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1 **First direct dating of the Late Neanderthal remains from Subalyuk Cave in Northern**  
2 **Hungary**

3  
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21

22 With 6 figures and 1 table

23

24 **Summary**

25 The Subalyuk hominin remains were uncovered in 1932 in a cave of the same name in the  
26 Bükk Mountains, near the village of Cserépfalu in Borsod-Abaúj-Zemplén county, Northern  
27 Hungary. The remains represent two individuals, an adult and a young child who have been  
28 described in a few publications since their discovery, providing substantial anthropological  
29 data and general assessments of their Neanderthal affiliation. They were associated with Late  
30 Mousterian industry. Thus, the Bükk Mountains gain importance in the discussion concerning  
31 the contribution of East Central European sites to the debate on the peopling history of Europe  
32 during the Late Middle to Early Upper Palaeolithic transition. In this paper, we summarize the  
33 archaeological and chronological context of the two individuals, and publish the first direct  
34 dating results that place them among the Last Neanderthals of Central Europe.

35

36 **Keywords:** Neanderthal, Central Europe, Middle-Upper Palaeolithic transition, Subalyuk, <sup>14</sup>C  
37 dating

38

## 1 **Introduction**

2 In Central Europe, 25 sites yielded Neanderthal remains, 13 in the western part and 12 in the  
3 eastern part. However, we only possess direct dating from three sites: Kleine Feldhofer Cave  
4 in Germany, Vindija Cave in Croatia, and Šaľa in Slovakia (Ahern et al. 2013, Kuzmin &  
5 Keats 2014, Hopkins et al. 2022). After the well-known Krapina site in Croatia with the  
6 richest material representing at least 89 individuals, Subalyuk Cave in Hungary has yielded  
7 the most important Neanderthal fossils from East Central Europe (Ahern et al. 2013),  
8 including the cranial and postcranial remains of an adult and a child (Bartucz 1940). The cave  
9 is located near the village of Cserépfalu (Borsod-Abaúj-Zemplén County) in the Bükk  
10 Mountains of northeastern Hungary (**Fig. 1**), and was fully excavated by János Dancza and  
11 Ottokár Kadić in 1932. In addition to hominin remains (**Fig. 2**), a long sequence of human  
12 occupations with rich Middle Palaeolithic lithic assemblages, associated with Upper  
13 Pleistocene vertebrate fauna was unearthed (Bartucz et al. 1940).

14 Since the first description by Bartucz (1940), the Subalyuk hominin remains have been the  
15 subject of a few anthropological studies (Thoma 1963, Pap et al. 1995, 1996, Coqueugniot et  
16 al. 2014), and palaeopathological examinations were also carried out (Minnikin et al. 2020,  
17 Pálfi et al. 2020). From a taxonomic point of view, the hominin fossils were generally  
18 considered to be Neanderthals with no exact chronology available. Based on stratigraphic and  
19 palaeontological considerations, it has been estimated to the Lower Weichselian (Jánossy  
20 1986, Vörös 2000) or to the Lower Pleniglacial (MIS 4; Kordos & Ringer 1991, Ringer  
21 2002). Attempts to reassess the archaeological context and bone preservation (Mester 1989,  
22 1990, 2004, Mester & Patou-Mathis 2016) have provided an abundance of new information  
23 that shed light on the current issues regarding uncertainties about the conditions of the  
24 hominin fossils and their relative age estimates.

25 In the frame of the ongoing anthropological research project, the first direct radiometric  
26 dating has been performed on both Subalyuk 1 and 2 hominins (curated in the Hungarian  
27 Natural History Museum, Department of Anthropology). In this paper, we publish the dating  
28 results that place both individuals among the Late Neanderthals of Central Europe, and we  
29 summarize the archaeological and chronological context of the Subalyuk hominins.

## 31 **Archaeological context and relative chronology**

32 Subalyuk Cave is the most important Middle Palaeolithic site of Hungary (Gábori 1976). Its  
33 stratigraphic sequence was subdivided into 18 geological layers numbered from bottom to top  
34 (Kadić 1940) (**Fig. 3**). The whole sequence represents the Upper Pleistocene. Layer 1 can be  
35 attributed to the Last Interglacial (MIS 5e) by its plastic clayey sediment as well as its  
36 reconstructed warm and wet climate, and layer 17 represents the Last Glacial Maximum (MIS  
37 2) by the presence of wolverine (*Gulo gulo*), while layer 18 is the Holocene soil (Jánossy  
38 1986, Mester & Patou-Mathis 2016). Archaeological material was recorded from layers 1 to  
39 14, documenting different animal and human occupations, while all hominin remains were  
40 found in layer 11 (Bartucz et al. 1940, Mester & Patou-Mathis 2016). The hominin skeletal  
41 elements representing the two individuals were discovered within one week at different  
42 locations near the entrance of the cave on a 5 m × 5 m surface in a depth of 2–3 m (Bartucz  
43 1940, Mester 2004). Only those of the child were gathered together but not in articulation,  
44 while the adult remains were scattered. Bartucz (1940) had mentioned that similarities in the  
45 external aspect of the adult skeletal remains (i.e. same relatively dark color) suggested that all  
46 Subalyuk 1 elements were buried in the same layer. However, the spatial distribution of the  
47 hominin fossils within layer 11 (more than 1 meter thick) was a question that he could not  
48 resolve, as no direct field observations by an anthropologist were available. The fact that  
49 some of the bones were damaged at the time of discovery or later during preparation did not  
50 allow him to unequivocally recognize any traces of anthropic or animal activities that could

51 explain this spatial distribution within the site. Unlike the adult remains, the subadult skeletal  
52 elements appeared lighter in color. This observation led Bartucz (1940) to assume either that  
53 they came from a distinctly lighter coloured layer, or that they had fossilized in a different  
54 way than the adult remains, with no evidence for intentional funerary deposition. In a critical  
55 reassessment of the archaeological context, Mester (2004) argued that the two individuals had  
56 been deposited in different times and different conditions, a hypothetical interpretation that  
57 was reinforced by a new taphonomical analysis (Mester & Patou-Mathis 2016).  
58 Having revised the lithic assemblages, Mester (1989, 1990, 2008, 2022) classified the lithic  
59 industries from layers 7 to 14 as a Quina-type Mousterian, on the basis of typology, flake  
60 morphology, and lack of Levallois technology. According to the find inventory recorded at  
61 the excavation, 4437 lithic artefacts were unearthed in layer 11, from which 776 (i.e. 17.40%)  
62 were found in the same excavation units as the hominin remains. However, based on the  
63 documentation system applied in 1932 we cannot directly associate the lithics and the human  
64 remains.  
65 Recently, the available faunal assemblage coming from layer 11 were re-examined (Mester &  
66 Patou-Mathis 2016). 80 pieces of bone representing 9 species of carnivores were identified  
67 with a prevalence of cave bear (*Ursus spelaeus*), and 58 elements representing 6 species of  
68 herbivores (caprids, cervids, bovids, equids and hare) were also unearthed. The faunal  
69 assemblage in layer 11 together with its seasonal interpretation indicated that Neanderthals  
70 used the cave as a hunting station, and that the human occupation might be contemporaneous  
71 to the dry and cold conditions of MIS 4.  
72 Because of the few microfaunal remains in the palaeontological material recorded during the  
73 excavation, Jánossy and his colleagues collected original sediments adhering to the wall of the  
74 cave in 1956 and 1964. Sediment samples corresponding to layers 11 and 12 were wet sieved  
75 for microvertebrates. Jánossy (1960, 1986) reported remains of bats and rodents dominated by  
76 *Lagurus lagurus*. According to Kordos (1991), this phenomenon forms a “Lagurus-horizon”  
77 all over Europe which corresponds to the MIS 4 cold steppe period. Kordos & Ringer (1991)  
78 concluded that the dominance of *Lagurus* in the microfauna of layers 11 and 12 of Subalyuk  
79 could be related to a younger phase of MIS 4. According to Mester & Patou-Mathis (2016),  
80 the faunal spectrum of the cave suggests a tendency of warming from layer 11 to layer 14  
81 which should indicate the transition from MIS 4 to MIS 3.

82

## 83 **Materials and methods**

### 84 ***The Subalyuk hominin remains***

85 The adult specimen (Subalyuk 1, **Fig. 4**) consists of a mandible (lacking the right ramus), four  
86 vertebrae (atlas in three parts and three corpus vertebrae), a manubrium sterni, an incomplete  
87 sacrum, a left patella, three more or less complete metatarsals (second and third right one, left  
88 fourth one) and fragments of a second left metacarpal (Pap et al. 1996).

89 The Subalyuk 1 mandible retains several features that align it with the European Neanderthals  
90 (receding symphysis without mental depressions or eminences, backwards positioning of the  
91 mental foramen under the first permanent molar, gap between the back of the third molar and  
92 the front of the ramus). In contrast, the mandible exhibits some distinctive conditions in the  
93 corpus area that are evocative of an overall gracilization: value of robusticity index below the  
94 European Neanderthal mean ( $43.6 \pm 3.8$ ,  $N=14$ ), decrease of body height from the front to the  
95 level of the third molar, faint development of ligamentous and muscular attachments. In  
96 addition, on the medial surface of the left ramus the V-shaped mandibular foramen is opening  
97 backwards and upwards instead of a horizontal-oval form as described for instance on  
98 Neanderthal specimens from Vindija Cave in Croatia (Wolpoff et al. 1981). When compared  
99 to other Neanderthal mandibles, Subalyuk 1 exhibits a mosaic of morphological features,  
100 primitive retentions found in Neanderthals and apparent modern traits (Pap et al. 1996).

101 Most of the postcranial fragments of Subalyuk 1 do not show anatomical characteristics that  
102 could differentiate Neanderthals from modern humans (Pap et al. 1996). Yet, the manubrium  
103 sterni is especially well preserved and differs from those of modern specimens in a number of  
104 features (overall square shape resulting from a broad articular surface for the sternal body,  
105 extremely concave dorsal surface and bulging shape of the superior-sagittal border at the  
106 jugular notch).

107 The morphological analysis of adult bones in the site provided no argument to support the  
108 presence of more than one individual aged 25-35 years at death, despite the large spatial  
109 distribution of the remains (Pap et al. 1996).

110 The subadult remains (Subalyuk 2, **Fig 5**) consist of an incomplete cranium (basis not  
111 represented), two maxillae, an isolated left nasal bone, and a few corpus vertebrae. Recently, a  
112 3D reconstruction of both maxillae was performed to accurately evaluate the age at death of  
113 the child. Based on the deciduous dentition, an age at death between 2.5 and 3 years can be  
114 proposed (Coqueugniot et al. 2014) which is consistent with previous data (Thoma 1963, Pap  
115 et al. 1996). The virtual extraction of permanent tooth germs leads to a more contrasted result:  
116 when considering the incisors, the canines and the premolars, an older age around 4.5 years is  
117 reached, while the first molar supports the younger age of 3.5 years (Coqueugniot et al. 2014),  
118 compared to modern standards (Moorrees et al. 1963; AlQahtani et al. 2010). Using the  
119 current age estimates either for the deciduous or the permanent dentition, the Subalyuk child  
120 was definitely younger than the original estimation of 6–7 years proposed by Bartucz (1940).

121 The Subalyuk 2 calvaria differs from early modern children by the lack of parietal eminences,  
122 the rounded shape of the neurocranium in posterior view, and a low position of the maximum  
123 cranial breadth, all features that can be found on Neanderthals of similar developmental age  
124 (Tillier 2011). Like other young Neanderthal children, Subalyuk 2 retains juvenile features,  
125 e.g. incipient supraorbital thickening, and a mid-facial region not yet morphologically  
126 derived.

127 Interestingly, the mesio-distal length values of the upper deciduous incisors and canine  
128 crowns of Subalyuk 2 represent the lower limits of the range for European Neanderthals (Pap  
129 et al. 1996, Bailey & Hublin 2006, Tillier et al. 2013).

130 In summary, the combination of features exhibited by the two individuals from Subalyuk  
131 Cave, which includes primitive retentions and characteristics found in Neanderthals and  
132 “gracilized” features, is intriguing: it could be the product of individual variation or mosaic  
133 evolution during the Middle Palaeolithic in Central Europe. It opens up new perspectives on  
134 Neanderthal settlement in Central Europe.

135

### 136 ***Direct dating of the hominin remains***

137 Two hominin bone samples were used for radiocarbon dating at the Curt-Engelhorn-Centre  
138 Archaeometry, Mannheim (Germany) in 2013 and 2015. Sample 1 (MAMS 16562, sample  
139 name Subalyuk 1 ID 1353) was a vertebra from the adult Subalyuk 1. Sample 2 (MAMS  
140 25051, sample name GMP 157) was a left fragment of the occipital bone from Subalyuk 2  
141 child.

142 The bone collagen was extracted using a modified Longin method (Brown et al. 1988), ultra-  
143 filtered to remove molecules of chain length lower than 30 kDa, and freeze-dried. Sample 2  
144 (MAMS 25051) was additionally treated with organic solvents (including chloroform) in  
145 order to remove some sort of varnish used as a conservation treatment. A full description of  
146 the sample pretreatment, graphitization and sample measuring (using a MICADAS accelerator  
147 mass spectrometer (AMS) facility in the Mannheim laboratory) is given by Kromer et al.  
148 (2013).

149

## 150 **Results**

151 Detailed results of radiocarbon analyses of the Subalyuk Neanderthals are given in **Table 1**.  
152 The samples were calibrated using the software OxCal 4.4 (Bronk Ramsey 1995) with the  
153 INTCAL20 dataset (Reimer et al. 2020). Sample 1 (MAMS 16562) yielded a  $^{14}\text{C}$  age of  
154  $34,177 \pm 159$  years BP and a calibrated age between 39,732–39,076 cal. BP ( $2\sigma$ ). Sample 2  
155 (MAMS 25051) yielded a  $^{14}\text{C}$  age of  $31,370 \pm 140$  years BP with a calibrated age between  
156 36,117–35,387 cal. BP ( $2\sigma$ ). All analytical values like C:N and %C of both samples are in the  
157 normal range and the content of preserved collagen %Coll is good.  
158 Regarding sample 2 (MAMS 25051), it must be reported that the subadult bone fragment had  
159 been covered with a kind of varnish of unknown composition. As stated above the  
160 pretreatment procedure included washes with organic solvents in order to remove the varnish.  
161 However, it cannot be fully ruled out that little amounts of residual contamination remained.  
162 In order to qualitatively estimate the effect of a possible residual contamination, the varnish  
163 was dated as well. Its young conventional  $^{14}\text{C}$  age of  $1619 \pm 50$  years BP would shift the  $^{14}\text{C}$   
164 determination of sample 2 towards younger ages, if residual varnish was present.

165

## 166 **Discussion**

167 As it was mentioned above, the cave infilling of Subalyuk have been fully excavated in 1932  
168 with a good documentation at that time. It means that distinguishing layers was based on the  
169 colour of the sediment and the frequency of limestone rubbles in it. Faunal remains were  
170 collected without sieving by excavation units, but evaluated by layers only. As a result of  
171 these conditions, no possibility to have additional data about the sediments, as well as faunal  
172 assemblages of the light brown layers (11 and 14) cannot be separated. The relative  
173 chronology of the site was based on the interpretation of the stratigraphic sequence and the  
174 vertebrate fauna in relation to the Upper Pleistocene climatostratigraphy (Kretzoi & Vértes  
175 1965, Jánossy 1986, Kordos & Ringer 1991, Vörös 2000). In this respect, as marked changes  
176 were identified the appearance of limestone rubbles in the sediments from layer 7 up (Kadić  
177 1940) which probably corresponds to the increasing frost fracturing effects (Mester 2022),  
178 and by the increasing steppe-semidesert elements, including *Lagurus lagurus*, in the fauna of  
179 the upper layers group (10 to 16) (Jánossy 1986). Based on these considerations, layers 7 to  
180 12 were correlated to the MIS 4 stage, dated to between 72 and 60 ka (Kordos & Ringer  
181 1991).

182 The age of 39–40 and 35–36 ka of our direct dating place Subalyuk Neanderthals in the MIS 3  
183 stage, dated between 57 and 29 ka (Cohen & Gibbard 2012). The palaeoecological  
184 characterization of the Quaternary in the Carpathian basin using taxon-free methods (Pazonyi  
185 2011) demonstrated the presence of the ecological units of mammoth steppe environment  
186 from 90 to 27 ka. Within this period in small mammals assemblages the cold-adopted species,  
187 like *Lagurus* and *Ochotona*, constituted significant proportion until 47 ka. replaced by other  
188 steppe species, like *Alactaga*, *Spalax* and *Cricetus*, also recorded in the light brown layer of  
189 Subalyuk. As a conclusion, the accumulation of layer 11 should continue in MIS 3.

190 Since the Neanderthal remains were found in a relatively confined area within layer 11, the  
191 two individuals were longtime thought to be contemporaneous. The results of the direct  
192 radiocarbon dating may suggest two periods of Neanderthal occupation in layer 11 of  
193 Subalyuk Cave. The possibility of either residual contamination related to chemical treatment  
194 of the child's bones in the laboratory or a lower quality of the material could explain this age  
195 difference (Hublin 2017). However, Bartucz (1940) had already pointed out that the differing  
196 preservation patterns of the adult and child bones could suggest different depositional  
197 conditions. Archaeological considerations (Mester 2004) and detailed taphonomical  
198 observations (Mester & Patou-Mathis 2016) also argue in favour of two separate events of  
199 deposition. According to the reconstruction of the location of the human bones within layer 11  
200 using the original report and drawing by Dancza, the adult body may have been deposited and

201 decomposed on an earlier surface of the cave floor during the accumulation period of the  
202 layer. In the scale of the original drawing, the child's body was buried in a small pit dug from  
203 approximately the same surface (Mester 2004) (**Fig. 6**). This conclusion, however, does not  
204 exclude a difference of some thousands of years between the two events because we cannot  
205 estimate the dynamic of the accumulation of the cave sediment. According to the  
206 taphonomical observations, the adult body was exposed at a time on the surface when there  
207 were relatively humid conditions in the cave, while the child's body was buried when the cave  
208 was relatively dry (Mester & Patou-Mathis 2016). This conclusion argue in favour of an age  
209 difference between the two events. It is crucial for our understanding to obtain additional  
210 chronometric data from the associated faunal samples in order to further interpret the results  
211 obtained in this current study. Taking into account the thickness of the layer's sediment with  
212 same characteristics (from the excavators' points of view), a series of dating from different  
213 faunal elements can shed more light on the length of the accumulation period within which  
214 the deposition of the human bodies happened.

215 Whatever the precise age of the Subalyuk 2 child is, our new chronometric results propose  
216 that the hominins from Subalyuk Cave belong to the last Neanderthals in East Central Europe.  
217 As already mentioned, human remains from only two sites were directly dated from this  
218 region previously (Vindija Cave in Croatia and Šaľa in Slovakia). The cranial fragments of  
219 two adults, found in a secondary position near Šaľa in Western Slovakia, were recently  
220 radiocarbon dated by the single-amino-acid method (Hopkins et al., 2022). The obtained dates  
221 are (OxA-X-2731-16) > 44,800 <sup>14</sup>C years BP for Šaľa I and (OxA-X-2731-15) > 45,100 <sup>14</sup>C  
222 years BP for Šaľa II (Hopkins et al. 2022).

223 Chronologically more comparable to Subalyuk are the human remains from layer G<sub>1</sub> of  
224 Vindija Cave (Smith et al. 1999, Higham et al. 2006, Devière et al. 2017). Among the  
225 fragmentary hominin fossils unearthed in the Vindija G<sub>1</sub> layer, a right mandibular ramus (Vi-  
226 207) and a fragment of left parietal (Vi-208) have been directly radiocarbon dated by AMS  
227 method. The first dating was obtained with standard Oxford pretreatment and resulted 29,080  
228 ± 400 BP (OxA-8296) and 28,020 ± 360 BP (OxA-8295) respectively (Smith et al. 1999). By  
229 these dates, representing an age between 29,880 to 27,300 BP at two standard deviations, the  
230 Vindija specimens suggest a very late survival of the last Neanderthals in East Central  
231 Europe. Because of its crucial role in the debate on scenarios of the Middle to Upper  
232 Palaeolithic transition, both Vindija remains were re-dated using new ultrafiltration  
233 pretreatment method (Higham et al. 2006). This attempt produced older dates: 32,400 ± 1,800  
234 BP (OxA-X-2089-07) for Vi-207 and 32,400 ± 800 BP (OxA-X-2089-06) for Vi-208. These  
235 dates suggest an age estimation from 34,000 to 30,800 BP at two standard deviations.  
236 Recently, a new dating was performed for clarifying the supposed effect of presence of  
237 contaminants, suggested by the C:N ratios of previous datings (Devière et al. 2017). For this  
238 reason, a more robust purification method targeting the amino acid hydroxyproline has been  
239 used. This pretreatment seems to ensure removal of all contaminations. AMS measurements  
240 on these samples gave considerably older dates than earlier ones: 43,900 ± 2000 BP (OxA-X-  
241 2089-10) for Vi-207 and 42,700 ± 1600 BP (OxA-X-2089-09) for Vi-208. These new dates  
242 placed the late Neanderthals at Vindija Cave to between 47,900 and 39,500 BP at two  
243 standard deviations. The same procedure have been applied for redating the Neanderthal  
244 bones discovered in Spy Cave (Belgium), and similarly resulted up to 9,000 years older ages  
245 with robust purification as ultrafiltration pretreatment methods (Devière et al. 2021).

246 The dating history of Vindija and Spy hominin remains clearly shows how carefully we have  
247 to use radiometric dates in our interpretations. To achieve the most plausible conclusion, we  
248 need to use information from as many different sources as possible (Janković et al. 2011).

249 To compare our dates of the Subalyuk Neanderthal specimens to similar remains in East  
250 Central Europe, it is reasonable to use the dates OxA-X-2089-07 and OxA-X-2089-06 for the

251 Vindija hominins, since the same pretreatment method was used in both these Vindija and our  
252 Subalyuk specimens. In this case, both Subalyuk 1 and 2 are dated nearly to the same period.  
253 At two standard deviations, the range of Subalyuk dates (34,336–31,230) overlaps  
254 considerably with the Vindija dates (34,000–30,800).  
255 Late Neanderthals from Vindija Cave layer G<sub>1</sub> are associated with an archaeological  
256 assemblage containing stone and bone artefacts attributed to Middle and Upper Palaeolithic  
257 cultural units, including diagnostic Aurignacian bone points (Karavanić & Smith 1998, Ahern  
258 et al. 2013). This association should support the Assimilation Model of the origin of  
259 anatomically modern humans in Europe (Smith et al. 2005). However, the reliability of this  
260 association is highly criticized on the basis of chrono-cultural arguments, and an alternative  
261 taphonomical mixture has been proposed as an explanation (Zilhão 2009). On the contrary,  
262 the late Neanderthals from Subalyuk Cave are associated with homogenous archaeological  
263 material, attributed to the Quina-type Mousterian (Mester 1990, 2008, 2022). In this regard,  
264 our new direct dating results argue in favour of the persistence of Neanderthals and late  
265 Mousterian industries after 40 ka BP, not only in Western Europe (Finlayson et al. 2006), but  
266 also in East Central Europe. This conclusion appears to be in contrast to that of Higham et al.  
267 (2014) demonstrating that the end of the Mousterian should be dated between 41,030 and  
268 39,260 cal. BP at 95.4% probability. Their study did not include any other Central European  
269 Neanderthal sites or data than Vindija itself. Our age for the Subalyuk 1 specimen (39,732–  
270 39,076 cal. BP (2 $\sigma$ )) already fits well into their timeframe (**Table 1**), however the Mousterian  
271 industry is recorded in the subsequent three layers too. The age of Subalyuk 1 specimen  
272 corresponds well to the dates of 35,300  $\pm$  900 uncal BP (GrN-4443) obtained from charcoal of  
273 the hearths unearthed in the lower levels of the open-air site of Érd in Hungary (Vogel &  
274 Waterbolk 1967, Gábori-Csánk 1968, 1970). The archaeological context of the human  
275 occupations at Érd, also attributed to the Quina-type Mousterian, is quite identical to that in  
276 Subalyuk Cave (Daschek & Mester 2020, Mester 2022).  
277 Unfortunately, there is no clear anthropological evidence of Neanderthal persistence later in  
278 Hungary; the Remete-Felső Cave in Northern Hungary has yielded only a few isolated  
279 undiagnostic teeth, and the human tooth found during old excavations at Dzeravá skála  
280 (Pálffy Cave) in present-day Western Slovakia does not permit a more precise taxonomic  
281 attribution (Tillier et al. 2006).

282

## 283 **Conclusion**

284 In the last two decades, chronological assignments based on direct and indirect dating have  
285 documented the last surviving Neanderthals in Europe long after 40 ka BP. The possible  
286 cultural interaction between Neanderthals and early modern humans has become the focus of  
287 numerous studies (e.g. Bar Yosef & Pilbeam 2000, Conard 2006, Condemi & Weniger 2006,  
288 Ahern et al. 2013, Higham et al. 2014, Otte 2014, Benazzi et al. 2015, Talamo et al. 2016,  
289 Bard et al. 2020). Much discussion is devoted to the transitional period between 40 and 30 ka  
290 BP, and the role played by late Neanderthals in the origin of modern humans in Europe. The  
291 first direct dating of the two individuals unearthed in Subalyuk Cave that we report here  
292 contributes considerably to this debate. The time range of the two new dates (34,336–31,230  
293 BP) overlaps with the dating of the Vindija layer G<sub>1</sub> specimens (34,000–30,800 BP) published  
294 by Higham et al. (2006) obtained using the ultrafiltration pretreatment method. Also, the  
295 approximate date of 39 ka cal BP of Subalyuk 1 adult associated with Quina-type Mousterian  
296 industry fits well with the end of the Mousterian calculated by Higham et al. (2014). Our  
297 results suggest that Neanderthals living in Central Europe also survived the climatic changes  
298 at the beginning of the Interpleniglacial (MIS 3) as they did in Western Europe (Sánchez Goñi  
299 2022).



300 As in the rest of Europe, this period was probably complex and dynamic in Hungary. Yet,  
301 modern human remains are very fragmentary in the region, and inferences of their possible  
302 age come from geological evidence, in the absence of radiometric dating (Tillier et al. 2006).  
303 The *Homo sapiens* occipital bone found without clear archaeological context in the  
304 Görömböly-Tapolca Cave (Bükk Mts, Northeastern Hungary) was directly dated by AMS  
305 radiocarbon measurements using ultrafiltration pretreatment method and yielded  $30,300 \pm 300$   
306 BP (Thoma 1957, Davies & Hedges 2008–2009). Thus, the potential coexistence between late  
307 Neanderthal groups and modern humans developing Upper Palaeolithic technology is  
308 chronologically not yet established in Hungary. However, the arrival of modern humans in  
309 this part of Europe is evidenced as early as 41–37 ka in Peștera cu Oase Cave, Southwestern  
310 Romania (Trinkaus et al. 2003, Kuzmin & Keats 2014) and 47–43 ka in Bacho Kiro Cave,  
311 Central Bulgaria (Hublin et al. 2020). Although Oase 1 and 2 were found in a gallery of the  
312 cave without any archaeological material, Bacho Kiro individuals were associated with Initial  
313 Upper Palaeolithic (IUP) industry. Palaeogenetic (Oase 1, Bacho Kiro IUP) and  
314 morphological (Oase 2, Muierii) data show evidences of physical contacts (interbreeding) of  
315 these modern human populations with contemporary Neanderthals (Soficaru et al. 2006,  
316 Rougier et al. 2007, Fu et al. 2015, Hajdinjak et al. 2021). Cultural contacts have been  
317 assumed based on similarities between pendants found in the IUP industry of Bacho Kiro  
318 Cave and in the Chatelperronian layers of Grotte du Renne Cave in France made by  
319 Neanderthals (Hublin et al. 2020). Unfortunately, Neanderthal human remains were not  
320 discovered in this region of Southeastern Europe. The closest ones are known actually from  
321 layer G<sub>1</sub> of Vindija Cave and layer 11 of Subalyuk Cave. As it was discussed above, Vindija  
322 G<sub>1</sub> hominins have both Middle and Upper Palaeolithic cultural association but it is debated  
323 (Ahern et al. 2013, Zilhão 2009), however Subalyuk hominins have evident Quina-type  
324 Mousterian context. Middle Palaeolithic industries unearthed in the caves of the Southern  
325 Carpathians were often related to Quina-type Mousterian or Charentian (Gábori 1976,  
326 Păunescu 1989, Mertens 1996). In the Peștera Muierii, the Mousterian industry underlying the  
327 layer with modern human remains was dated to about 42 ka by conventional radiocarbon  
328 method (Soficaru et al. 2006, Doboş et al. 2010). Actually, there are not any archaeological  
329 evidences at our disposal witnessing contacts between Late Middle Palaeolithic and Early  
330 Upper Palaeolithic groups in the region, however it is worth to mention that an analysis using  
331 the whole assemblage behavioral indicator (WABI) method demonstrated a broad level of  
332 behavioral continuity during the transitional period in terms of land-use strategies,  
333 organizational flexibility and lithic technological organization (Riel-Salvatore et al 2008).  
334 Therefore, future studies with chronological precision will be important to further our  
335 understanding of the patterns of regional population movements, and the contribution of East  
336 Central European sites to the debate regarding the peopling history of Europe during the Late  
337 Middle to Early Upper Palaeolithic transition.

338

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352

### 353 **Declaration of competing interest**

354 The authors declare that there is no conflict of interest.

355

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696

## 697 **Figure legends**



698 Figure 1. Location of Subalyuk Cave and sites mentioned in the text. 1: Subalyuk, 2:  
699 Görömböly-Tapolca, 3: Remete-Felső, 4: Érd, 5: Šaľa, 6: Dzeravá skala, 7: Krapina, 8:  
700 Vindija, 9: Peștera cu Oase, 10: Peștera Muierii, 11: Bacho Kiro.

701  
702 Figure 2. Vertebral remains of the Subalyuk adult Neanderthal specimen in the original 1932  
703 boxes (photo courtesy of György Pálfi).

704  
705 Figure 3. Stratigraphic sequence of Subalyuk Cave (after Kadić 1940, modified); crosses in  
706 layer 11 represent the location of the hominin remains.

707  
708 Figure 4. Anterior (A) and lateral (B) view of the adult mandible (photos courtesy of Ildikó  
709 Pap).

710  
711 Figure 5. Superior (A) left side (B) and right side (C) view of the subadult calvaria (photos  
712 courtesy of György Pálfi (A) and Ildikó Pap (B and C)).

713  
714 Figure 6. Reconstruction of the location of the hominin bones in layer 11 at Subalyuk Cave;  
715 the circle represents the remains of the child; the squares show the adult bones. A: projection  
716 to the transversal section at line 0; B: projection to the longitudinal section (after Mester 2004,  
717 Figs 4 and 5).

718

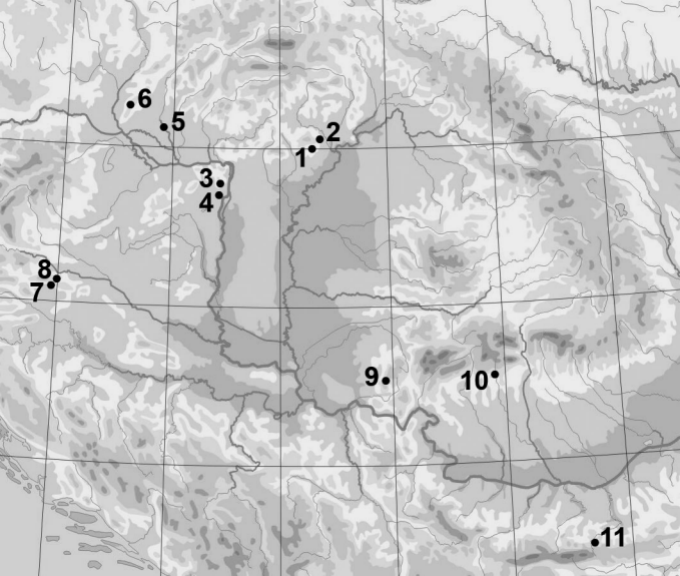
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720 **Table**

721 Table 1. Data of the radiocarbon analyses. Lab. code = laboratory code;  $^{14}\text{C}$  age = conventional date; BP = before present; cal. = calibrated date;  
 722  $1\sigma$  = 1 standard deviation (68.2% probability);  $2\sigma$  = 2 standard deviations (95.4% probability). The given  $\delta^{13}\text{C}$  values from measuring with AMS  
 723 are not comparable with data from isotope ratio mass spectrometry (IRMS).

Sample	Lab. code.	Material	$^{14}\text{C}$ age (BP)	$\delta^{13}\text{C}$ (‰)	Calendar age (cal. BP)		C:N	%C	%Coll
					$1\sigma$	$2\sigma$			
Sample 1	MAMS 16562	adult bone	$34,177 \pm 159$	-24.8	39,520–39,216	39,732–39,076	3.4	41.7	4.7
Sample 2	MAMS 25051	child bone	$31,370 \pm 140$	-34.8	35,971–35,549	36,117–35,387	3.1	40.0	3.5

724

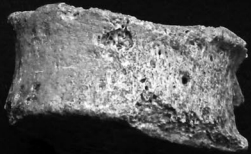


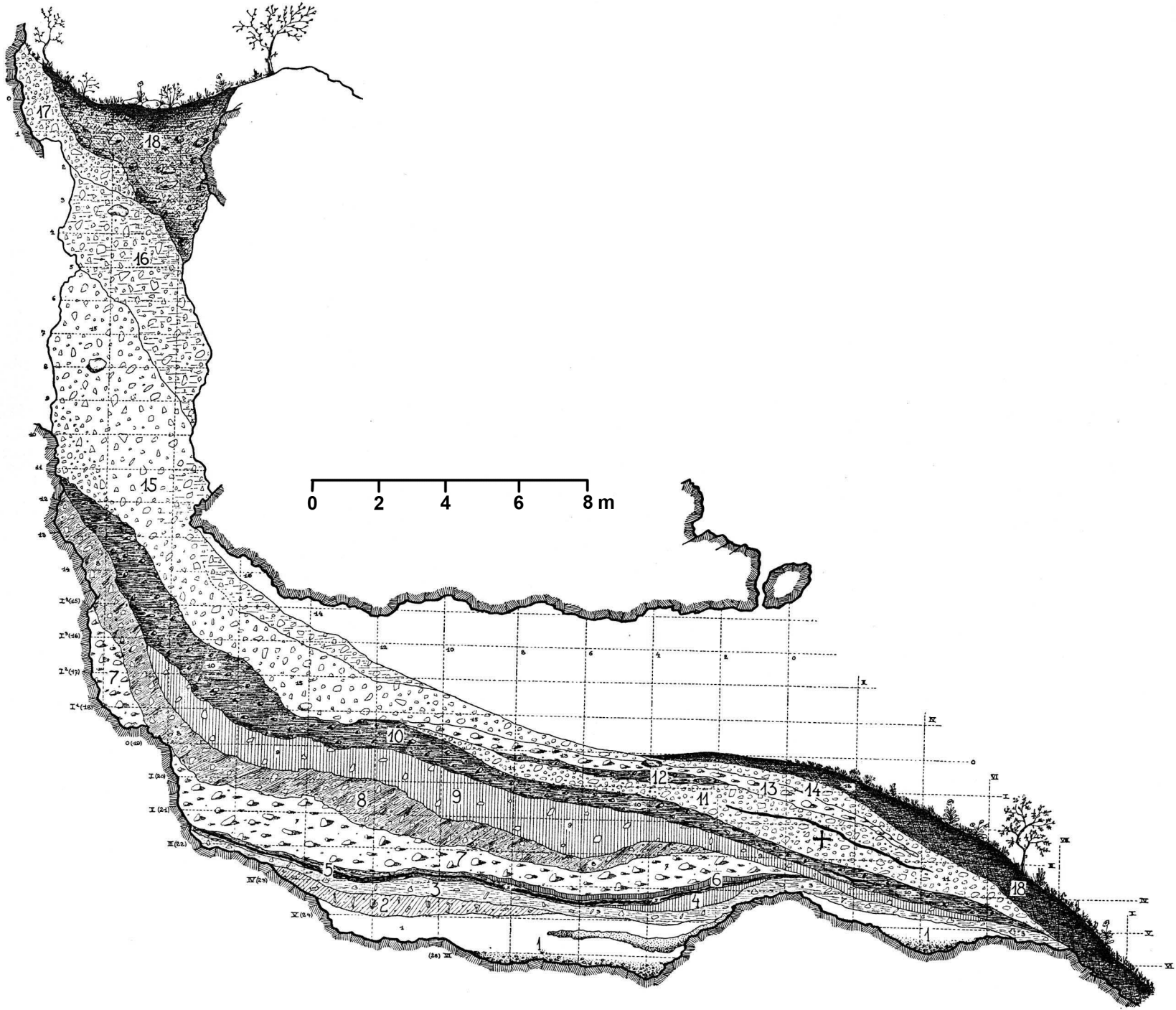
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68. 140. 6.



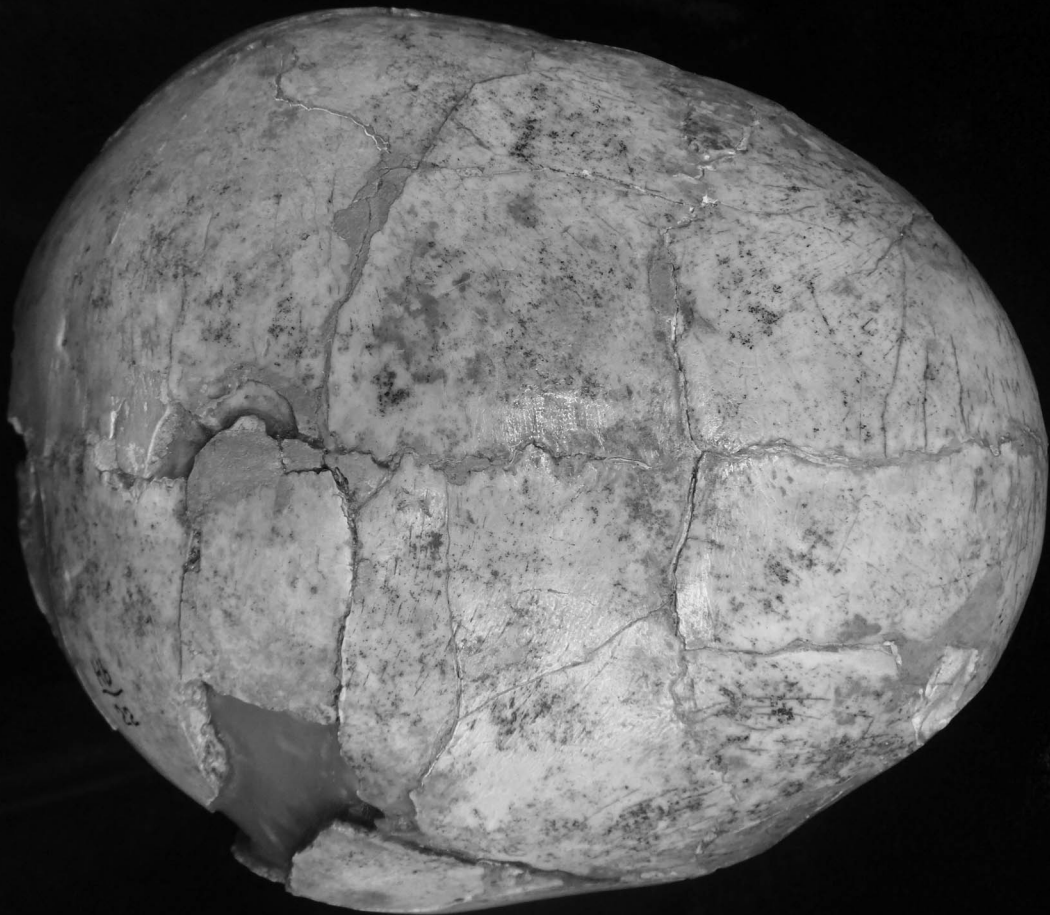
M. kir. Földtani Intézet  
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 M. sz. 1932  
*Homo primigenius* L.  
 (corp<sup>us</sup> vertebrae)  
 Lelőhely: *Mussolini-barlang*  
 K<sup>6</sup>7. k<sup>6</sup>ad<sup>6</sup> O. de. (Borsod-u)  
 35060 — Szénásy







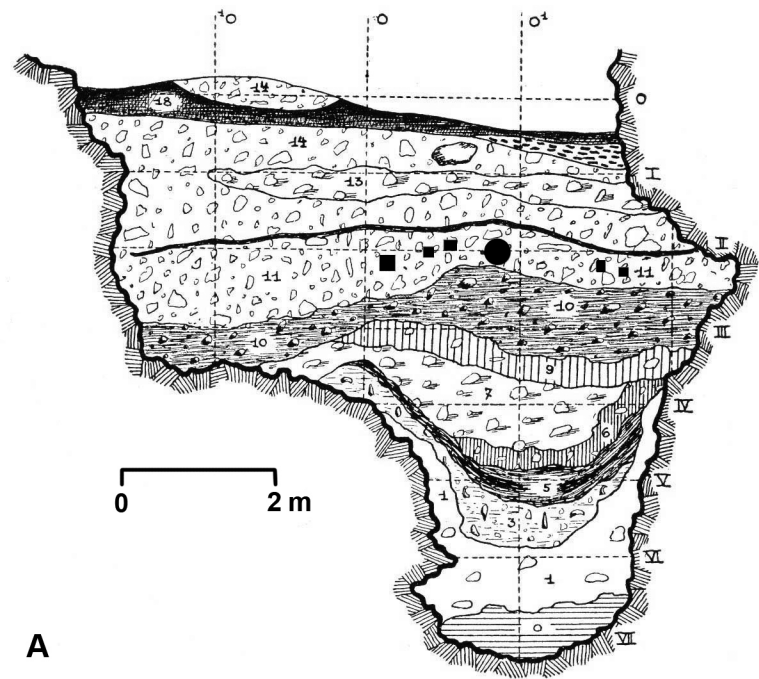




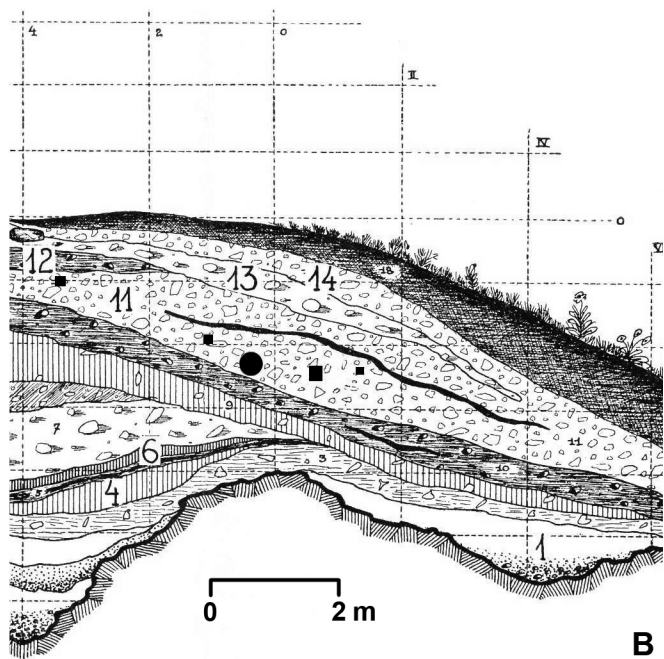








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