results, the Châtelperronian can be assigned to a window of time between 39 and 35 ka in ^{14}C chronology (c. 44–40 ka cal BP).

The Neandertal remains from the Grotte du Renne have been mostly discovered in the lowermost Châtelperronian layer of the site (layer X) (Leroi-Gourhan, 1958), but a smaller number of human fossils have also been discovered in the Châtelperronian layers IX and VIII. This distribution matches the richness of the different layers, layer X having by far yielded the largest amount of archaeological material. Among other material, 29 isolated teeth have been discovered (Hublin et al., 2006; Bailey and Hublin, 2006b). The series also encompasses various fragmentary post-cranial skeletal remains and an infant temporal bone (Hublin et al., 1996). There is little doubt on the Neandertal nature of these remains. The anatomical analysis of the inner ear of the temporal bone was the starting point of the description for the Neandertal morphology of the labyrinth and its interpretation as Neandertal was fully confirmed by later works (Spoor et al., 2003). The non-metrical and metrical features of the dentition have been assessed in several articles (Bailey and Hublin, 2006a, 2006b; Bailey et al., 2009) and confirm an indisputably Neandertal nature.

The association of Neandertal remains with the Châtelperronian assemblage, including body ornaments, has been challenged by two groups of authors. Bar-Yosef and Bordes (2010) have argued that the occurrence of Neandertal remains in the lowermost layers of the Châtelperronian deposits at the Grotte du Renne could have resulted from site-formation processes, reworking underlying layers. However, the migration of Neandertal remains from the underlying Mousterian layers into the Châtelperronian layers meets two objections. The uppermost layers of Mousterian at the Grotte du Renne have actually yielded very few human remains in comparison to what has been discovered in the Châtelperronian layers. Furthermore, Neandertal remains are not only found in the lowermost layer of the Châtelperronian. Two teeth of Neandertal morphology have also been found in the uppermost Châtelperronian layer (Layer VIII), in an undisturbed area of the site.

Layer admixture has also been proposed by Higham et al. (2010) on the basis of inconsistencies between stratigraphy and ^{14}C dates at the site to explain the association of body ornaments and Neandertal remains at the Grotte du Renne. This view has however been criticized on various grounds. When assessing the vertical and horizontal distribution of the lithic material at the Grotte du Renne, Caron et al. (2011) could not find any evidence of major material movement between Mousterian, Châtelperronian and Protoaurignacian layers in the site. The areas where bone tools have been found in the Châtelperronian layers of the Grotte du Renne do not match the areas where Aurignacian bone tools are found in overlying deposits. Furthermore, at Quinçay, where body ornaments have also been described in Châtelperronian context, the Châtelperronian layers are directly covered by large blocks and there is no later UP assemblage present in the stratigraphy. Additionally, the dating of 40 samples of well-preserved bone from the Grotte du Renne (with or without entropic marks) by Hublin et al. (2012a) did not replicate the results obtained by Higham et al. (2010). Although refits suggest some level of layer admixture between Châtelperronian sub-layers at the site, and/or a lack of reality of some of these stratigraphical divisions, no overlap was observed between the dates obtained in the Mousterian, the Châtelperronian and the Protoaurignacian layers. Low collagen yield may instead explain

some of the apparently too recent dates obtained by Higham et al. (2010) in the Châtelperronian layers.

Neandertal remains have also been recognized in the Châtelperronian Ejop SUP layer of Saint-Césaire. In 1979 a fragmentary skeleton (Saint-Césaire 1) was discovered in the site by F. Lévêque. This skeleton included the face and a large portion of the braincase, the mandible, and a good proportion of the post-cranial skeleton. Lévêque and Vandermeersch (1980) identified the specimen as Neandertal and partial descriptions by Stringer et al. (1984) and Trinkaus et al. (1999) have fully confirmed this identification. Bailey et al. (2009) have also shown that the dentition of this specimen displays a clear Neandertal morphological pattern with a computed posterior probability of 98% for Saint-Césaire 1 dentition to be assigned to a Neandertal. At Saint-Césaire, the Châtelperronian nature of this Neandertal skeleton has also been questioned by Bar-Yosef and Bordes (2010), who proposed that this individual could represent a secondary burial “planted” by contemporaneous Neandertals into the dwelling of modern humans. Primarily, these authors see no connection between the Châtelperronian and the earlier Mousterian of Acheulean Tradition and rather consider that some of the techno-typological traits of the Châtelperronian are reminiscent of the later Protoaurignacian in the region (but see Soressi and Rousset, 2014). The Saint-Césaire Neandertal has been directly dated between 41,950 and 40,660 cal BP (68.2% probability) (Hublin et al., 2012a), which corresponds to the upper range of the Châtelperronian dates obtained at the Grotte du Renne.

3.4. Uluzzian

The Uluzzian industry, named after the cave of Uluzzo (Italy) has been initially identified in southern Italy and more recently in Greece at the cave of Klissoura (Koumouzelis et al., 2001), as well as in northern Italy at the site of Fumane (Peresani, 2008, 2012) (Fig. 3). To some extent, the Uluzzian replicates some of the features observed in the Châtelperronian and it has long been considered as an Italian counterpart of this industry (Palma di cesnola, 1989; Mussi, 2001). The radiocarbon ages recently obtained also demonstrate a large chronological overlap between the two industries although the Uluzzian might have started slightly earlier (Hublin et al., 2012a; Douka et al., 2014). However, it should be underlined that in the Uluzzian the production of blades remains limited. It is a flake-dominated industry that displays a stronger MP signal than in the Châtelperronian. Blanks were produced by unipolar *débitage* by direct percussion and by bipolar knapping on an anvil, producing splintered pieces. Other *chaîne opératoire* for blank productions were also present, including centripetal cores. This is particularly the case at Fumane, where the oldest known Uluzzian layer has been initially assigned to the late Mousterian (Broglio et al., 1998–1999). Like the Châtelperronian, the Uluzzian displays a prevalence of backed pieces in the form of crescents that can represent a large proportion of the assemblage. It has also yielded some bone tools and body ornaments made of shells (Riel-Salvatore, 2009).

Only two sites have yielded human remains assigned to this assemblage, Fumane and Grotta del Cavallo. At Fumane, a fragment of a permanent molar (Fumane 6) was found in layer A3-I. However, post-depositional disturbance due to frost action have affected the sequence between layers A4 and D3 in the part of the site where the tooth was found and produced the intrusion of some Protoaurignacian artefacts in the underlying layers. The assignment of this fragmented tooth to the Uluzzian therefore remains uncertain. Furthermore, it does not display any morphological features helpful for taxonomic identification, either as Neandertal or modern human (Benazzi et al., 2014).

At Grotta del Cavallo, two deciduous molars have been found (Palma di Cesnola, 1966). Cavallo B is a left DM1 and Cavallo C is a right DM2. Cavallo B is said to come from the oldest Uluzzian layer of the site (layer EIII). Cavallo C was discovered in layer EIII-I, 50–20 cm above. At Cavallo, the Uluzzian layers are said to be sealed by a speleothem (DIa) and a volcanic ash (Layer CII), assigned to the Campanian Ignimbrite eruption, isolating them from overlying Epigravettian layers. The teeth were initially classified as modern human for Cavallo B and Neandertal for Cavallo C (Palma di Cesnola and Messeri, 1967). Later, they were assigned to Neandertals on metrical and morphological grounds, particularly in relation to some level of taurodontism (Churchill and Smith, 2000). However, a recent re-examination of the two specimens by Benazzi et al. (2011) concluded a modern assignment primarily based on the analysis of the crown outlines and of the enamel thickness. This assignment as well as the integrity of the stratigraphy in the site has been questioned by Banks et al. (2013), primarily reworking the arguments made by Gioia (1990) that layer D resulted from some admixture with later UP elements. These critiques have been addressed by Ronchitelli et al. (2014).

It seems difficult to dismiss the modern nature of the two deciduous teeth from Cavallo. However, it remains that the exact conformation of the stratigraphy at the place of their discovery is unknown and the description by Palma di Cesnola leaves open the possibility of intrusion from overlying layers (Palma di Cesnola, 1965, 1966). Recently, Douka et al. (2014) have provided a series of ^{14}C dates at Cavallo cave based on shell samples. These dates are mostly consistent with a pre-Campanian Ignimbrite age older than 40 ka cal BP. However, the dating OxA-21072 duplicated on two different fragments of a shell of *Cylope neritea* from layer DI was established at $19,685 \pm 75$ and $19,235 \pm 75$ ^{14}C BP. In these samples the ratio of aragonite/calcite and the carbon yield are fully satisfactory and this date may give substance to the claim that intrusion of material from overlying layers may have occurred at least in the upper parts of the Uluzzian levels. The modern nature of the Uluzzian makers will only be fully demonstrated with the discovery of new palaeontological evidence.

4. The Aurignacian complex and its origins

The Aurignacian complex has long been considered to be the oldest expression of a genuine UP and a proxy for the first spread of modern humans over western Eurasia (Mellars, 2006). Among the earliest phases of this complex one can recognize a “Protoaurignacian” —Aurignacian archaïque in Laplace terminology (Laplace, 1966)— and an “Early Aurignacian”. In southwest France, these two industries are found in chronological succession. However, further east they seem to have developed in different geographical domains. The Protoaurignacian, characterized by the production of large bladelets (Bartolomei et al., 1993; Bon, 2002) has been primarily recognized in southern Europe, with only one possible exception, north of the Alps at Krems Hundssteig (Teyssandier, 2007). In the Danubian region, where the Protoaurignacian is virtually unknown, early Aurignacian assemblages have been associated with ^{14}C dates as old as the first occurrence of the Protoaurignacian in the Mediterranean area (Haesaerts et al., 1996; Douka et al., 2012; Higham et al., 2012; Nigst and Haesaerts, 2012) (Fig. 3). This situation makes it difficult to simply consider the two assemblages as successive stages of the same techno-complex (Banks et al., 2013).

4.1. Protoaurignacian

The Protoaurignacian is characterized by the production of large straight bladelets, most likely representing the tips of long-distance

projectiles (Le Brun-Ricalens et al., 2009), a distinctive innovation in comparison to older assemblages in western Eurasia. Similar industries have been identified in Bulgaria, at Kozarnika (Sirakov et al., 2007) and further east in the Zagros (Otte et al., 2007; Tsanova et al., 2012) where they could have developed from the Early Ahmarian (Otte et al., 2011). Further east, the Protoaurignacian is still unknown and bladelet assemblages from central Asia and from the Altai seem to represent examples of a technological convergence with early phases of the Aurignacian (Zwyns and Flas, 2010). Most authors agree that this innovation spread out of the Levant where the Early Ahmarian seems to represent the first expression of this large ensemble of industries. The Ahmarian is represented over a large domain from the Sinai to the southern border of Turkey. In Israel, it is noticeably encountered at Boker in the Negev, in the Mount Carmel at Kebara and in Galilee at Qafzeh. It is also present over the IUP layers of Ksar Akil (Lebanon), Umm el Tlel (Syria) and Üçağızlı (Turkey). The first occurrence of the Early Ahmarian was dated by Rebollo et al. (2011) in Kebara Cave and by using a Bayesian model, these authors proposed a start of the Ahmarian sequence between 47,690 and 46,360 cal BP (68.2% probability). As for the IUP, the dates based on shells obtained at Ksar Akil are noticeably younger with a lower limit for the Ahmarian between 41.6 and 40.9 ka cal BP (68.2% probability) according to the model 2 by Douka et al. (2013). This is also the case at Üçağızlı, where the oldest date in Ahmarian context is $34,580 \pm 620$ ^{14}C BP and using Bayesian modelling, Douka et al. (2013) propose a starting age for the Ahmarian of this site around 41.6–40.3 ka cal BP (68.2% probability). In Europe, the Kozarnikian of Kozarnika (layer VII) yielded radiocarbon dates ranging from $39,310 \pm 100$ BP (Gifa-99662) to $36,200 \pm 510$ BP (Gifa-99706) (Guadelli et al., 2005), which would correspond to calibrated ages between 43.4 and 41.3 ka cal BP. Further west, the oldest occurrence of the Protoaurignacian has been identified at Riparo Mochi and Isturitz c. 42 ka cal BP (Szmidski et al., 2010; Douka et al., 2012).

If one assumes that the Early Ahmarian/Kozarnikian/Protoaurignacian represent a consistent wave of peoplings in western Eurasia, the identity of the makers of this assemblage would be primarily substantiated by the discovery of an immature individual in layer XVII of Ksar Akil (Lebanon), where the skull, mandible and some postcranial elements of a child aged between 7 and 9 years was discovered in 1938 and nicknamed Egbert. Although the original specimens have been lost, the discovery is still documented by photographs and casts. There is little doubt that this child belongs to an anatomically modern population (Bergman and Stringer, 1989). In Europe, human remains directly associated with assemblages of the Protoaurignacian group are to date very fragmentary. The skeletal fragments of a foetus or newborn were found in the Protoaurignacian layers from Le Piage (France), but their identification is inconclusive (Beckouche and Poplin, 1981). Some dental material was also later discovered at the site but remains unpublished. In Italy, two sites have yielded additional dental remains. At Riparo Bombrini, layer III yielded a left deciduous incisor of small dimension and modern morphology (Formicola, 1989). Further material from Fumane is currently under description.

In France, human remains have been assigned to the “Aurignacian” division of the stratigraphy at Isturitz Cave (“couche A” by Passemard, 1944; or “couche V” by Saint-Périer and Saint-Périer, 1952). These human remains are reported from layers that yielded assemblages displaying Protoaurignacian and Early Aurignacian characteristics as well as from other Upper Palaeolithic layers in the site. However, their origin is rather imprecise. Almost all the human fragments of Isturitz display cutmarks, and it has been suggested by Gambier (1990) and Henry-Gambier et al. (2013) that they might all be derived from the Magdalenian level of the site, which is by far the richest in human remains.

Finally, one should also mention the discoveries from the site of El Castillo (Spain), where H. Obermaier unearthed some cranial fragments, a second right lower molar and a fragmentary child mandible, bearing a dm1 and dm2 and an unerupted M1 on the right side. These remains are assigned to layer 18 of the stratigraphy of the cave. Advocating for a local emergence of the Aurignacian, [Cabrera-Valdés et al. \(2001\)](#) described the lithic assemblages of the layers 18b and 18c as transitional to an “archaic Aurignacian”. This interpretation results from the occurrence in these layers of Mousterian-like elements. However the additional presence of Châtelperronian elements in the same layers have led some ([Zilhao and d’Errico, 1999](#)) to question the homogeneity of the layer 18 assemblage. Its composite nature would be consistent with the broad spectrum of dates yielded by layer 18, which range from 42.2 to 37.1 ka ^{14}C BP (46.2–41.9 ka cal BP) and widely overlap well accepted dates for the late Mousterian, the Châtelperronian and the Protoaurignacian ([Cabrera-Valdés et al., 1996](#)). Another issue results from the difficulty to connect the material recovered by Obermaier with that more recently excavated and published ([Pastoors and Tafelmaier, 2013](#)). [Garralda et al. \(1992\)](#) has made available an unpublished description by the human remains by H. Vallois and this description is not quite conclusive in terms of the taxonomical assignment of these fossils.

4.2. Early Aurignacian

The oldest assemblages assigned to the Early Aurignacian in Europe have been yielded by layer 3 from Willendorf II (Austria) and layer AH III from Geißenklösterle (Germany). At Geißenklösterle, the layer AH III has yielded lithics rather characteristic of the Early Aurignacian, consisting of carinated and nosed end-scrapers as well as a small number of objects made of bone, ivory and antler, including several body ornaments ([Hahn, 1988](#)). This deposit has produced a series of dates around 38–37 ka ^{14}C BP, suggesting that the deposition in this layer would have started between 42,940 and 42,180 cal BP (68.2% probability) ([Higham et al., 2012](#)). Charcoals from layer 3 at Willendorf II were dated between c. 39–38 ka ^{14}C BP (c. 43–42.5 ka cal BP) ([Haesaerts et al., 1996](#); [Nigst and Haesaerts, 2012](#)). However, most of the assemblages formally assigned to the “Early Aurignacian” in western Europe are younger, especially in southwest France, where the chronological framework of the UP industries has been primarily established. In western Europe, the Early Aurignacian always overlays the Protoaurignacian when the two are encountered together in stratigraphy ([Banks et al., 2013](#)). This suggests a later penetration of Early Aurignacian populations in the far west of Europe. In the British Islands and across northwestern Europe, i.e. Belgium, central/northern Germany as well as southern Poland, only later phases of the Aurignacian are represented.

To date no human remains were found in direct association with the earliest phases of the Early Aurignacian. At the easternmost extension of the Aurignacian, the site of Markina Gora (Kostenki 14), Russia, has yielded a complete skeleton of an individual buried in a pit dug through a level of volcanic ash, generally assigned to the Campanian Ignimbrite eruption ([Pyle et al., 2006](#)). Although this short statured individual has only been partially described ([Debets, 1955](#); [Gerasimova, 1987](#)), there is no doubt it belonged to a modern human. This is fully confirmed by the complete mitochondrial DNA sequence that has been obtained by [Krause et al. \(2010\)](#). Direct dating of the skeleton has been obtained by single amino acid ^{14}C dating at $33,250 \pm 500$ ^{14}C BP, which would correspond to an age around 38 ka cal BP ([Marom et al., 2012](#)). Although the association of this individual with the Aurignacian assemblage found in the ash layer ([Sinityn, 2003](#); [Zwyns and Flas, 2010](#)) is still debated, its age is not incompatible with a radiocarbon date obtained on charcoal at

$32,420 \pm 440$ ^{14}C BP, yielded by the Aurignacian layer ([Haesaerts et al., 2004](#)). The individual of Markina Gora may be the only known complete skeleton of an Aurignacian individual, as well as the only one found to date in a burial. At Kostenki 1 (Layer 3) a human tibia and fibula have also been found associated with Aurignacian artefacts and have been directly dated at $32,600 \pm 1100$ ^{14}C BP (38.8–35.7 ka cal BP) ([Richards et al., 2001](#)).

In Crimea, the site of Buran-Kaya III has yielded a large number of fragmentary human remains of modern morphology. One of these fragments was directly dated at $31,900 \pm 240$ ^{14}C BP (36.7–35.7 ka cal BP) ([Prat et al., 2011](#)). Although the archaeological context has been described as “Gravettian”, radiometric ages obtained from the layers yielding these assemblages make this assignment quite unlikely. In Buran-Kaya III these layers have provided ages between $34,050 \pm 260$ ^{14}C BP – $34,910 \pm 950$ ^{14}C BP (c. 39–41 ka cal BP). This assemblage should most likely be considered as a non-Aurignacian Early Upper Palaeolithic assemblage, similar to those discovered further east ([Bar-Yosef et al., 2006](#); [Golovanova et al., 2006](#)).

West of the Black Sea, evidence of human remains discovered in direct association with Aurignacian-like industries is rather scarce. However, the human fossils from Peştera cu Oase, Romania, which were found in a karst outside of any archaeological context, have produced radiometric ages quite compatible with Early Aurignacian or Protoaurignacian assemblages from eastern Europe. The two main specimens are a mandible (Oase 1) and a skull from a second individual (Oase 2). The direct dating of Oase 2 provided only a minimum age of more than 29 ka ^{14}C BP ([Rougier et al., 2007](#)) but the direct dating of Oase 1 provided a more precise age of $34,290 + 970/-870$ ^{14}C BP, close to 40 ka cal BP, as well as an age of more than 35,200 ^{14}C BP ([Trinkaus et al., 2003](#)). The morphology of this specimen is indisputably modern. It has however been proposed that some peculiar features might be outside of the usual variation observed in recent modern humans and might be reminiscent of Neandertals, suggesting their occurrence would result from some gene flow between the two groups. Alternatively, these features may simply result from archaic persistence inherited from African ancestors in some of the oldest modern humans of Europe ([Rougier et al., 2007](#); [Hublin et al., 2012b](#); [Hublin, 2013](#)).

In Bacho Kiro, Bulgaria, a series of human fragments have been yielded by the layers 6 and 7 that overlie the IUP layers (Bachokirian). These layers have yielded a rather limited archaeological assemblage, defined as “Aurignacoid”. They include a fragment of parietal, a lower right permanent central incisor, a lower right lateral incisor, a right premolar, an upper right permanent canine, a deciduous lower central incisor and a fragment of immature right mandible ([Gleń and Kaczanowski, 1982](#)). These remains are generally considered to be modern ([Churchill and Smith, 2000](#); [Bailey et al., 2009](#)). Radiocarbon dates obtained in Bacho Kiro predate the development of refined pre-treatment techniques but for layer 7 a piece of charcoal has been dated at $32,200 \pm 780$ ^{14}C BP (c. 37.9–35.5 ka cal BP) ([Hedges et al., 1994](#)). It should also be noted that the human lower right molar from Dzeravá Skala (Slovakia) ([Kaminská et al., 2004](#)), which displays modern morphology ([Bailey et al., 2009](#)) could be associated to Early Aurignacian artefacts in a layer displaying clear disturbance, notably by cryoturbation ([Kaminská et al., 2005](#)).

In western Europe, Early Aurignacian human remains were discovered in several French sites. An upper first left incisor was found in La Ferrassie ([Gambier et al., 1990](#)). A fragmentary child mandible, an upper first molar and a fragmentary adult parietal may also be assigned to the older parts of the Aurignacian layers of Fontéchevade ([Garralda, 2006](#); [Chase and Teilhol, 2009](#)). However, the best evidence has been provided by the sites of La Quina-Aval ([Fig. 6](#)) and Brassempouy. At La Quina-Aval, Early Aurignacian

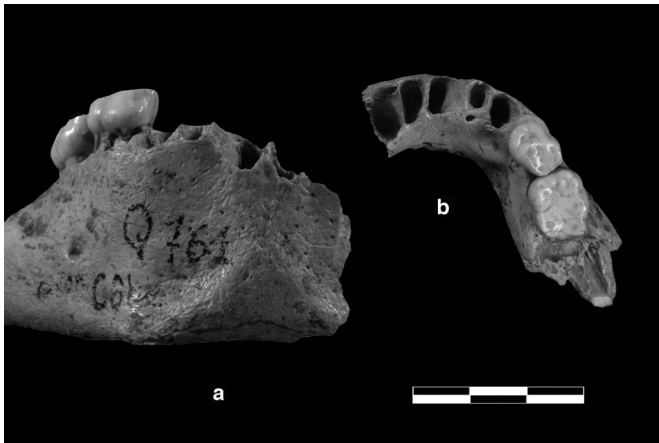


Fig. 6. Early Aurignacian specimens from La Quina-Aval (France). Mandible 4: a) anterior view b) occlusal view. Photo: Christine Verna.

level 3 has been dated at $33.3 \pm .33$ ka ^{14}C BP (c. 37.8 ka cal BP) (Dujardin, 2005). The layer has yielded two fragmentary mandibles, among which one (Quina-Aval 4) displays a full suite of modern features, including a clear bony chin (Verna et al., 2012).

Another securely dated set of specimens were found in the Early Aurignacian layers of Brassempouy. It mostly consists of a dental series but also includes a mandible fragment, a skull fragment and two distal hand phalanxes. These layers have been dated between 35 and 30 ka ^{14}C BP (c. 40.5–35 ka cal BP) (Henry-Gambier et al., 2004). A reassessment of the dental material, based on the frequency of non-metrical traits, clearly confirms the modern nature of this collection (Bailey and Hublin, 2005; Bailey et al., 2009).

In Italy, in one of the caves of the Monte Circeo at Fossellone, one fragmentary maxilla (Fossellone 1) has sometimes been assigned to a rather early phase of the Aurignacian (Mallegni and Segre-Naldini, 1992). It displays quite typical modern morphology with a deep canine fossa and a modern dental morphology for the associated second molar. Fossellone 2 consists of a scapula fragment but its precise stratigraphic origin in the site is uncertain. Finally, one should add the site of Fontana Nuova di Ragusa in the south of Sicily, where some human fragments (a left upper P3, a right upper M2, a frontal fragment, a parietal bone and a talus) (Chilardi et al., 1996) have also been associated to an Early Aurignacian lithic assemblage. However, the interpretation of the lithics (Martini et al., 2007), as well as the association of the bones that have been found in the backdirt of an ancient excavation, has led these specimens to be among the most uncertain Aurignacian human remains from western Europe.

4.3. Later Aurignacian

Later Aurignacian assemblages, postdating 35 ka cal BP, have yielded more complete specimens, in particular from the site of Mladeč (Czech Republic), where a large number of human remains were found in a karstic environment during the excavation at the turn of the 20th century. This series consisted of two skulls and two skullcaps, mandibles, postcranial bones, and some immature remains. Unfortunately, during the Second World War, a large portion of this collection was destroyed. The archaeological association is rather odd as it mostly consists of a series of bone points and some perforated teeth. Among these points, one should mention a type called “Mladeč point”, which have been found in various mid-Aurignacian sites throughout central Europe. The human remains have been directly dated and their average radiometric age is close

to 31 ka ^{14}C BP (c. 35.5 ka cal BP) (Wild et al., 2005). Svoboda (2000) has proposed that the layers excavated from the karst correspond to a secondary deposit of a block of sediment that may have fallen through a chimney opening to the surface. As in Peñteracu Oase, the anatomical features of the Mladeč series have been used to support the survival of phenotypical Neandertal features in the Early Upper Palaeolithic modern European populations (Freyer, 1986, 2006; Wolpoff et al., 2006). It is, however, unclear whether the possible Neandertal reminiscence described on some of these specimens really results from gene flow between the two groups at the time of the replacement or from the persistence of archaic features in these modern populations (Bräuer et al., 2006; Gunz and Harvati, 2007; Bailey et al., 2009).

Close in time to these findings is the human distal thumb phalanx from the cave of Oblazowa, Poland, directly dated at $31 \text{ ka} \pm 550$ ^{14}C BP, by Hedges et al. (1996). In Romania, two sites, Muierii and Cioclovina, have yielded well-preserved material. Although Aurignacian layers have been identified in both sites (Alexandrescu et al., 2010), the precise stratigraphical context of this material is unclear and they are mostly assigned to the Aurignacian based on direct radiocarbon dates. At Muierii, in addition to a mandible and some postcranial elements, a skull has been dated at $30,150 \pm 800$ ^{14}C BP (36.1–33.7 ka cal BP). At Cioclovina, a skull has also been found, and was dated to $29 \text{ ka} \pm 700$ ^{14}C BP (34.4–33.1 ka cal BP). In both sites, the human remains are anatomically modern (Soficaru et al., 2006, 2007; Harvati et al., 2007). Fragmentary remains have been found in Aurignacian complexes in the sites of La Adam, Bordu Mare, Peñteracu Mică and Malu Roșu (Alexandrescu et al., 2010). In Hungary, fragmentary remains of comparable age have been discovered at Istállós-kő and Görömböly-Tapolca. At Istállós-kő, the lower first molar most likely comes from the Upper Aurignacian layer, dated between 31 and 28 ka ^{14}C BP (36.1–32.2 ka cal BP) (Adams and Ringer, 2004), and is of modern morphology (Bailey et al., 2009). At the site of Görömböly-Tapolca a modern occipital bone (Thoma, 1971) has been directly dated at $30,300 \pm 300$ ^{14}C BP (35.0–34.6 ka cal BP) (Davies and Hedges, 2008–2009).

In western Europe, the most complete human remains coming from later phases of the Aurignacian have been found in France at La Crozade and Les Rois. In La Crozade, the most complete specimens are a frontal bone and a maxilla, both quite modern morphologically. The latter has been directly dated at $30,640 \pm 640$ ^{14}C BP (36.2–34.6 ka cal BP) (Henry-Gambier and Sacchi, 2008). In Les Rois, a series of 37 teeth has been found in addition to an immature mandible (Mandible A) and a smaller mandibular fragment (Mandible B). Anatomically, these remains are modern, especially regarding Mandible A (Vallois, 1958; Gambier, 1989; Verna et al., 2008) but see also (Ramirez Rozzi et al., 2009). This series has been found in layers ranging between 30 and 28 ka ^{14}C BP (34.6–32.4 ka cal BP) (Ramirez Rozzi et al., 2009). Finally, one should note an artificially perforated first or second left molar from the site of La Combe (France) (White et al., 2003).

In Germany, fragmentary human remains have been found in association with middle phases of the Aurignacian in the sites of Hohlenstein-Stadel, Sirgenstein, Kleine Olnet, Schafstall, and Geißenklösterle (Czarnetzki, 1983; Orschiedt, 2000; Street et al., 2006).

5. Conclusion

Although Europe and southwest Asia have provided one of the richest and best-studied archaeological and palaeontological records in the world, documenting the transition from Middle to Upper Palaeolithic, it is still difficult to provide an accurate picture of the exact process of the replacement of Neandertals by modern humans in western Eurasia. Primarily, the issue is obscured by the

scarcity or sometimes total absence of human fossil remains in several of the lithic assemblages from this time period. Furthermore, a large portion of the available material was discovered a long time ago, in the course of excavations that were not conducted and documented according to present-day standards. This situation has created a lot of uncertainty regarding the precise cultural assignment and geological age of key specimens. Furthermore, even when the stratigraphic assignment of specimens was well recorded, site formation processes may have led to the intrusion of archaeological or palaeontological material from one layer into another. This is especially true for small items such as teeth, which cannot always be directly dated. As a result, although morphometric techniques and palaeogenetics have dramatically improved our ability to determine the biological nature of the fossil evidence from this time period, there are still disagreements surrounding different scenarios of replacement. It remains, therefore, crucial to obtain more human fossil material in order to resolve the pending issues. However, considering the rhythm of discoveries and the fact that, for some assemblages, many key sites have been totally exhausted, one cannot be too optimistic.

Another issue relates to the extent to which one can extrapolate the biological nature of the makers of one assemblage from discoveries in one site where the concerned industry is represented. It seems rather parsimonious to conceive that the proven association of one type of humans (Neandertals or modern humans) with a given industry implies that the assemblage has been produced by this group across its whole geographical extension. This is probably true in most situations. However, the Levantine Mousterian provides examples of rather similar assemblages produced by Neandertals and anatomically modern humans in the same region. Moreover, the possibility that the remains of one individual may be found at a site yielding archaeological artefacts created by a different population cannot be totally discarded. Assuming the biological nature of the makers from a limited number of discoveries becomes even more problematic when large ensembles of apparently related industries are considered. This is especially true during the replacement period where people have been tempted to group very diverse lithic assemblages under denominations such as “intermediate” or “transitional” industries that are not independent from pre-conceived scenarios.

The dating itself of the human remains and of the archaeological layers that yield them is also often a matter of controversy. The past decade or two have witnessed spectacular improvements in the implementation of radiometric methods that have opened the possibility to revisit the chronology of some sites. In some cases, samples that had already been radiocarbon dated have been re-analysed, demonstrating that many published dates had provided clearly underestimated ages. One of the implications of this situation is that a statistical treatment of published dates that would mix results obtained with variably reliable techniques is worthless. A limited number of precise dates recently acquired with the most advanced techniques can provide decisive information when thousands of dates routinely referred to in the literature confuse the issue more than they clarify it. One should, however, not become overconfident. Technical improvements in radiocarbon dating, including ultrafiltration, were not obtained all at once and further improvements will certainly continue to occur in the future. The development of radiocarbon dates on marine shells, implying efficient pre-treatment, as well as accurate modelling of the reservoir effect for ^{14}C , is a good example of this ongoing progress (Russo et al., 2010; Reimer et al., 2013). The use of the single amino acid technique to avoid the bias of contamination certainly represents a breakthrough but its development is still limited by the need for a larger amount of organic matter to be extracted from bone samples. Still, different labs using the most up-to-date

techniques, but different sampling strategies, can resolve the chronology of the same site stratigraphy in contradicting ways (e.g. Higham et al., 2011a vs. Hublin et al., 2012a). The control of the quality of the samples still represents a crucial issue and when high-quality samples are available, the type of pre-treatment implemented on charcoals (e.g. classical ABA or more advanced ABOx) has been proven to have less influence on the obtained results than the choice of a laboratory where the measurements are performed (Haesaerts et al., 2013). Finally, one should keep in mind that the radiocarbon dates obtained from various materials have a different weight in their ultimate interpretation, depending on the very samples that were used to establish them. Many available dates of hominins are indirect, and only based on the dating of their geological or archaeological context, while others result from directly dating fossil hominins. In both cases, the relation between a given archaeological context and a hominin may or may not be well-established.

Reviewing the whole spectrum of lithic assemblages present in the time period between 50 and 35 ka cal BP provides us with a complex archaeological landscape (Fig. 7). Although some assemblages have a very ubiquitous presence, many are documented only in limited geographical domains and sometimes for rather short periods of time. This makes the assignment of these assemblages to one biological group of hominins or another even more challenging. Although it has long been considered that the development of the Aurignacian complex documented the first colonization of Europe by modern humans, there is growing evidence that the earliest occurrence of modern humans in the middle latitude of western and central Eurasia is much older. The archaeological proxy for this early colonization is to be found among older lithic assemblages. Among the various assemblages predating the Aurignacian, two groups can be delineated. One group consists of the industries assigned to the IUP and is represented in the Levant as well as in eastern Europe and central Asia. In most regions, this ensemble does not seem to result from a local transition but rather from the intrusion of allochthonous populations. Over a geographical domain, covering a large portion of Eurasia, the IUP displays a number of shared features in terms of blank production. Although its exact chronology is still under investigation, the start of its expansion out of southwest Asia most likely predates 47 ka cal BP, as suggested by the dates obtained at Bohunice (Richter et al., 2009) and Kara-Bom (Goebel et al., 1993). This early expansion would be more in agreement with an older date for the beginning of the IUP (Marks, 1983) than with those produced at Ksar Akil (Douka et al., 2013) and Üçağızlı (Kuhn et al., 2009). The recent discovery of the femur of Ust-Ischim in Siberia, directly dated at 45 ka BP and indisputably modern both anatomically and genetically, completes the more fragmentary discoveries from Ksar Akil (layer XXV), Üçağızlı and Bacho Kiro (layer 11), and brings support to the notion that the IUP represents a wave of migrations of fully modern humans. This wave, however, might not have been completely successful and apparently did not make it to western Europe.

At the time of the eastern European IUP, western Europe provides a complex picture where several TAs have been described and where directly dated Neandertal remains are known from Spy (Belgium) and Saint-Césaire (France). However, the situation in this region is still unclear. Claims have been made that the Lincombian in England and Uluzzian in Italy were produced by modern humans. However, the evidence provided by the sites of Kents Cavern and Cavallo still need to be confirmed. Unfortunately, the material yielded by these two sites is very fragmentary and the stratigraphic contexts, from excavations conducted in the middle of the 20th century, are cause for debate. In terms of the abundance and completeness of specimens that have been directly or indirectly assigned to the Châtelperronian and LRJ, the balance clearly

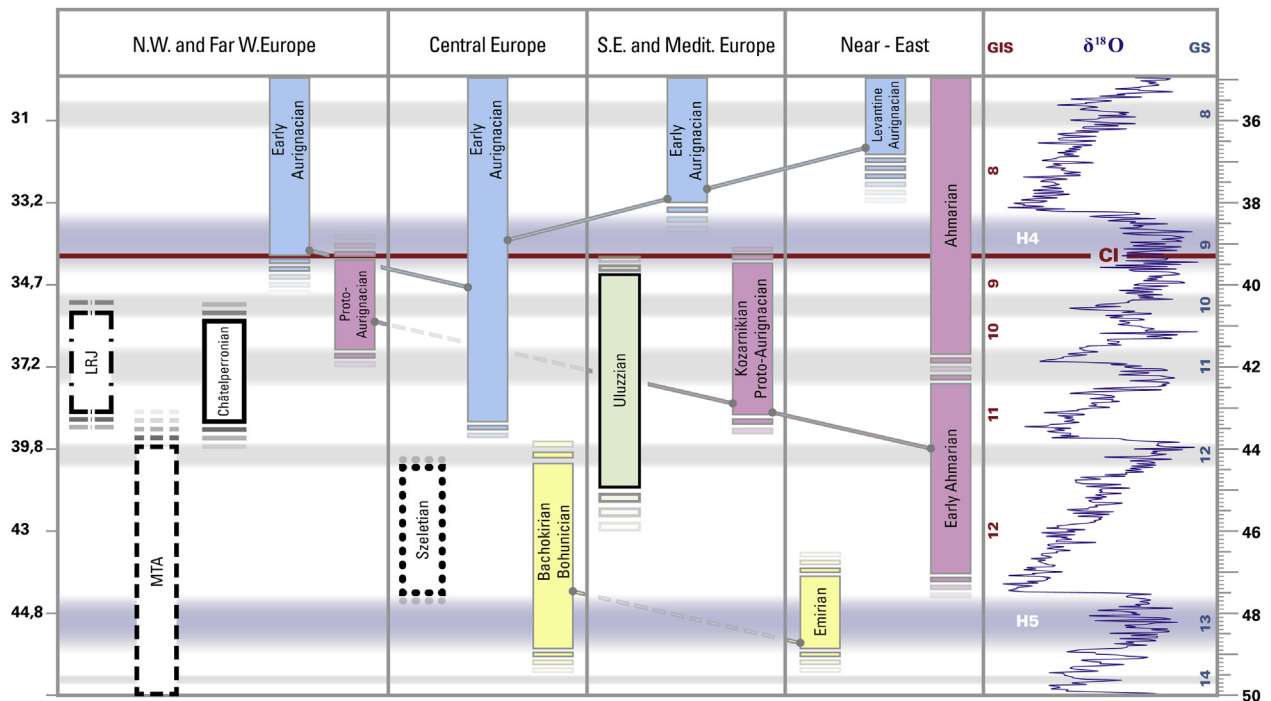


Fig. 7. Synthetic table of the assemblages discussed in the text with their estimated chronological span. The colour code matches that of Fig. 1 and 3. The calibrated timeline on the right side and the ^{14}C timeline on the left are scaled using Bronk Ramsey (2009) and Reimer et al. (2009). The $\delta^{18}\text{O}$ variations established by the North Greenland Ice-Core Project (NGRIP) are taken from <http://www.gfz.ku.dk/~www-glac/data/gripdelta.dat>. Cold stadials (GS) are indicated by grey horizontal bands and interstadial periods (GIS) by white horizontal bands. The red line indicates the time of the Campanian Ignimbrite (CI) and the blue bands the Heinrich Events 4 (H4) and 5 (H5).

tilts toward the Neandertal side. Another aspect to take into consideration relates to the fact that, to some degree, contrary to what is observed with the IUP further east, some arguments support local continuity for some of these western European assemblages. The case seems stronger for the LRJ, but it should also be considered for the Uluzzian and for the Châtelperronian. If some or all of these assemblages were really produced by Neandertals, and taking into account that they display clear UP features, it is tempting to consider that the cultural changes at work in the Neandertal world of western Europe since the final Mousterian phases (Soressi et al., 2013) might result from cultural stimulus diffusion (*sensu* Kroeber, 1940) from adjacent regions where modern humans had already been settled. The source of this stimulus diffusion would be represented first by the IUP, possibly as early as 48 ka cal BP and later by the first phases of the Aurignacian complex. Although there is no evidence for prolonged local co-existence of Neandertals and modern humans in any region of Europe, the ages of the latest directly dated Neandertals of Western Europe (Spy and Saint-Césaire) suggest that the chronological overlap between the two groups might have been quite long on a continental scale.

One can likely assign most, if not all, of the early phases of the Aurignacian to modern humans, although the biological nature of the makers of these earliest phases is poorly documented in western Europe. In the Mediterranean world, the Early Ahmarian/Kozarnikian/Protoaurignacian seems to represent a rather consistent techno-typological ensemble, spreading rather quickly, most likely out of the Levant. Its occurrence in northern Italy and the Pyrenees region predates the Campanian Ignimbrite and after 40 ka BP it further expanded in both central France and central Italy. Current stratigraphical and radiocarbon evidence suggest a partial chronological overlap with the Châtelperronian and Uluzzian. The limited development of body ornaments in both assemblages as well as the production of bladelets in the Châtelperronian with a

chaîne opératoire different from that of the Protoaurignacian has been suggested to result from direct cultural diffusion between these groups (e.g. Mellars, 2005; Rousset, 2011; Hublin, 2012; Hublin et al., 2012a). The earliest stages of the Early Aurignacian are documented north of the Alps at Willendorf II and Geißenklösterle c. 43–42 ka cal BP and may derive from the same source as the Protoaurignacian encountered south of the Alps. Its extension further west as well as further east, and ultimately into the Levant, occurred later. Although the fossil record of the Early Aurignacian is limited and has been yielded by the later phases of this industry, to date its modern nature is quite clear, which is consistent with the later Aurignacian fossil evidence.

In addition to a clarification of the chronology, a better understanding of the evolution of the various assemblages present in Europe during this crucial period of recent human evolution is essential to elucidate the dynamic of the modern human migration into western Eurasia, including the possible cultural interactions with and eventual replacement of the local Neandertal populations. Palaeogenetics are also expected to provide new insight into the biological aspects of these processes.

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References

- Adams, B., Ringer, Á., 2004. New C14 dates for the Hungarian early Upper Palaeolithic. *Curr. Anthropol.* 45, 541–551.

- Alexandrescu, E., Olariu, A., Skog, G., Stenström, K., Hellborg, R., 2010. Human fossil bones from the Muierii Cave and the Cioclovina Cave, Romania. *Anthropologie* 114, 341–353.
- Allsworth-Jones, P., 1990. The Szeletian and the stratigraphic succession in central Europe and adjacent areas: main trends, recent results, and problems for resolution. In: Mellars, P. (Ed.), *The Emergence of Modern Humans: an Archaeological Perspective*. Cornell University Press, New York, pp. 160–242.
- Armitage, S.J., Jasim, S.A., Marks, A.E., Parker, A.G., Usik, V.I., Uerpmann, H.-P., 2011. The Southern route “Out of Africa”: evidence for an early expansion of modern humans into Arabia. *Science* 331, 453–456.
- Bailey, S., Weaver, T.D., Hublin, J.-J., 2009. Who made the Aurignacian and other early Upper Paleolithic industries? *J. Hum. Evol.* 57, 11–26.
- Bailey, S.E., Hublin, J.-J., 2005. Who made the early aurignacian? a reconsideration of the Brassempouy dental remains. *Bull. Mém. la Société d'Anthropol. Paris* 17, 115–121.
- Bailey, S.E., Hublin, J.-J., 2006a. Did Neanderthals make the Châtelperronian assemblage from La Grotte du Renne (Arcy-sur-Cure, France)? In: Harvati, K., Harrison, T. (Eds.), *Neanderthals Revisited: New Approaches and Perspectives*. Springer, New York, pp. 191–210.
- Bailey, S.E., Hublin, J.J., 2006b. Dental remains from the Grotte du Renne at Arcy-sur-Cure (Yonne). *J. Hum. Evol.* 50, 485–508.
- Banks, W.E., d'Errico, F., Zilhão, J., 2013. Human–climate interaction during the early Upper Paleolithic: testing the hypothesis of an adaptive shift between the proto-Aurignacian and the early Aurignacian. *J. Hum. Evol.* 64, 39–55.
- Bar-Yosef, O., 1998. The chronology of the Middle Paleolithic of the Levant. In: Akazawa, T., Aoki, K., Bar-Yosef, O. (Eds.), *Neanderthals and Modern Humans in Western Asia*. Plenum Press, pp. 39–56.
- Bar-Yosef, O., 2003. Reflections on selected issues of the Upper Palaeolithic. In: Goring-Morris, A.N., Belfer-Cohen, A. (Eds.), *More than Meets the Eye. Studies on Upper Palaeolithic Diversity in the Near East*. Oxbow Books, Oxford, pp. 265–273.
- Bar-Yosef, O., 2007. The archaeological framework of the Upper Paleolithic revolution. *Diogenes* 214, 3–18.
- Bar-Yosef, O., Belfer-Cohen, A., Adler, D., 2006. The implications of the middle–Upper Paleolithic chronological boundary in the Caucasus to Eurasian prehistory. *Anthropologie XLIV*, 49–60.
- Bar-Yosef, O., Bordes, J.-G., 2010. Who were the makers of the Châtelperronian culture? *J. Hum. Evol.* 59, 586–593.
- Bartolomei, G., Broglio, A., Cassoli, P., Cremaschi, M., Giacobini, G., Malerba, G., Maspero, A., Peresani, M., Tagliacozzo, A., 1993. Risultati Preliminari Delle Nuove Ricerche al Riparo di Fumane. In: *L'Annuario Storico Della Valpolicella 1991–1992–1993*, pp. 9–64.
- Beckouche, S., Poplin, F., 1981. Les vestiges humains. In: *Champagne, F., Espalié, R. (Eds.), Le Piage, Site Préhistorique du Lot. Société Préhistorique Française, Paris*, pp. 159–160.
- Benazzi, S., Douka, K., Fornai, C., Bauer, C.C., Kullmer, O., Svoboda, J., Pap, I., Mallegni, F., Bayle, P., Coquerelle, M., Condemi, S., Ronchitelli, A., Harvati, K., Weber, G.W., 2011. Early dispersal of modern humans in Europe and implications for Neanderthal behaviour. *Nature* 479, 525–528.
- Benazzi, S., Bailey, S.E., Peresani, M., Mannino, M.A., Romandini, M., Richards, M.P., Hublin, J.-J., 2014. Middle Paleolithic and Uluzzian human remains from Fumane cave, Italy. *J. Hum. Evol.* 70, 61–68. <http://dx.doi.org/10.1016/j.jhevol.2014.03.001>.
- Bergman, C.A., Stringer, C.B., 1989. Fifty years after: Egbert, an early upper Palaeolithic juvenile from Ksar Akil, Lebanon. *Paléorient* 15, 99–111.
- Bodu, P., Salomon, H., Leroyer, M., Naton, H.-G., Lacarriere, J., Dessoles, M., 2014. An open-air site from the recent Middle Palaeolithic in the Paris Basin (France): les Bossats at Ormesson (Seine-et-Marne). *Quat. Int.* 331, 39–59. <http://dx.doi.org/10.1016/j.quaint.2013.10.029>.
- Bon, F., 2002. L'Aurignacien entre Mer et Océan. Réflexion sur l'unité des phases anciennes de l'Aurignacien dans le sud de la France. In: *Mémoire de la Société Préhistorique Française*, vol. X, p. 253.
- Bräuer, G., Broeg, H., Stringer, C.B., 2006. Earliest Upper Paleolithic crania from Mladec, Czech Republic, and the question of Neanderthal-modern continuity: metrical evidence from the fronto-facial region. In: Harvati, K., Harrison, T. (Eds.), *Neanderthals Revisited: New Approaches and Perspectives*. Springer, New York, pp. 269–280.
- Brock, F., Higham, T., Bronk Ramsey, C., 2007. Radiocarbon Dating Bone Samples Recovered from Gravel Sites. In: *Research Department Report Series*, pp. 1–25. London.
- Broglio, A., Cremaschi, M., Peresani, M., 1998–1999. Lo Stato delle Ricerche nella Grotta di Fumane all'anno 1998. In: *Annuario Storico Della Valpolicella*, pp. 11–18.
- Bronk Ramsey, C., 2009. Bayesian analysis of radiocarbon dates. *Radiocarbon* 51, 337–360.
- Brown, T.A., Nelson, D.E., Vogel, J.S., Southon, J.R., 1988. Improved collagen extraction by modified Longin method. *Radiocarbon* 30, 171–177.
- Cabrera-Valdés, V., Valladas, H., Bernaldo de Quiros, F., Gomez, M.H., 1996. La transition Paléolithique Moyen-Paléolithique supérieur a El castillo (Cantabrie): Nouvelles datations par le carbone 14. In: *Comptes Rendus de l'Académie des Sciences Paris*, vol. 322, pp. 1093–1098.
- Cabrera-Valdés, V., Maillo, J.M., Lloret, M., Bernaldo de Quiros, F., 2001. La transition vers le Paléolithique supérieur dans la grotte du Castillo (Cantabrie, Espagne): la couche 18. *L'Anthropologie* 105, 505–532.
- Caron, F., d'Errico, F., Del Moral, P., Santos, F., Zilhão, J., 2011. The Reality of Neanderthal Symbolic Behavior at the Grotte du Renne, Arcy-sur-Cure, France. *PLoS ONE* 6, e21545.
- Chase, P., Teilhol, V., 2009. The Fossil human remains. In: Chase, P.G., Debénath, A., Dibble, H.L., McPherron, S.P. (Eds.), *The Cave of Fontéchevade: Recent Excavations and Their Paleoanthropological Implications*. Cambridge University Press, Cambridge, pp. 103–116.
- Chilardi, S., Frayer, D.W., Gioia, P., Macchiarelli, R., Mussi, M., 1996. Fontana Nuova di Ragusa (Sicily, Italy): southernmost Aurignacian site in Europe. *Antiquity* 70, 553–563.
- Churchill, S.E., Smith, F.H., 2000. Makers of the early Aurignacian of Europe. *Am. J. Phys. Anthropol.* 113, 61–115.
- Connet, N., 2002. Le Châtelperronien: Réflexions sur l'unité et l'identité technico-économique de l'industrie lithique. In: *L'apport de L'analyse Diachronique des Industries Lithiques des couches Châtelperroniennes de la Grotte du Renne a Arcy-sur-Cure (Yonne)*. Université de Lille 1, Lille, p. 445.
- Cooper, L.P., Thomas, J.S., Beamish, M.G., Gouldwell, A., Colcutt, S.N., Williams, J., Jacobi, R.M., Currant, A., Higham, T., 2012. An early Upper Palaeolithic open-air Station and mid-Devensian Hyaena Den at Grange Farm, glaston, Rutland, UK. *Proc. Prehist. Soc.* 78, 73–93.
- Copeland, L., Yazbeck, C., 2002. Inventory of Stone Age Sites in Lebanon. In: *New and Revised, Part III*, vol. 55. Mélanges de l' Université Saint-Joseph, pp. 121–325.
- Czarnetzki, A., 1983. Zur Entwicklung des Menschen in Südwestdeutschland. In: Müller-Beck, H. (Ed.), *Urgeschichte in Baden-Württemberg*. Konrad Theiss Verlag, Stuttgart, pp. 217–240.
- d'Errico, F., 2003. The invisible frontier. A multiple species model for the origin of behavioral modernity. *Evol. Anthropol.* 12, 188–202.
- d'Errico, F., Zilhão, J., Baffier, D., Julien, M., Pelegrin, J., 1998. Neanderthal acculturation in Western Europe? A critical review of the evidence and its interpretation. *Curr. Anthropol.* 39, S1–S44.
- Desbrosse, R., Koslowski, J., 1988. Hommes et Climats à l'âge du Mammouth. Le Paléolithique Supérieur d'Eurasie Centrale. Masson, Paris.
- Davies, W., Hedges, R., 2008–2009. Dating a type site: fitting Szeleta cave into its regional Chronometric context. *Praehistoria* 9–10, 35–45.
- Debets, G.F., 1955. Paleoanthropological finds from Kostenki (Preliminary notes). *Sov. Etnogr.* 1, 43–53.
- Douka, K., Bergman, C.A., Hedges, R.E.M., Wesselingh, F.P., Higham, T.F.G., 2013. Chronology of Ksar Akil (Lebanon) and implications for the colonization of Europe by anatomically modern humans. *PLoS ONE* 8, e72931.
- Douka, K., Grimaldi, S., Boschian, G., del Lucchese, A., Higham, T.F.G., 2012. A new chronostratigraphic framework for the Upper Palaeolithic of Riparo Mochi (Italy). *J. Hum. Evol.* 62, 286–299.
- Douka, K., Higham, T.F.G., Wood, R., Boscato, P., Gambassini, P., Karkanas, P., Peresani, M., Ronchitelli, A.M., 2014. On the chronology of the Uluzzian. *J. Hum. Evol.* 68, 1–13.
- Dujardin, V., 2005. Débitage lamellaire aurignacien à La Quina aval (Gardes-le-Pontaroux) et à la grotte des Renardières (Les Pins, Charente, France). In: *Le Brun-Ricalens, F., Bordes, J.-G., Bon, F. (Eds.), Productions Lamellaires Attribuées à l'Aurignacien: Chaînes Opératoires et Perspectives Techno-culturelles*, first ed., Actes de la Table-ronde organisée dans le cadre du XVe Congrès de l'UISPP, Liège, 2001 Archéologiques, Luxembourg, pp. 273–295.
- Duller, G., 2008. Single-grain optical dating of Quaternary sediments: why aliquot size matters in luminescence dating. *Boreas* 37, 589–612.
- Ewing, J.F., 1963. A probable neanderthaloid from Ksar 'Akil, Lebanon. *Am. J. Phys. Anthropol.* 21, 101–104.
- Flas, D., 2006. La transition du Paléolithique moyen au supérieur dan la plaine septentrionale de l'Europe. Université de Liège, Liège, p. 318.
- Flas, D., 2011. The middle to Upper Paleolithic transition in Northern Europe: the Lincmbian-Ranisian-Jerzmanowician and the issue of acculturation of the last Neanderthals. *World Archaeol.* 43, 605–627.
- Formicola, V., 1989. Early Aurignacian deciduous incisor from riparo bombrini at Balzi Rossi (Grimaldi, Italy). *Riv. Antropol.* 67, 287–292.
- Frayer, D.W., 1986. Cranial variation at Mladec and the relationship between Mousterian and Upper Paleolithic hominids. In: Novotný, V., Mizerová, A. (Eds.), *Fossil Man: New Facts - New Ideas. Papers in Honour of Jan Jelinek's Life Anniversary*. Anthropos Institute- Moravian Museum, Brno, pp. 243–256.
- Frayer, D.W., Jelinek, A., Oliva, M., Wolpoff, M.H., 2006. Aurignacian male crania, jaws and teeth from the Mladec Caves, Moravia, Czech Republic. In: Teschler-Nicola, M. (Ed.), *Early Modern Humans at the Moravian Gate: the Mladec Caves and Their Remains*. Springer, Wien, pp. 185–272.
- Gábori-Csánk, V., 1983. La Grotte Remete 'Felső' (Supérieure) et le 'Szeletian de Transdanubie. *Acta Archaeol. Acad. Sci. Hung.* 35, 249–285.
- Gambier, D., 1989. Fossil hominids from the early upper palaeolithic (Aurignacian) of France. In: Mellars, P., Stringer, C. (Eds.), *The Human Revolution: Behavioural and Biological Perspectives on the Origins of Modern Humans*. Edinburgh University Press, Edinburgh, pp. 194–211.
- Gambier, D., 1990. Les vestiges humains du Gisement d'Isturitz (Pyrénées-Atlantiques). *Etude Anthropologique et Analyse des Traces D'action Humaine Intentionnelle*. Antiquités Nationales, pp. 10–25.
- Gambier, D., Houet, F., Tillier, A.M., 1990. Dents de Font de Gaume (Châtelperronien et Aurignacien) et de la Ferrassie (Aurignacien ancien) en Dordogne. *Paléo* 2, 143–152.
- Garralda, M.D., 2006. Las gentes del Paleolítico superior antiguo de Europa occidental. In: Maillo, J.M., Baquedano, E. (Eds.), *Miscelánea en homenaje a*

- Victoria Cabrera, vol. 1. Museo Arqueológico Regional, Alcalá de Henares, pp. 320–335.
- Garralda, M.D., Tillier, A.M., Vandermeersch, B., Cabrera, V., Gambier, D., 1992. Restes humains de l'Aurignacien archaïque de la Cueva de El Castillo. *Anthropologie* 32, 159–164.
- Gerasimova, M.M., 1987. *Metricheskiye kharakteristiki skeleta Markina Gora* (Metric characteristics of the Markina Gora skeleton). *Vopr. Antropol.* 78, 21–28.
- Gibbons, A., 2014. Oldest Homo sapiens genome pinpoints neandertal input. *Science* 343, 1417.
- Gioia, P., 1990. An aspect of the transition between middle and Upper Paleolithic in Italy: the Uluzzian. In: Farizy, C. (Ed.), *Paléolithique moyen récent et Paléolithique supérieur ancien en Europe. Ruptures et transitions: examen critique des documents archéologiques, Actes du Colloque international de Nemours 9-10-11 Mai 1988. Musée de Préhistoire d'Ile de France, Nemours*.
- Gleń, E., Kaczanowski, K., 1982. Human remains. In: Kozłowski, J. (Ed.), *Excavation in the Bacho Kiro Cave (Bulgaria): Final Report. Panstwowe Wydawnictwo Naukowe, Warszawa*, pp. 75–79.
- Goebel, T., Derevianko, A.P., Petrin, V.T., 1993. Dating the middle-to-Upper Paleolithic transition at Kara-Bom. *Curr. Anthropol.* 34, 452–458.
- Golovanova, L.V., Cleghorn, N.E., Doronichev, V.B., Hoffecker, J.F., Burr, G.S., Sulergizkiy, D., 2006. The early Upper Paleolithic in the northern Caucasus (new data from Mezmaiskaya Cave, 1997 excavation). *Eurasian Prehistory* 4, 43–78.
- Granger, J.-M., Lévêque, F., 1997. Parure castelperronienne et aurignacienne: étude de trois séries inédites de dents percées et comparaisons. *Comptes Rendus De L'Académie Des. Sci. Paris, Sci. De. la terre Et. Des. Planètes* 325, 537–543.
- Green, R.E., Krause, J., Briggs, A.W., Maricic, T., Stenzel, U., Kircher, M., Patterson, N., Li, H., Zhai, W.W., Fritz, M.H.Y., Hansen, N.F., Durand, E.Y., Malaspina, A.S., Jensen, J.D., Marques-Bonet, T., Alkan, C., Prüfer, K., Meyer, M., Burbano, H.A., Good, J.M., Schultz, R., Aximu-Petri, A., Butthof, A., Höber, B., Höffner, B., Siegemund, M., Weihmann, A., Nusbaum, C., Lander, E.S., Russ, C., Novod, N., Affourtit, J., Egholm, M., Verna, C., Rudan, P., Brajkovic, D., Kucan, Z., Gušić, I., Doronichev, V.B., Golovanova, L.V., Lalueza-Fox, C., de la Rasilla, M., Fortea, J., Rosas, A., Schmitz, R.W., Johnson, P.L.F., Eichler, E.E., Falush, D., Birney, E., Mullikin, J.C., Slatkin, M., Nielsen, R., Kelsey, J., Lachmann, M., Reich, D., Pääbo, S., 2010. A draft sequence and preliminary analysis of the Neandertal genome. *Science* 328, 710–722.
- Guadelli, J.-L., Sirakov, N., Ivanova, S., Sirakova, S., Anastassova, E., Courtaud, P., Dimitrova, I., Djabarska, N., Fernandez, P., Ferrier, C., Fontugne, M., Gambier, D., Guadelli, A., Iordanova, D., Iordanov, N., Kovatcheva, M., Krumov, I., Leblanc, J.-C., Mallye, J.-B., Marinska, M., Miteva, V., Popov, V., Spassov, R., Taneva, S., Tisserat-Laborde, N., Tsanova, T., 2005. Une séquence Du Paléolithique Inférieur Au Paléolithique récent Dans Les Balkans : la Grotte Kozarnika A Orechts (Nord-Ouest De La Bulgarie). In: Molines, N., Moncel, M.-H., Monnier, J.-L. (Eds.), *Données récentes sur les modalités de peuplement et sur le cadre chronostratigraphique, géologique et paléogéographique des industries du Paléolithique inférieur et moyen en Europe*, pp. 87–103.
- Gunz, P., Harvati, K., 2007. The Neandertal "chignon": variation, integration, and homology. *J. Hum. Evol.* 52, 262–274.
- Haesaerts, P., Damblon, F., Bachner, M., Trnka, G., 1996. Revised stratigraphy and chronology of the Willendorf II sequence, lower Austria. *Archaeol. Austriaca* 80, 25–42.
- Haesaerts, P., Damblon, F., Nigst, P.R., Hublin, J.J., 2013. ABA and ABOx radiocarbon Cross-dating on charcoal from middle Pleniglacial Loess deposits in Austria, Moravia, and western Ukraine. *Radiocarbon* 55, 1–7.
- Haesaerts, P., Damblon, F., Sinitsyn, A., Van der Plicht, J., 2004. Kostienki 14 (Voronezh, Central Russia): new data on stratigraphy and radiocarbon chronology. In: Dewez, M., Noiret, P., Teheux, E. (Eds.), *Acts of the XIVth UISPP Congress (Liège, 2001). General Sessions and Posters. Section 6. The Upper Paleolithic, British Archaeological Reports (BAR), International Series*, pp. 169–180. Oxford.
- Hahn, J., 1988. *Das Geisenklösterle I. Konrad Theiss, Stuttgart*.
- Harvati, K., Gunz, P., Grigorescu, D., 2007. Cioclovina (Romania): affinities of an early modern European. *J. Hum. Evol.* 53, 732–746.
- Hedges, R.E.M., Housley, R.A., Bronk, R.C., Klinken, G.J.v., 1994. Radiocarbon dates from the Oxford ams system: archaeometry datelist 18. *Archaeometry* 36, 337–374.
- Hedges, R.E.M., Housley, R.A., Law, I.A., Bronk, C.R., 1989. Radiocarbon dates from the Oxford AMS system: archaeometry datelist 9. *Archaeometry* 31, 207–234.
- Hedges, R.E.M., Housley, R.A., Pettitt, P.B., Bronk Ramsey, C., van Klinken, G.J., 1996. Radiocarbon dates from the Oxford AMS system: archaeometry datelist 21. *Archaeometry* 38, 181–207.
- Henry-Gambier, D., Maureille, B., White, R., 2004. Vestiges humains des niveaux de l'Aurignacien ancien du site de Brassempouy (Landes). *Bull. Mém. la Société d'Anthropol. Paris* 16, 49–87.
- Henry-Gambier, D., Sacchi, D., 2008. La crouzade V-VI (Aude, France) : un des plus anciens fossiles d'anatomie moderne en Europe Occidentale. *Bull. Mém. la Société Anthropol. Paris* 20, 79–104.
- Henry-Gambier, D., Normand, C., Petillon, J.-M., 2013. Datation radiocarbone directe et attribution culturelle des vestiges humains paléolithiques de la grotte d'Isturitz (Pyrénées-Atlantiques). *Bull. La Société Préhistorique Française* 110, 645–656.
- Higham, T., Basell, L., Jacobi, R., Wood, R., Ramsey, C.B., Conard, N.J., 2012. Testing models for the beginnings of the Aurignacian and the advent of figurative art and music: the radiocarbon chronology of Geißenklösterle. *J. Hum. Evol.* 62, 664–676.
- Higham, T., Brock, F., Bronk Ramsey, C., Davies, W., Wood, B.A., Basell, L., 2011a. Chronology of the site of Grotte du Renne, Arcy-sur-Cure, France: implications for Neandertal symbolic behaviour. *Before Farming* 2011 (2), 1–9.
- Higham, T., Compton, T., Stringer, C., Jacobi, R., Shapiro, B., Trinkaus, E., Chandler, B., Groning, F., Collins, C., Hillson, S., O'Higgins, P., FitzGerald, C., Fagan, M., 2011b. The earliest evidence for anatomically modern humans in northwestern Europe. *Nature* 479, 521–524.
- Higham, T., Jacobi, R., Julien, M., David, F., Basell, L., Wood, R., Davies, W., Bronk Ramsey, C., 2010. Chronology of the Grotte du Renne (France) and implications for the context of ornaments and human remains within the Châtelperronian. *Proc. Natl. Acad. Sci. U. S. A.* 107, 20234–20239.
- Higham, T., Brock, F., Peresani, M., Broglio, A., Wood, R., Douka, K., 2009. Problems with radiocarbon dating the middle to Upper Palaeolithic transition in Italy. *Quat. Sci. Rev.* 28, 1257–1267.
- Hillebrand, J., 1914. *Az 1913 évi barlangkutatósaím eredményei. Barlangkutató* 2, 115–124.
- Hoffecker, J.F., 2009. The spread of modern humans in Europe. *Proc. Natl. Acad. Sci. U. S. A.* 106, 16040–16045.
- Hublin, J.-J., 2009. The origin of Neandertals. *Proc. Natl. Acad. Sci. U. S. A.* 106, 16022–16027.
- Hublin, J.-J., 2012. The earliest modern human colonization of Europe. *Proc. Natl. Acad. Sci.* 109, 13471–13472.
- Hublin, J.-J., 2013. The makers of the early Upper Paleolithic in Western Eurasia. In: Smith, F.H., Ahern, J.C.M. (Eds.), *The Origins of Modern Humans : Biology Reconsidered*, Second ed. Wiley-Blackwell, Hoboken, New Jersey, pp. 223–252.
- Hublin, J.-J., Soressi, M., Bailey, S.E., 2006. Spatial analysis of Human Remains from the Châtelperronian Layers at Arcy-sur-Cure and Saint-Césaire (France). *J. Hum. Evol. abstract for the 2006 Paleoanthropology Society Meetings, April 2006, Puerto Rico*, pp. A98.
- Hublin, J.-J., Spoor, F., Braun, M., Zonneveld, F., Condemi, S., 1996. A late Neandertal associated with Upper Palaeolithic artefacts. *Nature* 381, 224–226.
- Hublin, J.-J., Talamo, S., Julien, M., David, F., Connet, N., Bodu, P., Vandermeersch, B., Richards, M.P., 2012a. Radiocarbon dates from the Grotte du Renne and Saint-Césaire support a Neandertal origin for the Châtelperronian. *Proc. Natl. Acad. Sci.* 109, 18743–18748.
- Hublin, J.-J., Verna, C., Bailey, S., Smith, T., Olejniczak, A.J., Sbihi-Alaoui, F.Z., Zouak, M., 2012b. Dental evidence from the Aterian human populations of Morocco. In: Hublin, J.-J., McPherron, S.P. (Eds.), *Modern Origins: a North African Perspective*. Springer, Dordrecht, pp. 189–204.
- Jacobs, Z., Roberts, R.G., 2007. Advances in optically stimulated luminescence dating of individual grains of quartz from archeological deposits. *Evol. Anthropol. Issues, News, Rev.* 16 (6), 210–223.
- Kaminská, L., Kozłowski, J.K., Svoboda, J.A., 2004. The 2002-2003 excavation in the Dzeravá skala cave, West Slovakia. *Anthropologie* 42, 321–332.
- Kaminská, L., Kozłowski, J.K., Svoboda, J., 2005. Pleistocene Environments and Archaeology of the Dzeravá Skala Cave, Lesser Carpathians, Slovakia. *Polish Academy of Arts and Sciences, Krakow*, p. 226.
- Koumouzelis, M., Ginter, B., Kozłowski, J.K., Pawlikowski, M., Bar-Yosef, O., Albert, R.M., Litynska-Zajac, M., Stworzewicz, E., Wojtal, P., Lipceki, G., Tomek, T., Bochenki, Z.M., Pazdur, A., 2001. The early Upper Palaeolithic in Greece: the excavations in Klisoura cave. *J. Archaeol. Sci.* 28, 515–539.
- Kozłowski, J.K., 1983. *Le Paléolithique supérieur en Pologne. L'Anthropologie* 87, 49–832.
- Kozłowski, J.K., 2002. La Grande Plaine de l'Europe avant le Tardiglaciaire. In: Otte, M., Kozłowski, J. (Eds.), *Préhistoire de la Grande Plaine du Nord de l'Europe. Les Échanges entre l'Est et l'Ouest dans les Sociétés Préhistoriques. ERAUL, Liège*, pp. 53–65.
- Krause, J., Briggs, A.W., Kircher, M., Maricic, T., Zwyns, N., Derevianko, A., Pääbo, S., 2010. A complete mtDNA genome of an early modern human from Kostenki, Russia. *Curr. Biol.* 20, 231–236.
- Kroeber, A.L., 1940. Stimulus diffusion. *Am. Anthropol.* 42, 1–20.
- Kuhn, S.L., 2003. In what sense is the Levantine initial Upper Paleolithic a "transitional" industry? In: Zilhao, J., d'Errico, F. (Eds.), *The Chronology of the Aurignacian and of the Transitional Technocomplexes: Dating, Strategies, Cultural Implications. Instituto Portugues de Arqueologia, Lisbon*, pp. 61–70.
- Kuhn, S.L., Stiner, M.C., Gülec, E., Özer, I., Yilmaz, H., Baykara, I., Açıkkol, A., Goldberg, P., Molina, K.M., Ünay, E., Suata-Alpaslan, F., 2009. The early Upper Paleolithic occupations at Uçağizli cave (Hatay, Turkey). *J. Hum. Evol.* 56, 87–113.
- Kuhn, S.L., Zwyns, N., 2014. Rethinking the initial Upper Paleolithic (in press). *Quat. Int.*
- Laplace, G., 1966. *Recherches sur l'origine et l'évolution des complexes lepéolithiques*. Brocard, Paris.
- Le Brun-Ricalens, F., Bordes, J.-G., Eizenberg, L., 2009. A crossed-glance between southern European and Middle-Near Eastern early Upper Palaeolithic lithic technocomplexes. Existing models, new perspectives. In: Camps, M., Szmíd, C. (Eds.), *The Mediterranean from 50 000 to 25 000 BP: Turning Points and New Directions*. Oxbow Books, Oxford, pp. 11–33.
- Leroi-Gourhan, A., 1958. Etude des restes humains fossiles provenant des grottes d'Arcy-sur-Cure. *Ann. Paléontol.* 44, 87–148.
- Lévêque, F., Vandermeersch, B., 1980. Découverte de restes humains dans un niveau castelperronien à Saint-Césaire (Charente-Maritime). *Comptes-Rendus L'Académie Sci. Paris* 291, 187–189.

- Mallegni, F., Segre-Naldini, E., 1992. A human maxilla (Fossellone 1) and scapula (Fossellone 2) recovered in the Pleistocene layers of the Fossellone Cave, Mt. Circeo, Italy. *Quaternaria Nuova* 11, 211–225.
- Mania, D., Toepfer, V., 1973. Königsaue. Gliederung, Ökologie und Mittelpaläolithische Funde des Letzten Eiszeit. In: Veröffentlichungen des Landesmuseums für Vorgeschichte in Halle, vol. 26. VEB Deutscher Verlag der Wissenschaften.
- Marks, A.E., 1983. Prehistory and Palaeoenvironments in the Central Negev, Israel. SMU Press, Dallas.
- Marom, A., McCullagh, J.S.O., Higham, T.F.G., Sinityn, A.A., Hedges, R.E.M., 2012. Single amino acid radiocarbon dating of Upper Paleolithic modern humans. *Proc. Natl. Acad. Sci.* 109, 6878–6881.
- Martini, F., Lo Vetere, D., Colonese, A.C., De Curtis, O., Di Giuseppe, Z., Locatelli, E., Sala, B., 2007. L'Epigravettiano Finale in Sicilia. In: Martini, F. (Ed.), *L'Italia tra 15000 e 10000 Anni fa. Cosmopolitismo e regionalità nel Tardoglaciale*. Atti Della Tavola rotonda, Firenze 18 Novembre 2005. Museo Fiorentino di Preistoria, Florence, pp. 209–253.
- Mellars, P., 2005. The impossible coincidence: a single-species model for the origins of modern human behavior in Europe. *Evol. Anthropol.* 14, 12–27.
- Mellars, P., 2006. Archeology and the dispersal of modern humans in Europe: deconstructing the Aurignacian. *Evol. Anthropol.* 15, 167–182.
- Metni, M., 1999. A re-examination of a proposed Neandertal maxilla from Ksar' Akil Rock Shelter, Antelias, Lebanon. *Am. J. Phys. Anthropol.* 202 (Suppl. 28).
- Mook, W.G., 1982. Radiocarbon dating. In: Kozłowski, J. (Ed.), *Excavation in the Bacho Kiro Cave (Bulgaria): Final Report*. Państwowe Wydawnictwo Naukowe, Warszawa, p. 168.
- Müller, U.C., Pross, J., Tzedakis, P.C., Gamble, C., Kotthoff, U., Schmiel, G., Wulf, S., Christanis, K., 2011. The role of climate in the spread of modern humans into Europe. *Quat. Sci. Rev.* 30, 273–279.
- Mussi, M., 2001. *Earliest Italy. An Overview of the Italian Paleolithic and Mesolithic*. Kluwer Academic/Plenum Publishers, New York, NY.
- Nigst, P.R., 2012. The Early Upper Palaeolithic of the Middle Danube Region. Leiden University Press, Leiden.
- Nigst, P.R., Haesaerts, P., 2012. L'Aurignacien en Basse Autriche : résultats préliminaires de l'analyse technologique de la couche culturelle 3 de Willendorf II et ses implications pour la chronologie du Paléolithique supérieur ancien en Europe centrale. *L'Anthropologie* 116, 575–608.
- Orschiedt, J., 2000. Head burials from the Ofnet cave, southwest Germany: results of a reexamination. *J. Hum. Evol.* 38, A24–A25.
- Otte, M., Biglari, F., Flas, D., Shidrang, S., Zwyns, N., Mashkour, M., Naderi, R., Mohaseb, A., Hashemi, N., Darvish, J., Radu, V., 2007. The Aurignacian in the Zagros region: new research at Yafteh cave, Lorestan, Iran. *Antiquity* 81, 82–96.
- Otte, M., Shidrang, S., Zwyns, N., Flas, D., 2011. New radiocarbon dates for the Zagros Aurignacian from Yafteh cave, Iran. *J. Hum. Evol.* 61 (3), 340–346.
- Palma di Cesnola, A., 1965. Il paleolitico superiore arcaico (facies uluzziana) della grotta del cavallo, Lecce. *Riv. Sci. Preistoriche* XX, 33–62.
- Palma di Cesnola, A., 1966. Il Paleolitico superiore arcaico (facies uluzziana) della grotta del cavallo, Lecce. *L'uluzziano medio (o evoluto)*. *Riv. sci. Preistoriche* XXI, 3–59.
- Palma di cesnola, A., 1989. L'Uluzzian: Faciès italienne du leptolithique archaïque. *L'Anthropologie* 93, 783–812.
- Palma di Cesnola, A., Messeri, P., 1967. Quatre dents humaines Paléolithiques trouvées dans des cavernes de l'Italie Méridionale. *L'Anthropologie* 71, 249–262.
- Passermard, E., 1944. La caverne d'Isturitz en Pays Basque. In: *Préhistoire*, vol. 9, pp. 1–95.
- Pastors, A., Tafelmaier, Y., 2013. The Middle-Upper Palaeolithic transition at El Castillo (Spain). A re-evaluation of the lithic reduction systems from the Obermaier excavation. In: Pastors, A., Auffermann, B. (Eds.), *Pleistocene Foragers: their Culture and Environment*, pp. 35–50.
- Pelegrin, J., 1995. *Technologie Lithique: Le Châtelperronien de Roc-de-Combe (Lot) et de la Côte (Dordogne)*. CNRS, Paris.
- Peresani, M., 2012. Fifty thousand years of flint knapping and tool shaping across the Mousterian and Uluzzian sequence of Fumane cave. *Quat. Int.* 247, 125–150.
- Peresani, M., 2008. A new cultural frontier for the last Neanderthals: the Uluzzian in Northern Italy. *Curr. Anthropol.* 49, 725–731.
- Pirson, S., Flas, D., Abrams, G., Bonjean, D., Court-Picon, M., Di Monica, K., Draily, C., Dambon, F., Haesaerts, P., Miller, R., Rougier, H., Toussaint, M., Semal, P., 2012. Chronostratigraphic context of the Middle to Upper Palaeolithic transition: recent data from Belgium. *Quat. Int.* 259, 78–94.
- Prat, S., Péan, S.C., Crépin, L., Drucker, D.G., Puaud, S.J., Valladas, H., Lázníčková-Galetová, M., van der Plicht, J., Yanevich, A., 2011. The oldest anatomically modern humans from far Southeast Europe: direct dating, culture and behavior. *PLoS ONE* 6, e20834.
- Proctor, C., Higham, T., Proctor, J., Stringer, C., 2013. The KC4 Maxilla (Kent's Cavern, England) and the age of the arrival of early AMH to Western Europe. In: *Paper Given at the 3rd Annual Meeting of the European Society for the Study of Human Evolution* (Vienna, Austria).
- Prüfer, K., Racimo, F., Patterson, N., Jay, F., Sankararaman, S., Sawyer, S., Heinze, A., Renaud, G., Sudmant, P.H., de Filippo, C., Li, H., Mallick, S., Dannemann, M., Fu, Q., Kircher, M., Kuhlwilm, M., Lachmann, M., Meyer, M., Ongyerth, M., Siebauer, M., Theunert, C., Tandon, A., Moorjani, P., Pickrell, J., Mullikin, J.C., Vohr, S.H., Green, R.E., Hellmann, I., Johnson, P.L.F., Blanche, H., Cann, H., Kitzman, J.O., Shendure, J., Eichler, E.E., Lein, E.S., Bakken, T.E., Golovanova, L.V., Doronichev, V.B., Shunkov, M.V., Derevianko, A.P., Viola, B., Slatkin, M., Reich, D., Kelso, J., Paabo, S., 2014. The complete genome sequence of a Neanderthal from the Altai Mountains. *Nature* 505, 43–49.
- Pyle, D.M., Ricketts, G.D., Margari, V., van Andel, T.H., Sinityn, A.A., Praslov, N.D., Lisitsyn, S., 2006. Wide dispersal and deposition of distal tephra during the Pleistocene 'Campanian Ignimbrite/Y5' eruption, Italy. *Quat. Sci. Rev.* 25, 2713–2728.
- Ramirez Rozzi, F.V., d'Errico, F., Vanhaeren, M., Grootes, P.M., Kerautret, B., Dujardin, V., 2009. Cutmarked human remains bearing Neandertal features and modern human remains associated with the Aurignacian at Les Rois. *J. Anthropol. Sci.* 87, 153–185.
- Rebollo, N.R., Weiner, S., Brock, F., Meignen, L., Goldberg, P., Belfer-Cohen, A., Bar-Yosef, O., Boaretto, E., 2011. New radiocarbon dating of the transition from the Middle to the Upper Paleolithic in Kebara Cave, Israel. *J. Archaeol. Sci.* 38, 2424–2433.
- Reimer, P.J., Bard, E., Bayliss, A., Beck, J.W., Blackwell, P.G., Ramsey, C.B., Buck, C.E., Cheng, H., Edwards, R.L., Friedrich, M., Grootes, P.M., Guilderson, T.P., Hafflidason, H., Hajdas, I., Hatté, C., Heaton, T.J., Hoffmann, D.L., Hogg, A.G., Hughen, K.A., Kaiser, K.F., Kromer, B., Manning, S.W., Niu, M., Reimer, R.W., Richards, D.A., Scott, E.M., Southern, J.R., Staff, R.A., Turney, C.S.M., Van der Plicht, J., 2013. IntCal13 and Marine13 radiocarbon age calibration curves 0–50,000 Years cal BP. *Radiocarbon* 55, 1869–1887.
- Reimer, P.J., Baillie, M.G.L., Bard, E., Bayliss, A., Beck, J.W., Blackwell, P.G., Bronk Ramsey, C., Buck, C.E., Burr, G.S., Edwards, R.L., Friedrich, M., Grootes, P.M., Guilderson, T.P., Hajdas, I., Heaton, T.J., Hogg, A.G., Hogg, K.F., Kaiser, K.F., Kromer, B., McCormac, F.G., Manning, S.W., Reimer, R.W., Richards, D.A., Southon, J.R., Talamo, S., Turney, C.S.M., van der Plicht, J., Weyhenmeyer, C.E., 2009. Intcal09 and Marine09 radiocarbon age calibration curves, 0–50,000 Years Cal BP. *Radiocarbon* 51, 1111–1150.
- Richards, M.P., Pettitt, P.B., Stiner, M.C., Trinkaus, E., 2001. Stable isotope evidence for increasing dietary breadth in the European mid-Upper Paleolithic. *Proc. Natl. Acad. Sci.* 98, 6528–6532.
- Richter, D., Tostevin, G., Škrdl, P., Davies, W., 2009. New radiometric ages for the early Upper Palaeolithic type locality of Brno-Bohunice (Czech Republic): comparison of OSL, IRSL, TL and ¹⁴C dating results. *J. Archaeol. Sci.* 36, 708–720.
- Riel-Salvatore, J., 2009. What Is a 'transitional' industry? The Uluzzian of Southern Italy as a case study. In: Camps, M., Chauhan, P. (Eds.), *Sourcebook of Paleolithic Transitions*. Springer, New York, pp. 377–396.
- Ronchitelli, A., Benazzi, S., Boscato, P., Douka, K., Moroni, A., 2014. Comments on "Human-climate interaction during the Early Upper Paleolithic: testing the hypothesis of an adaptive shift between the Proto-Aurignacian and the Early Aurignacian" by William E. Banks, Francesco d'Errico, João Zilhão. *J. Hum. Evol.* 73, 107–111. <http://dx.doi.org/10.1016/j.jhevol.2013.12.010>.
- Rose, J.I., Usik, V.I., Marks, A.E., Hilbert, Y.H., Galletti, C.S., Parton, A., Geiling, J.M., Cerný, V., Morley, M.W., Roberts, R.G., 2011. The Nubian complex of Dhofar, Oman: an African middle Stone age Industry in southern Arabia. *PLoS ONE* 6, e28239.
- Rougier, H., Milota, S., Rodrigo, R., Gherase, M., Sarcină, L., Molcovan, O., Zilhão, J., Constantin, S., Franciscus, R.G., Zollikofer, C.P.E., de León, M.P., Trinkaus, E., 2007. Peștera cu Oase 2 and the cranial morphology of early modern Europeans. *Proc. Natl. Acad. Sci. U. S. A.* 104, 1165–1170.
- Roussel, M., 2011. Normes et Variations de la Production Lithique durant le Châtelperronien: la séquence de la Grande-Roche-de-la-Plématrie à Quincy (Vienne). *Préhistoire*. Université Paris Ouest Nanterre – La Défense, Paris, p. 566.
- Roussel, M., 2013. Méthodes et rythmes du débitage laminaire au Châtelperronien : comparaison avec le Protoaurignacien. *Comptes Rendus Palevol* 12, 233–241.
- Ruebens, K., 2013. Regional behaviour among late Neanderthal groups in Western Europe: a comparative assessment of late Middle Palaeolithic bifacial tool variability. *J. Hum. Evol.* 65, 341–362.
- Russo, C.M., Tripp, J.A., Douka, K., Higham, T.F.G., 2010. A new radiocarbon pretreatment method for molluscan shell using density fractionation of carbonates in bromoform. *Radiocarbon* 52, 1301–1311.
- Saint-Périer, R., Saint-Périer, S., 1952. La Grotte d'Isturitz III: les Solutréens, les Aurignaciens et les Moustériens. In: Masson (Archives de l'Institut de Paléontologie Humaine, Mémoire 25) (Paris).
- Semal, P., Rougier, H., Crevecoeur, I., Jungels, C., Flas, D., Hauzeur, A., Maureille, B., Germonpré, M., Bocherens, H., Pirson, S., Cammaert, L., De Clerck, N., Hambucken, A., Higham, T., Toussaint, M., van der Plicht, J., 2009. New data on the late Neanderthals: direct dating of the Belgian Spy fossils. *Am. J. Phys. Anthropol.* 138, 421–428.
- Shea, J.J., 2008. Transitions or turnovers? Climatically-forced extinctions of Homo sapiens and Neanderthals in the east Mediterranean Levant. *Quat. Sci. Rev.* 27, 2253–2270.
- Sinityn, A., 2003. A Palaeolithic "Pompeii" at Kostenki, Russia. *Antiquity* 77, 9–14.
- Sirakov, N., Tsanova, T., Sirakova, S., Taneva, S., Krumov, I., Dimitrova, I., Kovatcheva, N., 2007. Un nouveau faciès lamellaire du début du Paléolithique supérieur dans les Balkans. *Paléo* 19, 131–144.
- Škrdl, P., 2003. Comparison of Boker Tachtit and Stranska skala MP/UP transitional industries. *J. Israel Prehist. Soc.* 33, 37–73.
- Soficaru, A., Dobos, A., Trinkaus, E., 2006. Early modern humans from the Peștera Muierii, Baia de Fier, Romania. *Proc. Natl. Acad. Sci. U. S. A.* 103, 17196–17201.
- Soficaru, A., Petrea, C., Dobos, A., Trinkaus, E., 2007. The human Cranium from the Peștera cioclovina Uscata, Romania. *Curr. Anthropol.* 48, 611–619.
- Soressi, M., 2011. Révision taphonomique et techno-typologique des deux ensembles attribués au Châtelperronien de la Roche-à-Pierrot à Saint-Césaire. *Anthropologie* 115, 569–584.
- Soressi, M., McPherron, S.P., Lenoir, M., Dogandžić, T., Goldberg, P., Jacobs, Z., Mairiot, Y., Martisius, N.L., Miller, C.E., Rendu, W., Richards, M., Skinner, M.M.,

- Steele, T.E., Talamo, S., Texier, J.-P., 2013. Neandertals made the first specialized bone tools in Europe. *Proc. Natl. Acad. Sci.* 110, 14186–14190.
- Soressi, M., Rousset, M., 2014. European middle to Upper Paleolithic transitional industries: Châtelperronian. In: Smith, C. (Ed.), *Encyclopedia of Global Archaeology*. Springer, London, pp. 2679–2693.
- Spoor, F., Hublin, J.J., Braun, M., Zonneveld, F., 2003. The bony labyrinth of Neandertals. *J. Hum. Evol.* 44, 141–165.
- Street, M., Terberger, T., Orschiedt, J., 2006. A critical review of the German Paleolithic hominin record. *J. Hum. Evol.* 51, 551–579.
- Stringer, C.B., Hublin, J.-J., Vandermeersch, B., 1984. The origin of anatomically modern humans in Western Europe. In: Smith, F.H., Spencer, F. (Eds.), *The Origins of Modern Humans: a World Survey of the Fossil Evidence*. Alan R. Liss, New York, pp. 51–135.
- Svoboda, J., 2000. The depositional context of the early Upper Paleolithic human fossils from the Koneprusy (Zlatý kun) and Mladeč Caves, Czech Republic. *J. Hum. Evol.* 38, 523–536.
- Svoboda, J.A., Siman, K., 1989. The middle-Upper Paleolithic transition in South-eastern Central Europe (Czechoslovakia and Hungary). *J. World Prehistory* 3, 283–322.
- Szmidt, C.C., Normand, C., Burr, G.S., Hodgins, G.W.L., LaMotta, S., 2010. AMS ¹⁴C dating the Protoaurignacian/Early Aurignacian of Isturitz, France. Implications for Neanderthal-modern human interaction and the timing of technical and cultural innovations in Europe. *J. Archaeol. Sci.* 37, 758–768.
- Talamo, S., Soressi, M., Rousset, M., Richards, M., Hublin, J.-J., 2012. A radiocarbon chronology for the complete Middle to Upper Palaeolithic transitional sequence of Les Cottés (France). *J. Archaeol. Sci.* 39, 175–183.
- Talamo, S., Richards, M.P., 2011. A comparison of bone pretreatment methods for AMS dating of samples >30,000 BP. *Radiocarbon* 53, 443–449.
- Teyssandier, N., 2007. *En Route vers l'Ouest. Les Débuts de l'Aurignacien en Europe*. John and Erica Hedges, Oxford.
- Teyssandier, N., 2008. Revolution or evolution: the emergence of the Upper Paleolithic in Europe. *World Archaeol.* 40, 493–519.
- Thoma, A., 1971. Hungary. In: Oakley, K.P., Campbell, B.G., Molleson, T.I. (Eds.), *Catalogue of Fossil Hominids. Part II: Europe*. Trustees of the British Museum (Natural History), London, pp. 223–229.
- Thomsen, K.J., Murray, A.S., Bøtter-Jensen, L., Kinahan, J., 2007. Determination of burial dose in incompletely bleached fluvial samples using single grains of quartz. *Radiat. Meas.* 42, 370–379.
- Tostevin, G.B., 2003. A Quest for Antecedents: a comparison of the Terminal middle palaeolithic and early Upper Palaeolithic of the Levant. In: Goring-Morris, A.N., Belfer-Cohen, A. (Eds.), *More than Meets the Eye. Studies on Upper Palaeolithic Diversity in the Near East*. Oxbow Books, Oxford, pp. 54–67.
- Trinkaus, E., Churchill, S.E., Ruff, C.B., Vandermeersch, B., 1999. Long bone shaft robusticity and body proportions of the Saint-Césaire 1 Châtelperronian Neandertal. *J. Archaeol. Sci.*, 753–773.
- Trinkaus, E., Moldovan, C., Milota, T., Bîlgăr, A., Sarcina, L., Athreya, S., Bailey, S.E., Rodrigo, R., Mircea, G., Higham, T., Ramsey, C.B., van der Plicht, J., 2003. An early modern human from the Peștera cu Oase, Romania. *Proc. Natl. Acad. Sci. U. S. A.* 100 (20), 11231–11236.
- Tsanova, T., Zwyns, N., Eizenberg, L., Teyssandier, N., Le Brun-Ricalens, F., Otte, M., 2012. Le plus petit dénominateur commun : réflexion sur la variabilité des ensembles lamellaires du Paléolithique supérieur ancien d'Eurasie. Un bilan autour des exemples de Kozarnika (Est des Balkans) et Yafteh (Zagros central). *L'Anthropologie* 116 (4), 469–509.
- Tsanova, T., 2008. *Les débuts du Paléolithique supérieur dans l'Est des Balkans*. Archaeopress, Oxford.
- Tsanova, T., Bordes, J.-G., 2003. Contribution au débat sur l'origine de l'Aurignacien: Principaux résultats d'une étude technologique de l'industrie lithique de la couche 11 de Bacho Kiro. In: Tsonev, T., Montagnari Kokclj, E. (Eds.), *The Humanized Mienral World: Towards Social and Symbolic Evaluation of Prehistoric Technologies in South Eastern Europe*, Proceedings of the ESF Workshop. ERAUL, Sofia, pp. 41–50.
- Vallois, H.V., 1958. Les restes humains d'âge aurignacien de la grotte des Rois, Charente. *Bull. Mém. la Société d'Anthropol. Paris* 9, 138–159.
- Verna, C., Dujardin, V., Trinkaus, E., 2012. The early Aurignacian human remains from La Quina-Aval (France). *J. Hum. Evol.* 62, 605–617.
- Verna, C., Ramirez Rozzi, F.V., d'Errico, F., Lenoble, A., Michel, A., Renou, S., Vanhaeren, M., 2008. New Aurignacian human remains from les Rois (France). In: *Paleoanthropology Society Annual Meeting*. Canada, Vancouver.
- White, M., Pettitt, P., 2012. Ancient Digs and modern Myths: the age and context of the Kent's cavern 4 maxilla and the earliest Homo sapiens specimens in Europe. *Eur. J. Archaeol.* 15, 1–30.
- White, R., Henry-Gambier, D., Normand, C., 2003. Human-tooth ornaments from the French early Aurignacian: implications for early Upper Paleolithic treatment of the dead. In: *PaleoAnthropology 2003*.
- Wild, E.M., Teschler-Nicola, M., Kutschera, W., Steier, P., Trinkaus, E., Wanek, W., 2005. Direct dating of Early Upper Palaeolithic human remains from Mladeč. *Nature* 435, 332–335.
- Wolpoff, M.H., Frayer, D.W., Jelinek, A., 2006. Aurignacian female crania and teeth from the Mladeč Caves, Moravia, Czech Republic. In: Teschler-Nicola, M. (Ed.), *Early Modern Humans at the Moravian Gate: the Mladeč Caves and Their Remains*. Springer, Wien, pp. 273–340.
- Wood, R.E., Douka, K., Boscato, P., Haesaerts, P., Sinitsyn, A., Higham, T.F.G., 2012. Testing the ABOx-SC method: dating known-age charcoals associated with the Campanian Ignimbrite. *Quat. Geochronol.* 9, 16–26.
- Yazbeck, C., 2004. Le Paléolithique du Liban: bilan critique. *Paléorient* 30, 111–126.
- Zeuner, F.E., 1940. *The age of Neanderthal Man with Notes on the Cotte de St. Brelade, Jersey*. C.I. University of London, Institute of Archaeology, London.
- Zilhao, J., d'Errico, F., 1999. The chronology and taphonomy of the earliest Aurignacian and its implications for the understanding of Neanderthal extinction. *J. World Prehistory* 13, 1–68.
- Zwyns, N., 2012. *Laminar Technology and the Onset of the Upper Paleolithic in the Altai, Siberia*. Leiden University Press, Leiden.
- Zwyns, N., Flas, D., 2010. Qu'en est-il à l'est? In: Otte, M. (Ed.), *Les Aurignaciens*. éditions Errance, Paris, pp. 271–295.
- Zwyns, N., Rybin, E., Hublin, J.-J., Derevianko, A., 2012. Burin-core technology & laminar reduction sequence in the initial Upper Paleolithic from Kara-Bom (Gorny-Altai, Siberia). *Quat. Int.* 259, 33–47.