



HAL
open science

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

Zsolt Mester, H el ene Coqueugniot, Anne-Marie Tillier, Wilfried Rosendahl,
Ronny Friedrich, Albert Zink, Frank Maixner, Olivier Dutour, Zsolt Bereczki,
Mih aly Gasparik, et al.

► **To cite this version:**

Zsolt Mester, H el ene Coqueugniot, Anne-Marie Tillier, Wilfried Rosendahl, Ronny Friedrich, et al..
First direct dating of the Late Neanderthal remains from Subalyuk Cave in Northern Hungary. An-
thropologischer Anzeiger, In press, 81 (2), pp.169-181. 10.1127/anthranz/2023/1716 . hal-04336905

HAL Id: hal-04336905

<https://cnrs.hal.science/hal-04336905>

Submitted on 12 Dec 2023

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destin ee au d ep ot et  a la diffusion de documents scientifiques de niveau recherche, publi es ou non,  emanant des  tablissements d'enseignement et de recherche fran ais ou  trangers, des laboratoires publics ou priv es.

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

3
4 Zsolt Mester ^{1,2,*}, Hélène Coqueugniot ^{3,4}, Anne-marie Tillier ³, Wilfried Rosendahl ⁵, Ronny
5 Friedrich ⁶, Albert Zink ⁷, Frank Maixner ⁷, Olivier Dutour ^{3,4}, Zsolt Bereczki ⁸, Mihály
6 Gasparik ⁹, Ildikó Pap ^{8,10,11}, György Pálfi ⁸

7
8 ¹ Institute of Archaeological Sciences, Eötvös Loránd University, Budapest, Hungary

9 ² UMR 7194 HNHP CNRS/MNHN/UPVD, Institut de Paléontologie humaine, Paris, France

10 ³ UMR 5199 PACEA CNRS, Université de Bordeaux, Pessac, France

11 ⁴ Ecole Pratique des Hautes Etudes - PSL University, Paris, France

12 ⁵ Reiss-Engelhorn-Museen, Museum Weltkulturen Mannheim, Germany

13 ⁶ Curt-Engelhorn Center Archaeometry gGmbH, Mannheim, Germany

14 ⁷ Institute for Mummy Studies, Eurac Research, Bolzano, Italy

15 ⁸ Department of Biological Anthropology, University of Szeged, Szeged, Hungary

16 ⁹ Department of Palaeontology and Geology, Hungarian Natural History Museum, Budapest,
17 Hungary

18 ¹⁰ Department of Anthropology, Hungarian Natural History Museum, Budapest, Hungary

19 ¹¹ Department of Biological Anthropology, Eötvös Loránd University, Budapest, Hungary

20 * Corresponding author: mester.zsolt@btk.elte.hu

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, ¹⁴C
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 ± 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}C age of
154 $34,177 \pm 159$ years BP and a calibrated age between 39,732–39,076 cal. BP (2σ). Sample 2
155 (MAMS 25051) yielded a ^{14}C age of $31,370 \pm 140$ years BP with a calibrated age between
156 36,117–35,387 cal. BP (2σ). 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}C age of 1619 ± 50 years BP would shift the ^{14}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 Šal'a in Slovakia). The cranial fragments of
219 two adults, found in a secondary position near Šal'a 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 ¹⁴C years BP for Šal'a I and (OxA-X-2731-15) > 45,100 ¹⁴C
222 years BP for Šal'a II (Hopkins et al. 2022).

223 Chronologically more comparable to Subalyuk are the human remains from layer G₁ of
224 Vindija Cave (Smith et al. 1999, Higham et al. 2006, Devièse et al. 2017). Among the
225 fragmentary hominin fossils unearthed in the Vindija G₁ 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 (Devièse 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 (Devièse 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 G₁ 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 σ)) 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 G₁ 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 G₁ of Vindija Cave and layer 11 of Subalyuk Cave. As it was discussed above, Vindija
322 G₁ 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

339 **Acknowledgements**

340 We send our sincerest thanks to Dr. Bernd Kromer, Susanne Lindauer, MSc. and the technical
341 team of the ¹⁴C laboratory at Curt-Engelhorn-Centre Archaeometry gGmbH Mannheim for
342 the technical support, preparation and measuring the samples. We are indebted to the
343 Department of Anthropology of the Hungarian Natural History Museum in Budapest for
344 providing access to the important Subalyuk specimens under its care. We are grateful to each
345 member of staff at the Department of Anthropology for their courtesy and assistance. This
346 research was funded by a French-Hungarian PHC–Balaton program (“Ancient Hungarian
347 Human Peopling”, co-directed by György Pálfi and Olivier Dutour), and the Hungarian NRD
348 Fund (grant no. K 125561, directed by György Pálfi). The authors thank Luca Kis (University
349 of Szeged, Department of Biological Anthropology) for her contribution in editing the

350 pictures. Finally, we are indebted to the anonymous reviewer for very useful comments and
351 suggestions for improving our manuscript.

352

353 **Declaration of competing interest**

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

355

356 **References**

357 Ahern, J. C. M., Janković, I., Voisin, J.-L., & Smith, F. H. (2013). Modern Human Origins in
358 Central Europe. In F. H. Smith, & J. C. M. Ahern (Eds.), *The Origins of Modern Humans:
359 Biology Reconsidered, Second Edition* (pp. 151–221). Hoboken: John Wiley & Sons.

360

361 AlQahtani, S. J., Hector, M. P., & Liversidge, H. M. (2010). Brief Communication: The
362 London Atlas of Human Tooth Development and Eruption. *American Journal of Physical
363 Anthropology*, 142, 481–490. <https://doi.org/10.1002/ajpa.21258>

364

365 Bailey, S. E., & Hublin, J.-J. (2006). Dental remains from the Grotte du Renne at Arcy-sur-
366 Cure (Yonne). *Journal of Human Evolution*, 50, 485–508.
367 <https://doi.org/10.1016/j.jhevol.2005.11.008>

368

369 Bar Yosef, O., & Pilbeam, D. (Eds.) (2000). *The Geography of Neandertals and Modern
370 Humans in Europe and the Greater Mediterranean*. Peabody Museum Bulletins 8,
371 Cambridge: Peabody Museum of Archaeology and Ethnology, Harvard University.

372

373 Bard, E., Heaton, T. J., Talamo, S., Kromer, B., Reimer, R. W., & Reimer, P. J. (2020).
374 Extended dilation of the radiocarbon time scale between 40,000 and 48,000 y BP and the
375 overlap between Neanderthals and *Homo sapiens*. *Proceedings of the National Academy of
376 Sciences of the United States of America*, 117, 21005–21007.
377 <https://doi.org/10.1073/pnas.2012307117>

378

379 Bartucz, L. (1940). Der Urmensch der Mussolini-Höhle. In L. Bartucz, J. Dancza, F.
380 Hollendonner, O. Kadić, M. Mottl, V. Pataki, E. Pálosi, J. Szabó, & A. Vendl, *Die Mussolini-
381 Höhle (Subalyuk) bei Cserépfalu* (pp. 49–105). Geologica Hungarica Series Palaeontologica
382 14, Budapest: Editio Instituti Regii Hungarici Geologici.

383

384 Bartucz, L., Dancza, J., Hollendonner, F., Kadić, O., Mottl, M., Pataki, V., Pálosi, E., Szabó,
385 J., & Vendl, A. (1940). *Die Mussolini-Höhle (Subalyuk) bei Cserépfalu*. Geologica Hungarica
386 Series Palaeontologica 14, Budapest: Editio Instituti Regii Hungarici Geologici.

387

388 Benazzi, S., Slon, V., Talamo, S., Negrino, F., Peresani, M., Bailey, S. E., Sawyer, S.,
389 Panetta, D., Vicino, G., Starnini, E., Mannino, M. A., Salvadori, P. A., Meyer, M., Pääbo, S.,
390 & Hublin, J.-J. (2015). The makers of the Protoaurignacian and Implications for Neandertal
391 Extinction. *Science*, 348, 793–796. <https://doi.org/10.1126/science.aaa2773>

392

393 Bronk Ramsey, C. (1995). Radiocarbon calibration and analysis of stratigraphy: The OxCal
394 program. *Radiocarbon*, 37, 425–430. <https://doi.org/10.1017/S0033822200030903>

395

396 Brown, T. A., Nelson, D. E., Vogel, J. S., & Southon, J. R. (1988). Improved Collagen
397 Extraction by Modified Longin Method. *Radiocarbon*, 30, 171–177.
398 <https://doi.org/10.1017/S0033822200044118>.

399

400 Cohen, K. M., & Gibbard, P. L. (2012). *Regional chronostratigraphical correlation table for*
401 *the last 270,000 years. North Atlantic – Greenland – West, North, Central, Eastern Europe,*
402 *Russia – Siberia v. 2012b.* [https://www.nhm2.uio.no/norges/GTS2012_Quaternary-Poster-](https://www.nhm2.uio.no/norges/GTS2012_Quaternary-Poster-reg-GSA2012.pdf)
403 [reg-GSA2012.pdf](https://www.nhm2.uio.no/norges/GTS2012_Quaternary-Poster-reg-GSA2012.pdf) (Accessed: 06.07.2023)

404

405 Conard, N. (Ed.) (2006). *When Neanderthals and Modern Humans Met.* Tübingen: Kerns
406 Verlag.

407

408 Condemi, S., Weniger, G.-C. (Eds.) (2011). *Continuity and Discontinuity in the Peopling of*
409 *Europe. One Hundred Fifty Years of Neanderthal Study.* Vertebrate Paleobiology and
410 Paleanthropology, Dordrecht: Springer. <https://doi.org/10.1007/978-94-007-0492-3>

411

412 Coqueugniot, H., Tillier, A.-m., Pálfi, Gy., Dutour, O. J., Dutailly, B., Desbarats, P., Palkó, A.,
413 & Pap, I. (2014). Contribution of virtual 3D reconstruction and printing (VIRCOPAL®) to
414 paleoanthropology: The case of the Neanderthal Subalyuk 2 child skull (Bukk Mountains,
415 Hungary). *American Journal of Physical Anthropology*, 153 S58, 97.

416

417 Daschek, É. J., & Mester, Zs. (2020). A site with mixed occupation: Neanderthals and
418 carnivores at Érd (Hungary). *Journal of Archaeological Science: Reports*, 29, 102116.
419 <https://doi.org/10.1016/j.jasrep.2019.102116>

420

421 Davies, W., & Hedges, R. (2008–2009). Dating a Type Site: Fitting Szeleta Cave into its
422 Regional Chronometric Context. *Praehistoria*, 9–10, 35–45.

423

424 Devièse, T., Karavanić, I., Comeskey, D., Kubiak, C., Korlević, P., Hajdinjak, M., Radović,
425 S., Procopio, N., Buckley, M., Pääbo, S., & Higham, T. (2017). Direct dating of Neanderthal
426 remains from the site of Vindija Cave and implications for the Middle to Upper Paleolithic
427 transition. *Proceedings of the National Academy of Sciences of the United States of America*,
428 114, 10606–10611. <https://doi.org/10.1073/pnas.1709235114>

429

430 Devièse, T., Abrams, G., Hajdinjak, M., Pirson, S., De Groote, I., Di Modica, K., Toussaint,
431 M., Fischer, V., Comeskey, D., Spindler, L., Meyer, M., Semal, P., & Higham, T. (2021).
432 Reevaluating the timing of Neanderthal disappearance in Northwest Europe. *Proceedings of*
433 *the National Academy of Sciences of the United States of America*, 118, e2022466118.
434 <https://doi.org/10.1073/pnas.2022466118>

435

436 Doboş, A., Soficaru, A., & Trinkaus, E. (2010). The Prehistory and Paleontology of the
437 Peştera Muierii (Romania), *Etudes et Recherches Archéologiques de l'Université de Liège*,
438 124, Liège: Université de Liège.

439

440 Finlayson, C., Giles Pacheco, F., Rodríguez-Vidal, J., Fa, D. A., Gutierrez López, J. M.,
441 Santiago Pérez, A., Finlayson, G., Allue, E., Baena Preysler, J., Cáceres, I., Carrión, J. S.,
442 Fernández Jalvo, Y., Gledhill-Owen, C. P., Jimenez Espejo, F. J., López, P., López Sáez, J. A.,
443 Riquelme Cantal, J. A., Sánchez Marco, A., Giles Guzman, F., Brown, K., Fuentes, N.,
444 Valarino, C. A., Villalpando, A., Stringer, C. B., Martínez Ruiz, F., & Sakamoto, T. (2006).
445 Late Neanderthals at the southernmost extreme of Europe. *Nature*, 443, 850–853.
446 <https://doi.org/10.1038/nature05195>

447

448 Gábori, M. (1976). *Les civilisations du Paléolithique moyen entre les Alpes et l'Oural.*
449 *Esquisse historique.* Budapest: Akadémiai Kiadó.

450
451 Gábori-Csánk, V. (1968). *La station du Paléolithique moyen d'Érd – Hongrie*. Budapest:
452 Akadémiai Kiadó.
453
454 Gábori-Csánk, V. (1970). 14C dates of the Hungarian Palaeolithic. *Acta Archaeologica*
455 *Academiae Scientiarum Hungaricae*, 22, 3–11.
456
457 Hajdinjak, M., Mafessoni, F., Skov, L., Vernot, B., Hübner, A., Fu, Q., Essel, E., Nagel, S.,
458 Nickel, B., Richter, J., Moldovan, O. T., Constantin, S., Endarova, E., Zahariev, N., Spasov,
459 R., Welker, F., Smith, G. M., Sinet-Mathiot, V., Paskulin, L., Fewlass, H., Talamo, S., Rezek,
460 Z., Sirakova, S., Sirakov, N., McPherron, S. P., Tsanova, T., Hublin, J.-J., Peter, B. M.,
461 Meyer, M., Skoglund, P., Kelso, J., & Pääbo, S. (2021). Initial Upper Palaeolithic humans in
462 Europe had recent Neanderthal ancestry. *Nature*, 592, 253–257.
463
464 Higham, T., Bronk Ramsey, C., Karavanić, I., Smith, F. H., & Trinkaus, E. (2006). Revised
465 direct radiocarbon dating of the Vindija G₁ Upper Paleolithic Neandertals. *Proceedings of the*
466 *National Academy of Sciences of the United States of America*, 103, 553–557.
467 <https://doi.org/10.1073/pnas.0510005103>
468
469 Higham, T., Douka, K., Wood, R., Bronk Ramsey, C., Brock, F., Basell, L., Camps, M.,
470 Arrizabalaga, A., Baena, J., Barroso-Ruíz, C., Bergman, C., Boitard, C., Boscato, P.,
471 Caparrós, M., Conard, N. J., Draily, C., Froment, A., Galván, B., Gambassini, P., Garcia-
472 Moreno, A., Grimaldi, S., Haesaerts, P., Holt, B., Iriarte-Chiapusso, M.-J., Jelinek, A., Jordá
473 Pardo, J. F., Maíllo-Fernández, J.-M., Marom, A., Maroto, J., Menéndez, M., Metz, L., Morin,
474 E., Moroni, A., Negrino, F., Panagopoulou, E., Peresani, M., Pirson, S., de la Rasilla, M.,
475 Riel-Salvatore, J., Ronchitelli, A., Santamaria, D., Semal, P., Slimak, L., Soler, J., Soler, N.,
476 Villaluenga, A., Pinhasi, R., & Jacobi, R. (2014). The timing and spatiotemporal patterning of
477 Neanderthal disappearance. *Nature*, 512, 306–309. <https://doi.org/10.1038/nature13621>
478
479 Hopkins, R., Hajdinjak, M., Šefčáková, A., Comeskey, D., Devière, T., & Higham, T. (2022).
480 Single amino acid radiocarbon dating of two Neanderthals found at Šal'a (Slovakia).
481 *Radiocarbon*, 64(1), 87–100. <https://doi.org/10.1017/RDC.2021.113>
482
483 Hublin, J.-J. (2017). The last Neanderthal. *Proceedings of the National Academy of Sciences*
484 *of the United States of America*, 114, 10520–10522. <https://doi.org/10.1073/pnas.1714533114>
485
486 Hublin, J.-J., Sirakov, N., Aldeias, V., Bailey, S., Bard, E., Delvigne, V., Endarova, E.,
487 Fagault, Y., Fewlass, H., Hajdinjak, M., Kromer, B., Krumov, I., Marreiros, J., Martisius, N.
488 L., Paskulin, L., Sinet-Mathiot, V., Meyer, M., Pääbo, S., Popov, V., Rezek, Z., Sirakova, S.,
489 Skinner, M. M., Smith, G. M., Spasov, R., Talamo, S., Tuna, T., Wacker, L., Welker, F.,
490 Wilcke, A., Zahariev, N., McPherron, S. P., & Tsanova, T. (2020). Initial Upper Palaeolithic
491 *Homo sapiens* from Bacho Kiro Cave, Bulgaria. *Nature*, 581, 299–302.
492 <https://doi.org/10.1038/s41586-020-2259-z>
493
494 Janković, I., Karavanić, I., Ahern, J. C. M., Brajković, D., Lenardić, J. M., & Smith, F. H.
495 (2011). Archaeological, Paleontological and Genomic Perspectives on Late European
496 Neandertals at Vindija Cave, Croatia. In S. Condemi, & G.-C. Weniger (Eds.), *Continuity and*
497 *Discontinuity in the Peopling of Europe. One Hundred Fifty Years of Neanderthal Study* (pp.
498 299–313). Vertebrate Paleobiology and Paleoanthropology, Dordrecht: Springer.
499 https://doi.org/10.1007/978-94-007-0492-3_23

500
501 Jánossy, D. (1960). Wirbeltierkleinfauna aus dem Mousteriensichten der Subalyuk-Höhle
502 (NO-Ungarn). In R. Musil (Ed.), *Mammalia Pleistocaenica* (pp. 71–76). Supplement
503 Anthropos, Brno: Krajské Nakladatelství.
504
505 Jánossy, D. (1986). *Pleistocene vertebrate faunas of Hungary*. Developments in
506 Palaeontology and Stratigraphy 8, Amsterdam–Oxford–New York–Tokyo: Elsevier.
507
508 Kadić, O. (1940). Topographische, morphologische und stratigraphische Verhältnisse der
509 Höhle. In L. Bartucz, J. Dancza, F. Hollendonner, O. Kadić, M. Mottl, V. Pataki, E. Pálosi, J.
510 Szabó, & A. Vendl, *Die Mussolini-Höhle (Subalyuk) bei Cserépfalu* (pp. 29–46). Geologica
511 Hungarica Series Palaeontologica 14, Budapest: Editio Instituti Regii Hungarici Geologici.
512
513 Karavanić, I., & Smith, F. H. (1998). The Middle/Upper Paleolithic interface and the
514 relationship of Neanderthals and early modern humans in the Hrvatsko Zagorje, Croatia.
515 *Journal of Human Evolution*, 34, 223–248. <https://doi.org/10.1006/jhev.1997.0192>
516
517 Kordos, L. (1991). A közép-európai felső-pleisztocén pocokfauna fejlődése és
518 biosztratigráfiai értékelése (Evolution and biostratigraphic ranging of the Late Pleistocene
519 vole fauna in Central Europe). *A Magyar Állami Földtani Intézet Évi Jelentése az 1989. évről*,
520 495–522.
521
522 Kordos, L., & Ringer, Á. (1991). A magyarországi felső-pleisztocén *Arvicolidae*-
523 sztratigráfiájának klimato- és archeosztratigráfiai korrelációja (Climatostratigraphic and
524 archeostratigraphic correlation of *Arvicolidae* stratigraphy of the Late Pleistocene in
525 Hungary). *A Magyar Állami Földtani Intézet Évi Jelentése az 1989. évről*, 523–534.
526
527 Kretzoi, M., & Vértes, L. (1965). The role of Vertebrate faunae and Palaeolithic industries of
528 Hungary in Quaternary stratigraphy and chronology. *Acta Geologica Hungarica*, 9, 125–144.
529
530 Kromer, B., Lindauer, S., Synal, H.-A., & Wacker, L. (2013). MAMS – A new AMS facility
531 at the Curt-Engelhorn-Centre for Achaeometry, Mannheim, Germany. *Nuclear Instruments*
532 *and Methods in Physics Research B*, 294, 11–13. <https://doi.org/10.1016/j.nimb.2012.01.015>
533
534 Kuzmin, Y. V., Keats, S. G. (2014). Direct radiocarbon dating of Late Pleistocene hominids in
535 Eurasia: Current status, problems, and perspectives. *Radiocarbon*, 56, 753–766.
536 <https://doi.org/10.2458/56.16936>
537
538 Mertens, S. B. (1996). The Middle Paleolithic in Romania. *Current Anthropology*, 37, 515–
539 521. <https://www.jstor.org/stable/2744551>
540
541 Mester, Zs. (1989). A Subalyuk-barlang középső paleolitikus iparainak újraértékelése (La ré-
542 évaluation des industries du Paléolithique moyen de la grotte de Subalyuk). *Folia*
543 *Archaeologica*, 40, 11–35.
544
545 Mester, Zs., 1990. La transition vers le Paléolithique supérieur des industries moustériennes
546 de la montagne de Bükk (Hongrie). In: Farizy, C. (Ed.), Paléolithique moyen récent et
547 Paléolithique supérieur ancien en Europe. Ruptures et transitions : examen critique des
548 documents archéologiques. Actes du Colloque international de Nemours 9-10-11 Mai 1988.

549 Mémoires du Musée de Préhistoire d'Île de France 3, Ed. A.P.R.A.I.F., Nemours, pp. 111–
550 113.

551

552 Mester, Zs. (2004). Újabb megfontolások a suba-lyuki neandervölgyi temetkezés kérdéséhez
553 (Nouvelles considérations sur les sépultures néandertaliennes de la grotte Suba-lyuk). In G.
554 Ilon (Ed.), *ΜΩΜΟΣ III. – Őskoros Kutatók III. Összejövetelének konferenciakötete –*
555 *Halottkultusz és temetkezés* (pp. 309–321). Szombathely: Kulturális Örökségvédelmi
556 Szakszolgálat– Vas megyei Múzeumok Igazgatósága.

557

558 Mester, Zs. (2008). A Suba-lyuk vadászai: két kultúra, két világ. In Cs. Baráz (Ed.), *A Suba-*
559 *lyuk barlang. Neandervölgyi ősember a Bükkben* (pp. 85–98). Eger: Bükki Nemzeti Park
560 Igazgatóság.

561

562 Mester, Zs. (2022). Certains aspects du Moustérien en Hongrie : Contribution au débat sur la
563 variabilité. In O. Cîrstina, E.-C. Nițu (Eds.), *O viață dedicată paleoliticului : studii in*
564 *honorem Marin Cârciumaru / A life dedicated to the paleolithic : studies in honorem Marin*
565 *Cârciumaru* (pp. 31–52). Târgoviște: Cetatea de scaun.

566

567 Mester, Zs., & Patou-Mathis, M. (2016). Nouvelle interprétation des occupations
568 néanderthaliennes de la grotte Subalyuk (Hongrie du Nord). *Acta Archaeologica Carpathica*,
569 51, 7–46.

570

571 Minnikin, D., Lee, O., Wu, H., Besra, G., Llwellyn, G., Williams, C., Pap, I., Pálfi, Gy.,
572 Maixner, F., Zink, A., & Jaeger, H. (2020). Lipid biomarkers for tuberculosis are present in
573 Neanderthal skeletal remains from Subalyuk, Hungary. In *26th EAA Virtual Annual Meeting –*
574 *Abstract Book* (p. 394). Prague: European Association of Archaeologists.

575

576 Moorrees, C. F. A., Fanning, E. A., & Hunt, E. E. (1963). Age Variation of Formation Stages
577 for Ten Permanent Teeth. *Journal of Dental Research*, 42, 1490–1502.
578 <https://doi.org/10.1177/00220345630420062701>

579

580 Otte, M. (Ed.) (2014). *Neandertal / Cro Magnon – La Rencontre*. Arles: Éditions Errance.

581

582 Pálfi, Gy., Pap, I., Tillier, A.-m., Szigeti, K., Molnár, E., Rosendhal, W., Krause, J., Posth, C.,
583 Maixner, F., & Zink, A. (2020). Re-examination of the Subalyuk Neanderthal Remains
584 (Subalyuk Cave, Hungary). In *26th EAA Virtual Annual Meeting – Abstract Book* (p. 393).
585 Prague: European Association of Archaeologists.

586

587 Pap, I., Tillier, A.-m., Arensburg, B., Weiner, S., & Chech, M. (1995). First scanning Electron
588 Microscope Analysis of Dental Calculus from European Neanderthals: Subalyuk (Middle
589 Paleolithic, Hungary). Preliminary report. *Bulletins et Mémoires de la Société*
590 *d'Anthropologie de Paris*, 7, 69–72. <https://doi.org/10.3406/bmsap.1995.2409>

591

592 Pap, I., Tillier, A.-m., Arensburg, B., & Chech, M. (1996). The Subalyuk Neanderthal
593 remains (Hungary): A re-examination. *Annales historico-naturales Musei nationalis*
594 *hungarici*, 88, 233–270.

595

596 Păunescu, A. (1989). Le Paléolithique et le Mésolithique de Roumanie (un bref aperçu).
597 *L'Anthropologie*, 93, 123–158.

598

599 Pazonyi, P. (2011). Palaeoecology of Late Pliocene and Quaternary mammalian communities
600 in the Carpathian Basin. *Acta Zoologica Cracoviensia*, 54A(1-2): 1–29. [2]
601 https://doi.org/10.3409/azc.54a_1-2.01-29
602

603 Reimer, P. J., Austin W. E. N., Bard, E., Bayliss, A., Blackwell, P. G., Bronk Ramsey, C.,
604 Butzin, M., Cheng, H., Edwards, R. L., Friedrich, M., Grootes, P. M., Guilderson, T. P.,
605 Hajdas, I., Heaton, T. J., Hogg, A. G., Hughen, K. A., Kromer, B., Manning, S. W.,
606 Muscheler, R., Palmer, J. G., Pearson, C., van der Plicht, J., Reimer, R. W., Richards, D. A.,
607 Scott, E. M., Southon, J. R., Turney, C. S. M., Wacker, L., Adolphi, F., Büntgen, U., Capano,
608 M., Fahrni, S. M., Fogtmann-Schulz, A., Friedrich, R., Köhler, P., Kudsk, S., Miyake, F.,
609 Olsen, J., Reinig, F., Sakamoto, M., Sookdeo, A., & Talamo, S. (2020). The IntCal20
610 Northern Hemisphere radiocarbon age calibration curve (0–55 cal kBP). *Radiocarbon*, 62,
611 725–757. <https://doi.org/10.1017/RDC.2020.41>
612

613 Riel-Salvatore, J., Popescu, G., Barton, M., 2008. Standing at the gates of Europe: Human
614 behavior and biogeography in the Southern Carpathians during the Late Pleistocene. *Journal*
615 *of Anthropological Archaeology*, 27, 399–417.
616

617 Ringer, Á. (2002). The chronostratigraphy and palaeo-humanecology of the Middle and
618 Upper Palaeolithic in Northeast Hungary, between 130,000 and 10,000 BP. *Praehistoria*, 3,
619 39–46.
620

621 Rougier, H., Milota, Ş., Rodrigo, R., Gherase, M., Sarcină, L., Moldovan, O., Zilhão, J.,
622 Constantin, S., Franciscus, R. G., Zollikofer, C. P. E., Ponce de León, M., & Trinkaus, E.
623 2007. Peștera cu Oase 2 and the cranial morphology of early modern Europeans. *Proceedings*
624 *of the National Academy of Sciences of the United States of America*, 104, 1165–1170.
625 <https://doi.org/10.1073/pnas.0610538104>
626

627 Sánchez Goñi, M. F. (2022). The climatic and environmental context of the Late Pleistocene.
628 In F. Romagnoli, F. Rivals, S. Benazzi (Eds.), *Updating Neanderthals. Understanding*
629 *Behavioural Complexity in the Late Middle Palaeolithic* (pp. 17–38). Dordrecht: Elsevier.
630 <https://doi.org/10.1016/C2019-0-03240-2>
631

632 Smith, F. H., Janković, I., & Karavanić, I. (2005). The assimilation model, modern human
633 origins in Europe, and the extinction of Neandertals. *Quaternary International*, 137, 7–19.
634 <https://doi.org/10.1016/j.quaint.2004.11.016>
635

636 Smith, F. H., Trinkaus, E., Pettitt, P. B., Karavanić, I., & Paunović, M. (1999). Direct
637 radiocarbon dates for Vindija G₁ and Velika Pećina Late Pleistocene hominid remains.
638 *Proceedings of the National Academy of Sciences of the United States of America*, 96, 12281–
639 12286. <https://doi.org/10.1073/pnas.96.22.12281>
640

641 Soficaru, A., Doboş, A., & Trinkaus, E. 2006. Early modern humans from the Peștera Muierii,
642 Baia de Fier, Romania. *Proceedings of the National Academy of Sciences of the United States*
643 *of America*, 103, 17196–17201. <https://doi.org/10.1073/pnas.0608443103>
644

645 Talamo, S., Hajdinjak, M., Mannino, M. A., Fasani, L., Welker, F., Martini, F., Romagnoli,
646 F., Zorzin, R., Meyer, M., & Hublin, J.-J. (2016). Direct radiocarbon dating and genetic
647 analyses on the purported Neanderthal mandible from the Monti Lessini (Italy). *Scientific*
648 *Reports*, 6, 29144. <https://doi.org/10.1038/srep29144>

649
650 Thoma, A., 1957. A Homo sapiens fossilis nyakszirtesontjának töredéke a Tapolcai
651 sziklafülkéből. (Un fragment d'occipital [Homo sapiens fossilis] provenant de l'abri de
652 Tapolca.) *Herman Ottó Múzeum Évkönyve*, 1, 60–69.

653
654 Thoma, A. (1963). The dentition of the Subalyuk Neanderthal child. *Zeitschrift für*
655 *Morphologie und Anthropologie*, 54, 127–150. <https://www.jstor.org/stable/25754835>
656

657 Tillier, A-m. (2011). Facts and Ideas in Palaeolithic Growth Studies (Paleauxology). Evidence
658 from Neanderthals in Europe. In S. Condemi, G.-C. Weniger (Eds.), *Continuity and*
659 *Discontinuity in the Peopling of Europe. One Hundred Fifty Years of Neanderthal Study* (pp.
660 139–154). Vertebrate Paleobiology and Paleoanthropology, Dordrecht: Springer.
661 https://doi.org/10.1007/978-94-007-0492-3_12
662

663 Tillier, A-m., Mester, Zs., Henry-Gambier, D., Pap, I., Ringer, Á., & Gyenis, Gy. (2006). The
664 Middle-Upper Palaeolithic transition in Hungary: an anthropological perspective. In V.
665 Cabrera-Valdés, F. Bernaldo de Quirós Guidotti, J. M. Maíllo Fernández (Eds.), *En el*
666 *centenario de la Cueva de El Castillo: el ocaso de los Neandertales* (pp. 89–106). Madrid:
667 Centro Asociado a la Universidad Nacional de Educación a Distancia en Cantabria.
668

669 Tillier, A-m., Sansilbano-Collilieux, M., David, F., Enloe, J. G., Girard, M., Hardy, M.,
670 D'iatchenko, V., Roblin-Jouve, A., & Tolmie, C. (2013). Les vestiges néanderthaliens
671 provenant des niveaux moustériens I et J de la Grotte du Bison à Arcy-sur-Cure (Yonne) :
672 bilan actuel. *Bulletins et Mémoires de la Société d'Anthropologie de Paris*, 25, 39–54.
673 <https://doi.org/10.1007/s13219-012-0061-7>
674

675 Trinkaus, E., Moldovan, O., Milota, Ş., Bilgăr, A., Sarcina, L., Athreya, S., Bailey, S. E.,
676 Rodrigo, R., Gherase, M., Higham, T., Bronk Ramsey, C., & van der Plicht, J. (2003). An
677 early modern human from the Peștera cu Oase, Romania. *Proceedings of the National*
678 *Academy of Sciences of the United States of America*, 100, 11231–11236.
679 <https://doi.org/10.1073/pnas.2035108100>
680

681 Vogel, J. C., & Waterbolk H. T. (1967). Groningen radiocarbon dates VII. *Radiocarbon*, 9,
682 107–155.
683

684 Vörös, I. (2000). Macro-mammal remains on Hungarian Upper Pleistocene sites. In V. T.
685 Dobosi (Ed.), *Bodrogheresztúr–Hénye (NE Hungary), Upper Palaeolithic site* (pp. 186–212).
686 Budapest: Hungarian National Museum.
687

688 Wolpoff, M. H., Smith, F. H., Malez, M., Radovčić, J., & Rukavina, D. (1981). Upper
689 Pleistocene Human remains from Vindija Cave, Croatia, Yugoslavia. *American Journal of*
690 *Physical Anthropology*, 54, 499–545. <https://doi.org/10.1002/ajpa.1330540407>
691

692 Zilhão, J. (2009). Szeletian, Not Aurignacian: A Review of the Chronology and Cultural
693 Associations of the Vindija G1 Neandertals. In M. Camps, P. Chauhan (Eds.), *Sourcebook of*
694 *Palaeolithic Transitions. Methods, Theories, and Interpretations* (pp. 407–426). New York:
695 Springer. https://doi.org/10.1007/978-0-387-76487-0_27
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

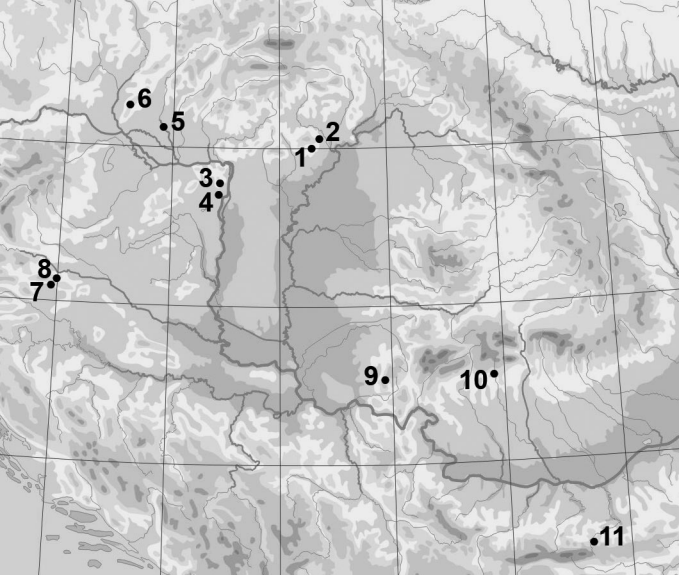
719

720 **Table**

721 Table 1. Data of the radiocarbon analyses. Lab. code = laboratory code; ^{14}C age = conventional date; BP = before present; cal. = calibrated date;
 722 1σ = 1 standard deviation (68.2% probability); 2σ = 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}C age (BP)	$\delta^{13}\text{C}$ (‰)	Calendar age (cal. BP)		C:N	%C	%Coll
					1σ	2σ			
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

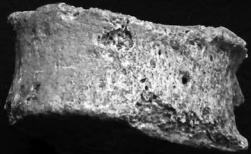


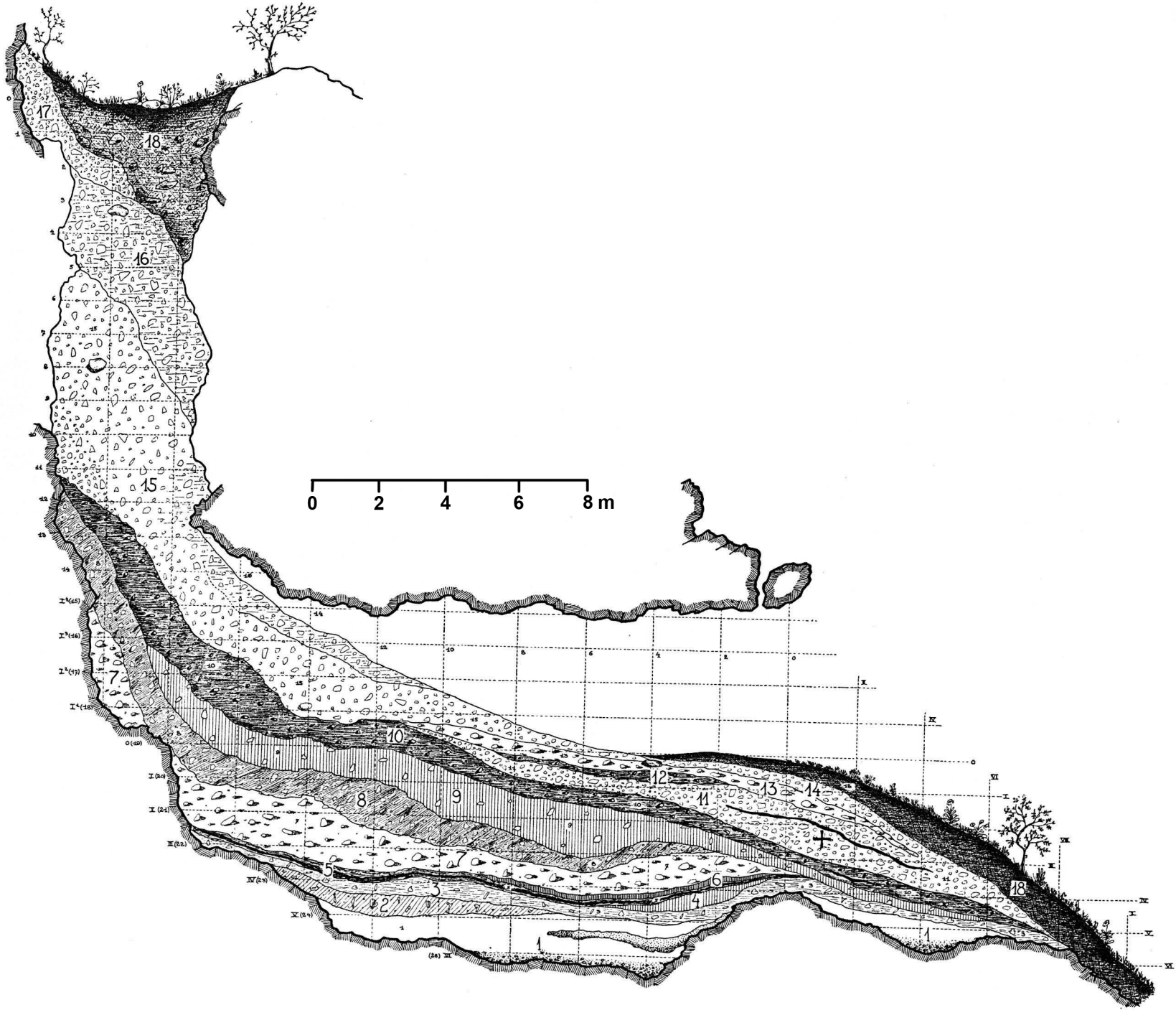
Atlas

68. 140. 6.



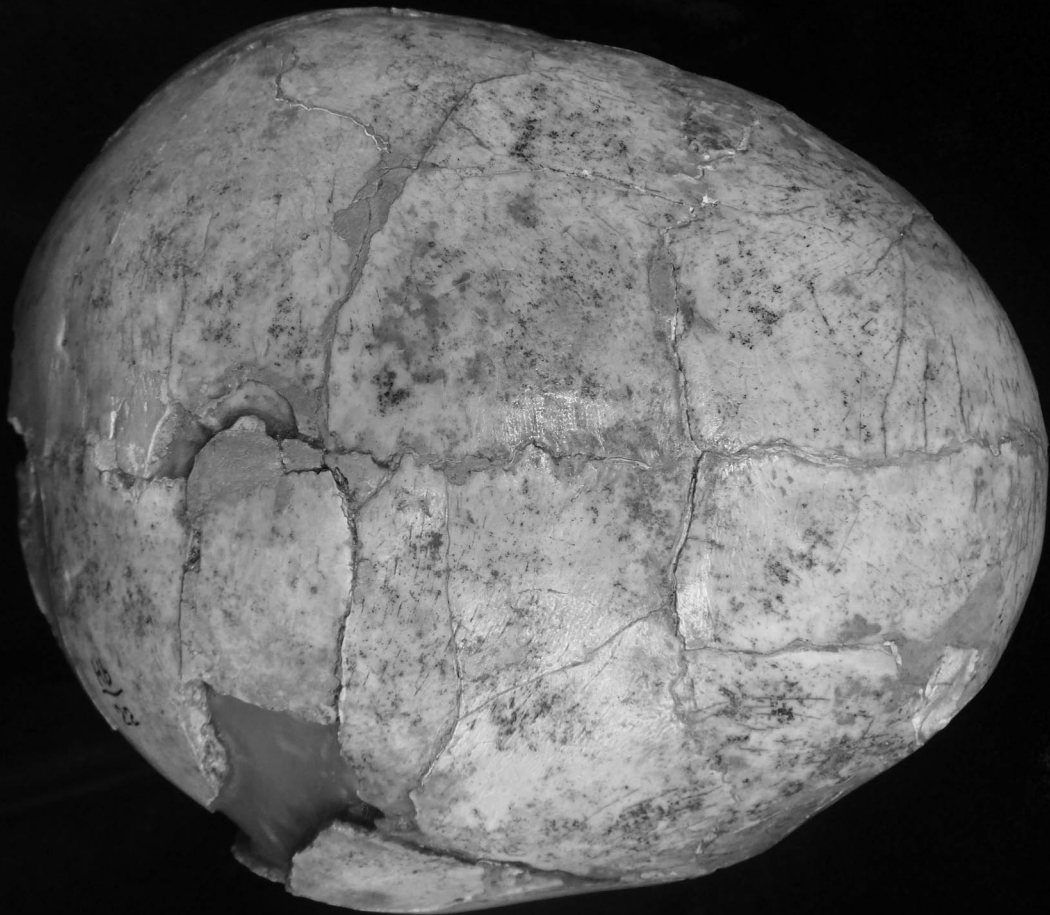
M. kir. Földtani Intézet
Hé. M. sz. 1932
Homo primigenius L.
(corpus vertebrae)
Lelőhely: Mussolini-barlang
Köz. Kádics O. dr. (Börönd-ú.)
35060 — Szénásy





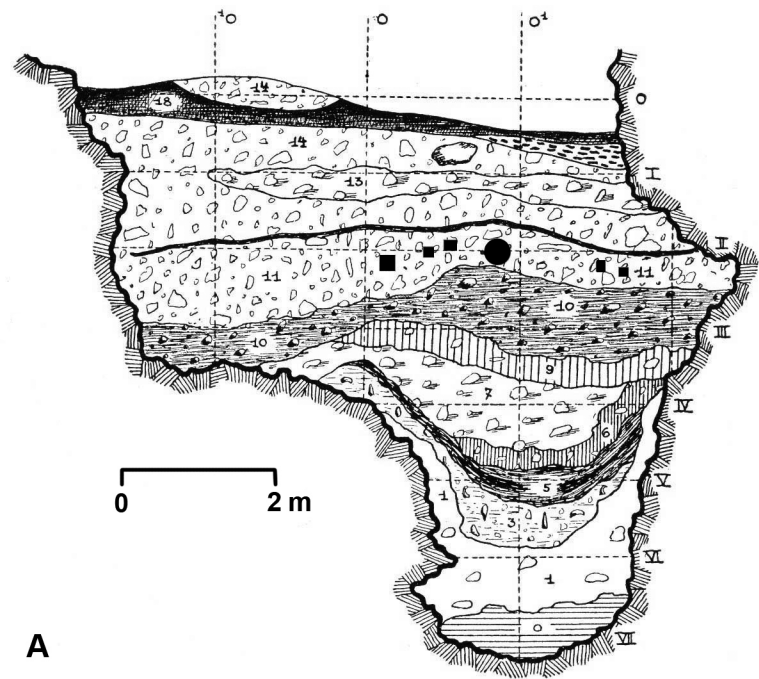




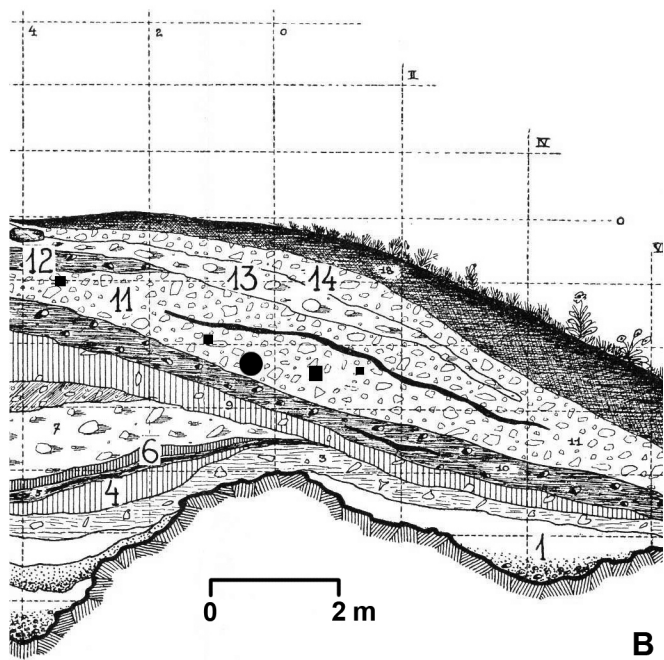








A



B