Vindija Cave and The Modern Human Peopling of Europe

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A B S T R A C T

Vindija cave in Croatia has yielded the youngest securely dated Neandertal skeletal remains in Central/Eastern Europe. In addition, these remains have been found in association with archaeological material exhibiting Upper Paleolithic elements. Due to its geographic location and date, the Vindija remains are particularly crucial for the understanding of initial modern human peopling of Europe and the nature of the Neandertal demise. The significance of archaeological and paleontological finds and hominin fossils from this site is discussed in the light of new finds at Vindija and recent developments in the fields of paleoanthropology and prehistoric archaeology. Furthermore, the impact of revised chronology for several crucial specimens and sites throughout Europe, including Vindija, is discussed.

Key words: Vindija cave, modern human origins, Neandertals, human evolution, Upper Paleolithic

Introduction and Brief Site History

The site of Vindija is a large cave, about 50 m in length, 28 m in width, and almost 20 m in height (Figure 1). It is located in the Hrvatsko Zagorje region of Croatia, 9 km northwest of Ivanec and about 20 km west from the center of Varaždin[1] It was first mentioned as a potentially interesting archaeological site by D. Hirc[2]. Initial archaeological excavations were conducted by S. Vuković[3–5] starting in 1928, but it was not until the mid-1970s that large-scale excavations started under the direction of M. Malez[1,6]. It was under his direction that the majority of the paleontological, archaeological, as well as the entire hominin sample was unearthed between 1974 and 1986[7–9]. Since then, several additional hominin fossils have been identified[10–12], and the archaeological and faunal assemblage has been a subject of detailed analyses[12–18].

The stratigraphic sequence of the site is complex, consisting of over 12 m of deposits, divided into 13 basic stratigraphic units (A–M). Complexes F, G and K are further subdivided into Fg, Fs, Fd, Fd/d, G_1 to G_5, and K_1 to K_3 layers[12,19,20]. Units A to D are Holocene, while units D to M yielded material dated to the Pleistocene (Figure 2).

Faunal and sedimentological analysis suggests that the climate during the formation of complex G (OIS 3) was variable but at times similar to the recent one, while the younger complex E/F (OIS 2) was deposited under somewhat cooler climatic conditions. Of major interest for the modern human origins debate in Europe is the material from complex G. This stratigraphic unit yielded most of the Neandertal bones from the site. The archaeological assemblage is quite complex. While the tools from G_3 are attributed to the Mousterian with some Upper Paleolithic elements present, the G_1 assemblage provides a more complicated picture[12,15]. It is in this layer that a Neandertal mandible (Vi-207) was found in association with Aurignacian or Aurignacian like split base bone point (Vi-3437) (Figure 3). Additionally, three massive-base bone points (so-called Mladeč type) were found in the same layer. Such bone points are distinctly Upper Paleolithic tools. The stone tool assemblage from G_1 exhibits a mixture of Mousterian and Upper Paleolithic types[15] (Figure 4). One well-made bifacial stone point made from non-local raw material shows similarities to material from Hungary usually attributed to the Szele-

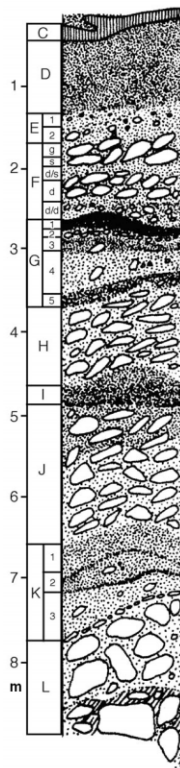*Fig. 1: Vindija cave (photo: I. Karavanić).*

Fig. 2: Stratigraphic profile of the Vindija Cave (modified after Rukavina 1983).

tian industry (Figure 4; 4). Whether the archaeological material from G_1 represents the Aurignacian or some other variant of the initial Upper Paleolithic, as a »transitional« industry (e.g. Szeletian), or the late Mousterian with Upper Paleolithic components remains uncertain[15,21–23]. Complex F has yielded archaeological material attributable to the Aurignacian *sensu lato* (layer Fd/d) and Epigravettian (layers Fd/s, Fs, and Fg), while

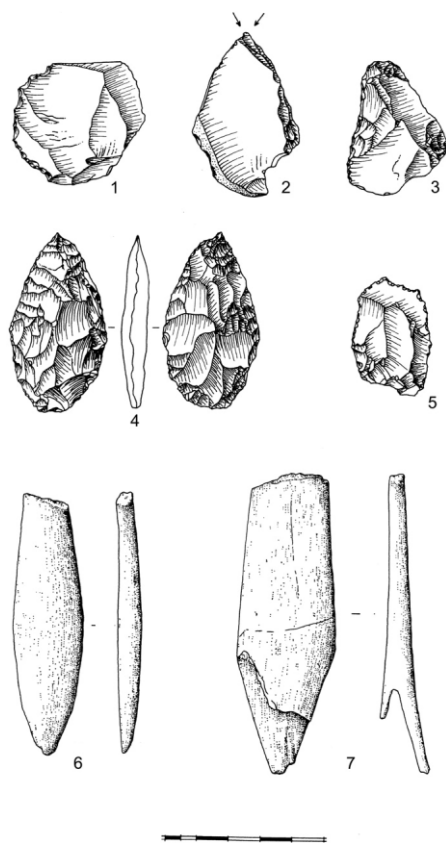*Fig. 3: Split-base bone point Vi 3437 and hominin mandible Vi 207.*

Fig. 4: Selected artefacts from Vindija level G1: 1. probable a pseudo- tool (previously published as denticulated piece), 2. burin. 3. sidescraper. 4. leaf-shaped bifacial piece, 5. flake with marginal retouch on distal end (previously published as an endscraper on flake), 6. massive base bone point, split base bone points. (Modified after Karavanić 1995: Fig. 3; Drawing by Marta Perkić.

the E layer is Epigravettian[12–14]. In layer D, modern human (*Homo sapiens sapiens*) skeletal material has been found alongside material attributed to the Epigravettian. The majority of the anatomically modern human sample comes from this layer, although the inscriptions on several fragments suggests that they were found near the border with the E sequence, and a few fragments might belong to the Holocene layer B. In this paper, we will concentrate on the finds from complex G, as those are crucial to the »Neandertal question« and the modern human peopling of Europe.

Vindija Faunal Sample

During the Upper Pleistocene, Vindija cave was situated on the southern edge of the Alpine ice sheet, which at the times of the glacial maximum covered the Alps. However, Vindija also lies near the edge of the Pannonian Plain, which explains the steppe elements in the classical forest faunal community during the OIS 2 and 3. As majority of the Vindija finds are faunal, the zooarchaeological sample from this site has been studied at numerous
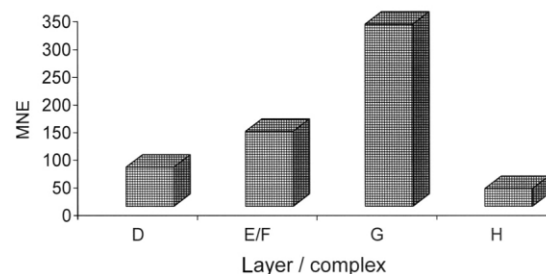

Fig. 5: Accumulated fossil remains of ungulata in taphodermes of layers/complexes D, E/F, G, and H.

times[19,20,24–26]. With a better understanding of taphonomy of the site and more detailed studies of specific taxa, new patterns emerged.

A recent revision of the ungulate fauna removes *Coelodonta antiquitatis* (woolly rhino), *Saiga tatarica* (saiga antelope), and *Equus* cf. *germanicus* from D, E/F, and G complexes at Vindija[18]. The presence of the first two taxa was considered to be evidence of extremely cold paleoclimatic conditions, while the equid was considered indicative of open, steppe environments during the period in which these complexes were deposited[19]. *Rangifer tarandus* (reindeer) is representative of the tundra zones and more open parts of the taiga. Fossil remains of reindeer were reported to be present in complexes D, E, F, and G[19], but now we know that only a few skeletal remains (MNE 5) were accumulated in complexes E/F and G. On the other hand, our recent revision has added *Capreolus caprolus* (roe deer) to the faunal lists of the E/F and G complexes. Results have shown that the abundance of ungulate remains is highest in complex G (Figure 5). The revised faunal associations better accord with the palaeoclimatic reconstructions based on sedimentological characteristics[27] and paleovegetation[28]. Results of this new revision of the Vindija faunal assemblage call into question the previous reconstruction of alternating »cold« and »warm« faunal communities during the deposition of the E, F and G complexes.

The Vindija ungulate assemblage has undergone a complex taphonomic history. Traces of animal modification (e.g. gnaw marks) point to the activities of small-sized carnivores (e.g. fox and marten) and rodents. Of the larger-sized carnivores, *Ursus spelaeus* (cave bear) is ubiquitous throughout the Vindija sequence, and it is the only large carnivore present in the lowest strata of complex G[19]. Cave bears probably occupied the cave for hibernation[17]. The other larger-sized carnivores are *Panthera spelaea* (cave lion) and *Canis lupus* (wolf); both are present in the assemblages of complexes D, E, F and G. There are only rare gnaw marks, most probably from wolf, on the ungulate remains, and these appear to have been made on bone refuse left by the hominins. In contrast, our new taphonomic analyses have produced widespread evidence of hominin selection and modification (e.g. body part selection, breakage patterns, butchery marks). This shows that hominins were the most important accumulators of the ungulate assemblage.

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Chronometric Dating and the Early Modern Human Sequence in Europe

The significance of establishing a reliable chronological framework in human evolutionary studies cannot be overemphasized, and improvement in dating techniques and redating of a number of finds has led to major reevaluations of both data and interpretations concerning modern human origins[29]. Recently, several key fossils have been redated by more precise methods. This led to exclusion of several specimens previously held to be among the earliest modern humans in Europe from the debate (e.g., Vogelherd and Velika Pećina, now dated to the Neolithic[30,31]). As the Vindija Neandertal remains are crucial to the debate, dating of various stratigraphic layers of this site has been attempted several times, but not without problems[32]. Neandertal remains from later G_1 were directly dated by AMS and yielded a date of 28–29 kya, thus making them the youngest Neandertals in the region[30]. Recently, the new technique of ultrafiltration of collagen samples has been applied and the same G_1 fossils have been redated to 32–33 000 ^{14}C years ago[33]. Until the same methods are applied to other crucial specimens of approximately same time period (both late Neandertals and early anatomically modern humans in the region) it is impossible to create the much needed timeframe of overlap of these two populations in Europe. The main problem with radiocarbon dating is a high error margin for material older than about 30 kya. Newer techniques, such as AMS, ultrafiltration, etc., add to the accuracy of dating and make these methods less destructive[34]. However when the time of overlap is expected to be several thousand years at best, the error margin is still unacceptably high. Further, many specimens from this crucial time period (e.g. Mladeč, Kostenki, etc.) are likely to be older than reported[35,36]. Therefore, the redating of the Vindija specimens does not necessarily widen the temporal gap between indigenous European Neandertals and anatomically modern newcomers.

At present, and based on the radiocarbon dates of the finds, candidates for the oldest anatomically modern human remains from Europe are those from Kent's Cavern, England, Brassempouy and La Quina in France, Kostenki in Russia, Oase, Cioclovina and Baia de Fier in Romania, and Mladeč in Czech Republic. However, there are problems with all of these sites. Kent's Cavern 4 is a human maxillary fragment found in 1927 in a large cave system near Torquay, England[37]. It was found below the layer containing what was described as »Aurignacoid« industry[22,38–40], making the association of archeological industry and human fossil questionable. The fossil was directly dated to around 31 kya[40,41], but it may be as old as 35–37 kya[42]. Although this specimen was described as modern in morphology, the fragmentary state makes this assesment uncertain[36] and new analyses are still in progress. The exact nature of the »Aurignacoid« industry also needs to be subjected to careful re-analysis. Several isolated teeth and phalanges found at Brassempouy in France yielded dates between 30000 and 33500 years ago[43]. As is the case with Kent's Cavern finds, the archae-

ological industry of this site needs serious reexamination before it can be confirmed as Aurignacian *sensu stricto*. An additional problem is that the metric values of the human fossils fall both within modern human and Neandertal ranges[43] contra [44]. La Quina 25 is stratigraphically associated with the radiocarbon date of around 32 kya[45], and not directly dated. Further, the specimen is juvenile which always presents an additional problem in taxonomic assesments. The Kostenki 1 specimen has recently been directly dated to around 32 kya[46], but a detailed morphological analysis is still unpublished.

Recently, human fossils from several Romanian sites have been directly dated[47]. A skull, tibia and scapula from the Woman's cave (Baia de Fier) were found in 1952 and the postcranial remains have been dated to around 30 kya[48]. The archaeological finds from the site have been described as Mousterian, while the upper layers contain some type of Upper Paleolithic industry. As the layers in the cave are mixed, the association of archaeological industries, as well as various human fossil elements are unclear. The skull from Cioclovina cave, most likely male[49] is now dated to around 29 kya[50] has been described by Rainer and Simionescu[51] as »*Homo sapiens fosillis*…with Neanderthalian characters«, and although it is morphologically modern in overall gestalt, its supraorbital region is very robust and there is bunning on the occipital bone[22,36,49]. Cranial and postcranial remains from Pestera Muierii[48] are approximately 30 000 years old[50], but not associated with archaeological industry. The most recent finds come from Pestera cu Oase in Romania and are dated to arround 35 kya[52,53]. These were also not found in association with archaeological material. Trinkaus and colleagues[52,53] note the presence of several archaic features on these otherwise anatomically modern specimens (e.g. pronounced juxtamastoid eminence on Oase 3, robust and laterally oriented zygomatic bones and large molars in Oase 2). At least one feature (lingual bridging of the mandibular foramen present on the left ramus of Oase 1 mandible) is unknown in modern humans predating Oase remains but is common in Neandertals and some of the later modern humans in Europe[52–53]. No archaeological industry was found at this important site, limiting our knowledge of these earliest anatomically modern humans in Europe to their anatomical features.

New direct dating of the human remains from Mladeč (Lautsch) in Moravia, Czech Republic[54] suggests an age of around 31 kya for these anatomically modern humans[55]. Although the association with Aurignacian lithics was previously suggested, the exact nature of the deposition at the site is uncertain[22] and while Mladeč type bone points were found, the lithic material is scarce, and the split base bone points that are common in other Aurignacian-like industries of the earliest Central/Eastern European Upper Paleolithic are absent[22]. Therefore, the question of whether these tools represent an early Aurignacian-like (transitional) industry, or later Aurignacian *sensu stricto*, remains open. In addition, as in Oase sample, several archaic features are seen in some of

the Mladeč specimens. These include occipital bunning in Mladeč 3, 5 and 6, and robust supraorbital regions in Mladeč 5 and 6, as well as large palatal and dental dimensions and some other anatomical details in the sample[22,49,55–64], all features that are common in earlier Neandertal populations.

Industries of the Earliest Upper Paleolithic of Europe

If we use the traditional approach based primarily on typology and technology in order to define Middle (Mousterian and its variants) vs. Upper Paleolithic industries in Europe, we face the problem of several so-called 'transitional' industries. These include the Châtelperronian of France and northern Spain, Szeletian and Jankovichian of central and parts of eastern Europe, Uluzzian of Italy (Tuscany, Calabria, southern Adriatic part, Uluzzo Bay, etc.), Streletskian of eastern Europe, Jerzmanowician of eastern Germany and Poland, Althmülian of southern Germany, Bohunician of Czech Republic, Brynzeny and Kostenki Szeletian of Russia and several other unnamed or site-specific assemblages from Poland, Slovakia, Czech Republic, Romania, etc. in which various elements of Mousterian appear alongside the Upper Paleolithic types or types produced using technology commonly associated with the Upper Paleolithic. All these industries seem to have their origin in local Mousterian variants and no abrupt change can be seen[22,65–97]. Except for documented associations of Neandertal remains and Châtelperronian artifacts from La Roche à Pierrot at St. Cesaire and Grotte du Renne at Arcy-sur-Cure[98–101] there are no diagnostic hominin fossils associated with any of these earliest Upper Paleolithic finds[22,102–103]. Thus, even if we accept the earliest Aurignacian as a single industrial complex that has its origins outside this area[104] (both of these premises being far from proven) and attribute it to anatomically modern newcomers (for which there are no known hominin/industrial associations) we are left with the problem of who is responsible for these pre-Aurignacian assemblages.

Typological thinking is responsible for the acceptance of the Aurignacian as a single widespread complex commonly associated with the spread of morphologically modern humans into Europe[21,22]. We believe that, in light of the currently available evidence (or the lack thereof) this view should be carefully reexamined. Simplification of this model can be summarized as follows:

As more and more studies[66–70,73,75,76,78,81,82,105] show that the earliest Upper Paleolithic (»transitional«) industries in Europe develop within the local framework from (and including various elements of) the Mousterian complex, the earliest distinctly Upper Paleolithic industry associated with anatomically modern humans should be Aurignacian, brought here as they move into the region[106]. Here authors vary in opinion on whether and how much influence modern newcomers and their culture had on the technological/behavioral change of late Neandertals. Thus, in this model, the Aurignacian is re-

garded as a single imported complex that can be recognized in the archaeological record by the appearance of certain tool types and automatically assigned to anatomically modern populations.

While this sounds simple enough, it is not. First, detailed archaeological studies show that several tool types (especially bone tools) used as indicative of Aurignacian are in fact commonly found in various aforementioned »transitional« industries[21,67,89,95,107,108]. Further, the Early Aurignacian differs from the Late Aurignacian[21]. Finally, there are great differences between assemblages of typical Aurignacian from Western Europe, and that of Central/Eastern Europe[15,21,90,108].

All this makes it clear that there may be a different pattern of behavioral, and most likely, populational change in Western vs. Central/Eastern Europe. This is in agreement with several anatomical studies[49,57,109]. While this transition (whatever the mode of it) was more abrupt in Western Europe, evidence suggests a more gradual pattern for Central and Eastern areas of this region. Therefore, we believe it is quite likely that some Neandertal populations had a significant role in the formation of early modern European gene pool (via assimilation into anatomically more modern populations), while other Neandertal groups had none.

As in the case of the initial Upper Paleolithic (aka »transitional«) industries, except for the Châtelperronian, makers of the earliest Aurignacian *sensu lato* are unknown as there is no clear association of diagnostic hominin and archaeological material. Although a new study and dating of an interstratified sequence of Châtelperronian and supposed Aurignacian suggests coexistence of these industries at least in some sites[110], determination of this industry as Aurignacian should be reexamined. As mentioned, tool types indicative of Aurignacian commonly appear in other transitional industries of Central Europe. Again, no association of human bones was found in these layers, therefore all we can say is that there are two contemporaneous yet somewhat different cultural traditions present at the site. One of these is known to be associated with late Neandertals.

One more point concerning the appearance of the Aurignacian should be mentioned. Although its origins were commonly seen in the Middle Eastern assemblages of anatomically modern humans, some authors trace its initial rise in several independent centers in Europe[111]. This explanation makes more sense if the Aurignacian is not a single widespread complex but actually represents different Early Upper Paleolithic assemblages that share several tool types (previously considered to be indicative of a single industrial complex). In this light there is no need to see these industries as a product of a single population. This also raises possibilities of different explanations for shared similarities (trade, influence, population mixing, etc). However, we should bear in mind that population contacts differ in their pattern. Interbreeding and peaceful coexistence, trade, etc., might dominate some of these interactions, while in others patterns of contact might differ. Therefore, models based on data from Western Europe should not be used for Central/Eastern Europe.

The Middle to Upper Paleolithic Transition at Vindija and its Significance for the Modern Human-Peopling of Europe

Vindija Cave has an important place in the understanding of the initial anatomically modern human peopling of Europe. The significance of the association of Neandertal remains with an Upper Paleolithic industry has been a subject of a considerable debate[15,80,112–114], as it has been argued that the association is in fact artificial and the result of the cryoturbation that has been noted in some parts of the cave. A partial Neandertal mandible (Vi-207) found in direct association with the characteristic Upper Paleolithic tool type (a split-based bone point, Vi-3437) adds to the complexity of the picture. We contend that the arguments presented in favor of artificial mixing of these are weakened by careful consideration of data.

It is true that the excavations at Vindija, in many ways, followed techniques that had already been abandoned in Paleolithic archaeology at that time in most of Europe (especially in France where the past mistakes of numerous excavations during the early part of the 20th century led to deeper understanding of the importance of careful and detailed collecting and documenting of finds and features). However, such arguments can only go so far. Practice of selective collecting of »more important« or bigger and diagnostic finds of recognizable importance does not automatically cast a shadow on all of the data. While important data was lost, resulting from non-collecting or selective collecting of items (such as debitage or smaller non-diagnostic fragmentary bones etc), the majority of recognizable tools, bones, bigger pieces of debitage etc. were collected and recorded according to stratigraphic units.

Cryoturbation, while present at the site[115], has not been noted for the part of the cave where the associated mandible and bone point have been found[8,12,15,112]. Further, G_1 consists of characteristic reddish clay, easily recognizable and distinct from both upper and lower parts of the sequence. This reddish clay was embedded in both

Vi-207 mandible and the Vi-3437 bone point and can still be observed on another massive bone point from this stratigraphic layer. In a recent paper, Ahern and colleagues[12] reported additional Neandertal remains, one of which (a proximal radial shaft Vi 13.8) has embedded reddish clay sediment that is characteristic of layer G_1. Neandertal attribution of this specimen[12] is suggested by the strong curvature of the shaft and the medial orientation of radial tuberosity[116,117]. The presence of further Neandertal specimens from layer G_1 additionally disproves the claim for artificial mixing of layers and arguments against the Neandertal association with the G_1 Upper Paleolithic industry.

There is an interesting pattern when we compare archaeological assemblages of various Vindija layers. In older layers (unit K) typical Mousterian tools predominate and there is a clear evidence of the use of Levallois technology that is common in most European Mousterian assemblages. The most abundant raw material in unit K is local quartz[16,118], and flake technology predominates in tool production. Level G_3 presents a mixture of typical Mousterian tools, such as sidescrapers, but there are also Upper Paleolithic types of stone tools (such as endscrapers), and alongside flake technology, bifacial and blade technology was used in production of tools from this layer. It is important to note that no evidence of Levallois technology is seen in layer G_3 of Vindija[15]. There is also evidence of more selective use of raw material, as there are more tools on chert in this layer[12,16,118].

The level G_1 assemblage shows an even more pronounced shift towards the use of higher quality raw material (i.e., chert) compared to the older layers of the site, and there are no tools made on quartz[12,16,118]. Upper Paleolithic elements in stone tools are more abundant than in layer G_3, and bone points from G_1 layer represent a new distinctly Upper Paleolithic element that is not seen in any of the older layers[13–15].

At several Slovenian sites, such as Divje Babe I and Mokriška Jama, bone tools similar to those of Vindija have also been found[119–120]. Similarly »Aurignacian« as-
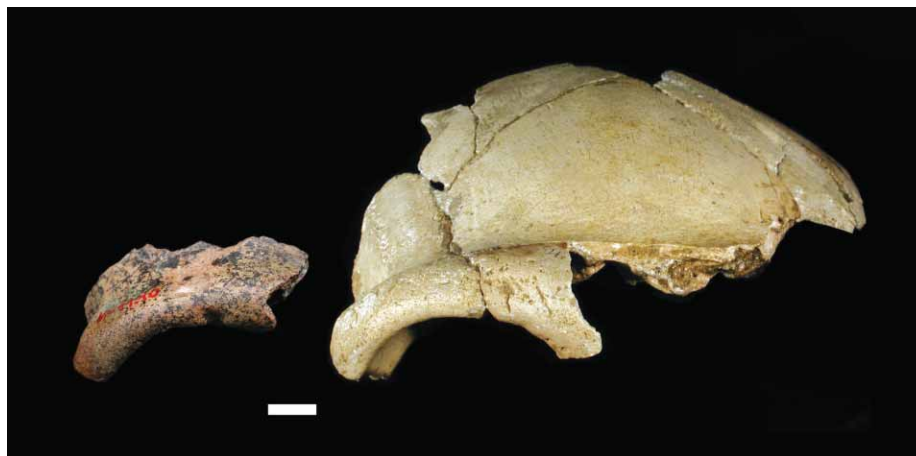

Fig. 6: Comparison of Vindija 202 (left) and Krapina 4 (right) frontal bones (photo: J.C.M. Ahern).

semblage of Potočka Zijalka also differs in pattern from the »classical Aurignacian« assemblages[120]. In fact, this assemblage was previously referred to as Olschewian[121].

All hominins from the Vindija G complex can be recognized as a part of Neandertal populations on the basis of their overall gestalt. However, most of the commonly noted »Neandertal features« (for a detailed list see[64,122–129] and references therein) do not represent autapomorphies, but are instead either plesiomorphic characters inherited from preceding archaic hominins or shared with contemporary and/or post-Neandertal populations[60]. It is clear that there are many temporal and geographic differences. Several studies have shown that later Neandertals differ in morphological details from earlier »classic« members of this population, for instance in the reduction of facial dimensions and projection[8,9,12,49,56,130–131] as well as in other details of their anatomy. This is true for the Vindija G_1 Neandertals, as shown by several studies, especially on the supraorbital and mandibular material[56,130,132]. Analyses reveal the intermediate position of the Vindija supraorbitals, both in projection and shape compared to the older Krapina sample (Figure 6). The Vindija supraorbital tori have relatively greater degrees of pinching above the orbits compared to the earlier Neandertals[49,130,133,134]. Recent study of a newly reconstructed partial cranial vault from G_3 level comprised of supraorbital and frontal fragments (Vi 284, Vi 230, Vi 255, Vi 256) again suggests anatomical change in the direction of anatomically more modern morphology[12]. Change in the direction toward a more modern human pattern is also seen in the Vindija mandibular sample, suggesting facial reduction, and the Vindija mandibles have more vertical symphyses than earlier Neandertals and exhibit incipient eminences, though not a true modern human chin[133,135–136]. Observed gracility and change in shape is not due to body size[109] or age and/or sex bias in the sample[12,131,132,136] and could suggest gene exchange with anatomically modern populations. »Neandertal« traits are not present in earlier anatomically modern humans (samples predating 40 kya from Africa and Asia) that are the likely ancestors of Upper Paleolithic populations that came to Europe. Thus, the appearance of several »Neandertal« traits in the youngest modern groups in Europe (such as Mladeč or Predmostí)[49,56,60,63,137,138] and the later Gravettian child from Lagar Velho[139] is easily explained by interbreeding and best fit within the framework of the Assimilation model of modern human origins[36,57–58].

The Impact of Molecular Data on the Modern Human Origins Debate

After the field of genetics entered the modern human origins debate with the initial claims for exclusively African origins[140], several authors emphasized that the results could be explained in different ways[141–145]. Moreover, mtDNA results do not seem to be in agreement with results obtained from other parts of genome[146,147]. Newer analyses of mtDNA isolated directly from Neandertal bones added another dimension to the debate[148–152]. Although these sequences are different from those of living humans, various processes (e.g. bottlenecks, selection, drift, populational expansions etc.) could cloud our insight into the past events. Among these specimens, several Vindija fossils were included[151–152] and were reported to fall outside both contemporary modern human, as well as Upper Paleolithic hominid ranges. However, ancient DNA was extracted from Vindija fossils that are both undiagnostic and of uncertain context (Vi 77, Vi 80, Vi 75). While a more meaningful insight into the question of whether or not Neandertals and anatomically modern humans interbred could be provided by extraction of DNA from the earliest modern humans in Europe[152], alas, problems with extraction and contamination of ancient DNA, as well as with the small size of the available fossil sample of these crucial specimens makes it impossible to answer this question solely based on genetic evidence. In sum, some amount of interbreeding between these two late Pleistocene populations cannot be excluded and distinction of Neandertals at the species level is refuted by the current evidence[58,141–143,147,148,151,152,154]. Any molecular analysis dealing with the question of Neandertal and anatomically modern human interaction must take into account the complex pattern of population movements, population size, bottlenecks, etc. Even then, known problems such as small sample size and difficulties with extraction and contamination of DNA would make such analyses questionable. Until these questions are answered, the genetic picture drawn from both ancient DNA studies, as well as of models based on contemporary modern human genetic research allows for different explanations and should not be taken as a proof that no interbreeding between these populations took place.

Conclusion

Vindija cave in Croatia has yielded the youngest securely dated Neandertal skeletal remains in Central/Eastern Europe. In addition, these remains have been found in association with archaeological material exhibiting Upper Paleolithic elements. Due to its geographic location and date, the Vindija remains are particularly crucial for the understanding of the initial modern human peopling of Europe and the nature of the Neandertal demise. We argue that the association of an early Upper Paleolithic industry with late Neandertals at Vindija is not likely to be a result of artificial mixing of specimens from different strata, but rather that these artifacts are reasonably considered to be products of the Vindija Neandertals. Although similar archaeological samples in Europe have traditionally been regarded as Aurignacian and automatically assigned to anatomically modern humans, we believe that many of earliest Upper Paleolithic assemblages are in fact derived from the local Mousterian, and the question of which population is responsible for the production of these assemblages remains open.

The so-called transitional industries such as Uluzzian of Italy and Szeletian of Hungary and adjacent areas were quite likely a product of local Neandertal groups, as they have their origin in preceeding local Mousterian. In Europe at least, only Neandertals have been associated with Mousterian assemblages. Likewise, the only clear association of hominin remains and the Initial Upper Paleolithic thus far has been Neandertals with the Châtelperronian (at Arcy-sur-Cure and St. Cesaire[98,100]). Although it can be argued that the anatomically modern newcomers are the likely producers of the earlier distinctly Upper Paleolithic industry of Europe (later Aurignacian, or Aurignacian *sensu stricto*), this still remains to be proven. However if, as we argue, Aurignacian should no longer be considered a single Pan-European industrial complex, but rather represents a number of local early Upper Paleolithic assemblages, the association of Neandertals and Early Upper Paleolithic is not so surprising.

The Upper Paleolithic industry at Vindija is not Aurignacian *sensu stricto*, but one of many »transitional« industry assemblages. This suggestion is supported by the presence of significant Mousterian types, one bifacial stone point typical of Szeletian, as well by significant differences in the assemblage compared to Western European sites[21,90,112,155]. While we cannot equal industry with biological populations, the simplest explanation would be that late Neandertals developed at least some of these »transitional« industries. Further, we should reexamine the Aurignacian sequence at various sites, especially in Central and Eastern Europe, and try to detect whether these are in fact Aurignacian *sensu stricto*, or another »transitional« industry. If the later proves to be the case, the association of the split-base bone point (and therefore the Upper Paleolithic sequence) and late Neandertals at Vindija should not come as a surprise at all.

The first modern people to come to Europe might have been small groups and it is unclear how much they contributed to the later modern human groups (e.g. Gravettians etc.). Therefore we must bear in mind that it is not only the issue of Neandertal genetic contribution to the initial anatomically modern newcomers, but also the relation of these first groups to the later modern humans that needs to be taken into account. Unfortunately the relatively short time frame of the populational overlap between late Neandertals and early moderns, possible differential site use, and numerous factors, including sedimentation rates, preservation of the sediment which is erroding more quickly than forming differences in site use, etc., will result in rare preservation of such evidence.

Therefore, the Vindija G_1 layer is a rare and important find. Anthropological analyses demonstrate that the late Neandertals at Vindija exhibit a more modern pattern of morphology compared to most other European Neandertals. We believe that both the anatomical and archaeological characteristics of Vindija are best explained by the Assimilation model of modern human origins.

The studies on the Vindija cave anthropological, archaeological and paleontological material is by no means over. New dating, DNA and various other skeletal analyses, as well as the recently published newly recognized hominids allow for a better insight into the human evolutionary past. There are many questions still to be answered and still more to be created by these answers. No doubt the material from the Vindija Cave will have a crucial part in answering some of them.

Acknowledgements

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ŠPILJA VINDIJA I DOLAZAK ANATOMSKI MODERNIH LJUDI NA PROSTORE EUROPE

SAŽETAK

U gornjopleistocenskim sedimentima špilje Vindije u SZ Hrvatskoj, u vertikalnoj sukcesiji s ostacima modernih ljudi, nađeni su ostaci najmlađih neandertalaca središnje i istočne Europe. Sedimentološki, paleontološki i arheološki sadržaji u autohtonim su startigrafskim relacijama s ostacima hominida, što Vindiju određuje kao ključno nalazište, koje se već nekoliko desetljeća interdisciplinarno istražuje. U potrazi za rasvjetljavanjem interakcije i sukcesije neandertalskih i modernih hominidnih populacija, dosadašnje spoznaje prezentirane su u svjetlu suvremenih saznanja i teorijskih pomaka. Izneseni su novi podaci o faunskim asocijacijama pojedinih stratigrafskih članova koji mijenjaju ranije spoznaje o prehrambenim resursima paleolitskih lovaca Vindije. Naglašen je značaj novih kronoloških podataka u repozicioniranju nekih ključnih gornjopleistocenskih nalaza i nalazišta Europe.