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

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- Zsolt Mester ^{1,2,*}, Hélène Coqueugniot ^{3,4}, Anne-marie Tillier ³, Wilfried Rosendahl ⁵, Ronny 4
- Friedrich ⁶, Albert Zink ⁷, Frank Maixner ⁷, Olivier Dutour ^{3,4}, Zsolt Bereczki ⁸, Mihály 5
- Gasparik⁹, Ildikó Pap^{8,10,11}, György Pálfi⁸ 6
- 7
- ¹ Institute of Archaeological Sciences, Eötvös Loránd University, Budapest, Hungary 8
- 9 ² UMR 7194 HNHP CNRS/MNHN/UPVD, Institut de Paléontologie humaine, Paris, France
- ³ UMR 5199 PACEA CNRS, Université de Bordeaux, Pessac, France 10
- ⁴ Ecole Pratique des Hautes Etudes PSL University, Paris, France 11
- ⁵ Reiss-Engelhorn-Museen, Museum Weltkulturen Mannheim, Germany 12
- ⁶ Curt-Engelhorn Center Archaeometry gGmbH, Mannheim, Germany 13
- ⁷ Institute for Mummy Studies, Eurac Research, Bolzano, Italy 14
- 15 ⁸ Department of Biological Anthropology, University of Szeged, Szeged, Hungary
- ⁹ Department of Palaeontology and Geology, Hungarian Natural History Museum, Budapest, 16
- 17 Hungary
- ¹⁰ Department of Anthropology, Hungarian Natural History Museum, Budapest, Hungary 18
- ¹¹ Department of Biological Anthropology, Eötvös Loránd University, Budapest, Hungary 19
- * Corresponding author: mester.zsolt@btk.elte.hu 20
- 21
- With 6 figures and 1 table 22

23 **Summary** 24

- The Subalyuk hominin remains were uncovered in 1932 in a cave of the same name in the 25 Bükk Mountains, near the village of Cserépfalu in Borsod-Abaúj-Zemplén county, Northern 26
- Hungary. The remains represent two individuals, an adult and a young child who have been 27
- 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
- during the Late Middle to Early Upper Palaeolithic transition. In this paper, we summarize the 32
- archaeological and chronological context of the two individuals, and publish the first direct 33
- dating results that place them among the Last Neanderthals of Central Europe. 34
- 35
- **Keywords:** Neanderthal, Central Europe, Middle-Upper Palaeolithic transition, Subalyuk, ¹⁴C 36
- 37 dating
- 38

1 Introduction

In Central Europe, 25 sites yielded Neanderthal remains, 13 in the western part and 12 in the 2 eastern part. However, we only possess direct dating from three sites: Kleine Feldhofer Cave 3 in Germany, Vindija Cave in Croatia, and Šal'a in Slovakia (Ahern et al. 2013, Kuzmin & 4 Keats 2014, Hopkins et al. 2022). After the well-known Krapina site in Croatia with the 5 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), including the cranial and postcranial remains of an adult and a child (Bartucz 1940). The cave 8 is located near the village of Cserépfalu (Borsod-Abaúj-Zemplén County) in the Bükk 9 Mountains of northeastern Hungary (Fig. 1), and was fully excavated by János Dancza and 10 Ottokár Kadić in 1932. In addition to hominin remains (Fig. 2), a long sequence of human 11 occupations with rich Middle Palaeolithic lithic assemblages, associated with Upper 12 Pleistocene vertebrate fauna was unearthed (Bartucz et al. 1940). 13 Since the first description by Bartucz (1940), the Subalyuk hominin remains have been the 14

- subject of a few anthropological studies (Thoma 1963, Pap et al. 1995, 1996, Coqueugniot et al. 2014), and palaeopathological examinations were also carried out (Minnikin et al. 2020, Pálfi et al. 2020). From a taxonomic point of view, the hominin fossils were generally considered to be Neanderthals with no exact chronology available. Based on stratigraphic and
- palaeontological considerations, it has been estimated to the Lower Weichselian (Jánossy
 1986, Vörös 2000) or to the Lower Pleniglacial (MIS 4; Kordos & Ringer 1991, Ringer
 2002). Attempts to reassess the archaeological context and bone preservation (Mester 1989,
- 1990, 2004, Mester & Patou-Mathis 2016) have provided an abundance of new information
 that shed light on the current issues regarding uncertainties about the conditions of the
 hominin fossils and their relative age estimates.
- In the frame of the ongoing anthropological research project, the first direct radiometric dating has been performed on both Subalyuk 1 and 2 hominins (curated in the Hungarian Natural History Museum, Department of Anthropology). In this paper, we publish the dating results that place both individuals among the Late Neanderthals of Central Europe, and we summarize the archaeological and chronological context of the Subalyuk hominins.
- 30

31 Archaeological context and relative chronology

Subalyuk Cave is the most important Middle Palaeolithic site of Hungary (Gábori 1976). Its 32 stratigraphic sequence was subdivided into 18 geological layers numbered from bottom to top 33 (Kadić 1940) (Fig. 3). The whole sequence represents the Upper Pleistocene. Layer 1 can be 34 attributed to the Last Interglacial (MIS 5e) by its plastic clayey sediment as well as its 35 reconstructed warm and wet climate, and layer 17 represents the Last Glacial Maximum (MIS 36 37 2) by the presence of wolverine (Gulo gulo), while laver 18 is the Holocene soil (Jánossy 1986, Mester & Patou-Mathis 2016). Archaeological material was recorded from layers 1 to 38 14, documenting different animal and human occupations, while all hominin remains were 39 found in layer 11 (Bartucz et al. 1940, Mester & Patou-Mathis 2016). The hominin skeletal 40 elements representing the two individuals were discovered within one week at different 41 locations near the entrance of the cave on a 5 m \times 5 m surface in a depth of 2–3 m (Bartucz 42 1940, Mester 2004). Only those of the child were gathered together but not in articulation, 43 44 while the adult remains were scattered. Bartucz (1940) had mentioned that similarities in the external aspect of the adult skeletal remains (i.e. same relatively dark color) suggested that all 45 Subalyuk 1 elements were buried in the same layer. However, the spatial distribution of the 46 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 some of the bones were damaged at the time of discovery or later during preparation did not 49 allow him to unequivocally recognize any traces of anthropic or animal activities that could 50

explain this spatial distribution within the site. Unlike the adult remains, the subadult skeletal elements appeared lighter in color. This observation led Bartucz (1940) to assume either that they came from a distinctly lighter coloured layer, or that they had fossilized in a different way than the adult remains, with no evidence for intentional funerary deposition. In a critical reassessment of the archaeological context, Mester (2004) argued that the two individuals had been deposited in different times and different conditions, a hypothetical interpretation that 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

- industries from layers 7 to 14 as a Quina-type Mousterian, on the basis of typology, flakemorphology, and lack of Levallois technology. According to the find inventory recorded at
- the excavation, 4437 lithic artefacts were unearthed in layer 11, from which 776 (i.e. 17.40%)
- were found in the same excavation units as the hominin remains. However, based on the 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 &
- Patou-Mathis 2016). 80 pieces of bone representing 9 species of carnivores were identified with a prevalence of cave bear (*Ursus spelaeus*), and 58 elements representing 6 species of herbivores (caprids, cervids, bovids, equids and hare) were also unearthed. The faunal assemblage in layer 11 together with its seasonal interpretation indicated that Neanderthals 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
- receivation, Jánossy and his colleagues collected original sediments adhering to the wall of the
- cave in 1956 and 1964. Sediment samples corresponding to layers 11 and 12 were wet sieved for microwatchrates. Idenausy (1960, 1986) reported remains of bats and reduced deviated by
- for microvertebrates. Jánossy (1960, 1986) reported remains of bats and rodents dominated by
 Lagurus lagurus. According to Kordos (1991), this phenomenon forms a "Lagurus-horizon"
- *Lagurus lagurus*. According to Kordos (1991), this phenomenon forms a "Lagurus-horizon"
 all over Europe which corresponds to the MIS 4 cold steppe period. Kordos & Ringer (1991)
- concluded that the dominance of *Lagurus* in the microfauna of layers 11 and 12 of Subalyuk
- resulting to a younger phase of MIS 4. According to Mester & Patou-Mathis (2016),
- 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

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

The Subalyuk 1 mandible retains several features that align it with the European Neanderthals (receding symphysis without mental depressions or eminences, backwards positioning of the

- 90 (recearing symphysis without mental depressions of enimences, backwards positioning of the 91 mental foramen under the first permanent molar, gap between the back of the third molar and
- 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
- 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
- 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

could differentiate Neanderthals from modern humans (Pap et al. 1996). Yet, the manubrium
 sterni is especially well preserved and differs from those of modern specimens in a number of

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
- proposed (Coqueugniot et al. 2014) which is consistent with previous data (Thoma 1963, Pap

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
- 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
- (Tillier 2011). Like other young Neanderthal children, Subalyuk 2 retains juvenile features,
 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

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

- The bone collagen was extracted using a modified Longin method (Brown et al. 1988), ultrafiltered to remove molecules of chain length lower than 30 kDa, and freeze-dried. Sample 2 (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
- 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 ¹⁴C 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 ¹⁴C 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

- pretreatment procedure included washes with organic solvents in order to remove the varnish.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 ¹⁴C age of 1619 ± 50 years BP would shift the ¹⁴C
- 164 determination of sample 2 towards younger ages, if residual varnish was present.
- 165

166 **Discussion**

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

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

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

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

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

Chronologically more comparable to Subalyuk are the human remains from layer G₁ of 223 Vindija Cave (Smith et al. 1999, Higham et al. 2006, Devièse et al. 2017). Among the 224 225 fragmentary hominin fossils unearthed in the Vindija G₁ layer, a right mandibular ramus (Vi-207) and a fragment of left parietal (Vi-208) have been directly radiocarbon dated by AMS 226 method. The first dating was obtained with standard Oxford pretreatment and resulted 29,080 227 \pm 400 BP (OxA-8296) and 28,020 \pm 360 BP (OxA-8295) respectively (Smith et al. 1999). By 228 229 these dates, representing an age between 29,880 to 27,300 BP at two standard deviations, the Vindija specimens suggest a very late survival of the last Neanderthals in East Central 230 Europe. Because of its crucial role in the debate on scenarios of the Middle to Upper 231 Palaeolithic transition, both Vindija remains were re-dated using new ultrafiltration 232 pretreatment method (Higham et al. 2006). This attempt produced older dates: $32,400 \pm 1,800$ 233 BP (OxA-X-2089-07) for Vi-207 and 32,400 ± 800 BP (OxA-X-2089-06) for Vi-208. These 234 dates suggest an age estimation from 34,000 to 30,800 BP at two standard deviations. 235 Recently, a new dating was performed for clarifying the supposed effect of presence of 236 contaminants, suggested by the C:N ratios of previous datings (Devièse et al. 2017). For this 237 reason, a more robust purification method targeting the amino acid hydroxyproline has been 238 used. This pretreatment seems to ensure removal of all contaminations. AMS measurements 239 on these samples gave considerably older dates than earlier ones: $43,900 \pm 2000$ BP (OxA-X-240 2089-10) for Vi-207 and 42,700 \pm 1600 BP (OxA-X-2089-09) for Vi-208. These new dates 241 placed the late Neanderthals at Vindija Cave to between 47,900 and 39,500 BP at two 242 standard deviations. The same procedure have been applied for redating the Neanderthal 243 244 bones discovered in Spy Cave (Belgium), and similarly resulted up to 9,000 years older ages with robust purification as ultrafiltration pretreatment methods (Devièse et al. 2021). 245

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

To compare our dates of the Subalyuk Neanderthal specimens to similar remains in East Central Europe, it is reasonable to use the dates OxA-X-2089-07 and OxA-X-2089-06 for the Vindija hominins, since the same pretreatment method was used in both these Vindija and our
Subalyuk specimens. In this case, both Subalyuk 1 and 2 are dated nearly to the same period.
At two standard deviations, the range of Subalyuk dates (34,336–31,230) overlaps
considerably with the Vindija dates (34,000–30,800).

Late Neanderthals from Vindija Cave layer G₁ are associated with an archaeological 255 256 assemblage containing stone and bone artefacts attributed to Middle and Upper Palaeolithic cultural units, including diagnostic Aurignacian bone points (Karavanić & Smith 1998, Ahern 257 et al. 2013). This association should support the Assimilation Model of the origin of 258 anatomically modern humans in Europe (Smith et al. 2005). However, the reliability of this 259 association is highly criticized on the basis of chrono-cultural arguments, and an alternative 260 taphonomical mixture has been proposed as an explanation (Zilhão 2009). On the contrary, 261 the late Neanderthals from Subalyuk Cave are associated with homogenous archaeological 262 material, attributed to the Quina-type Mousterian (Mester 1990, 2008, 2022). In this regard, 263 our new direct dating results argue in favour of the persistence of Neanderthals and late 264 Mousterian industries after 40 ka BP, not only in Western Europe (Finlayson et al. 2006), but 265 also in East Central Europe. This conclusion appears to be in contrast to that of Higham et al. 266 (2014) demonstrating that the end of the Mousterian should be dated between 41,030 and 267 39,260 cal. BP at 95.4% probability. Their study did not include any other Central European 268 Neanderthal sites or data than Vindija itself. Our age for the Subalyuk 1 specimen (39,732-269 39,076 cal. BP (2σ)) already fits well into their timeframe (**Table 1**), however the Mousterian 270 industry is recorded in the subsequent three layers too. The age of Subalyuk 1 specimen 271 corresponds well to the dates of $35,300 \pm 900$ uncal BP (GrN-4443) obtained from charcoal of 272 the hearths unearthed in the lower levels of the open-air site of Érd in Hungary (Vogel & 273 Waterbolk 1967, Gábori-Csánk 1968, 1970). The archaeological context of the human 274 275 occupations at Érd, also attributed to the Quina-type Mousterian, is quite identical to that in Subalyuk Cave (Daschek & Mester 2020, Mester 2022). 276

Unfortunately, there is no clear anthropological evidence of Neanderthal persistence later in
Hungary; the Remete-Felső Cave in Northern Hungary has yielded only a few isolated
undiagnostic teeth, and the human tooth found during old excavations at Dzeravá skala
(Pálffy Cave) in present-day Western Slovakia does not permit a more precise taxonomic
attribution (Tillier et al. 2006).

283 Conclusion

282

In the last two decades, chronological assignments based on direct and indirect dating have 284 documented the last surviving Neanderthals in Europe long after 40 ka BP. The possible 285 cultural interaction between Neanderthals and early modern humans has become the focus of 286 numerous studies (e.g. Bar Yosef & Pilbeam 2000, Conard 2006, Condemi & Weniger 2006, 287 Ahern et al. 2013, Higham et al. 2014, Otte 2014, Benazzi et al. 2015, Talamo et al. 2016, 288 Bard et al. 2020). Much discussion is devoted to the transitional period between 40 and 30 ka 289 BP, and the role played by late Neanderthals in the origin of modern humans in Europe. The 290 first direct dating of the two individuals unearthed in Subalyuk Cave that we report here 291 contributes considerably to this debate. The time range of the two new dates (34,336–31,230 292 BP) overlaps with the dating of the Vindija layer G₁ specimens (34,000–30,800 BP) published 293 294 by Higham et al. (2006) obtained using the ultrafiltration pretreatment method. Also, the approximate date of 39 ka cal BP of Subalyuk 1 adult associated with Quina-type Mousterian 295 industry fits well with the end of the Mousterian calculated by Higham et al. (2014). Our 296 297 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).

As in the rest of Europe, this period was probably complex and dynamic in Hungary. Yet, 300 modern human remains are very fragmentary in the region, and inferences of their possible 301 age come from geological evidence, in the absence of radiometric dating (Tillier et al. 2006). 302 The Homo sapiens occipital bone found without clear archaeological context in the 303 Görömböly-Tapolca Cave (Bükk Mts, Northeastern Hungary) was directly dated by AMS 304 305 radiocarbon measurements using ultrafiltration pretreatment method and yielded $30,300 \pm 300$ BP (Thoma 1957, Davies & Hedges 2008–2009). Thus, the potential coexistence between late 306 Neanderthal groups and modern humans developing Upper Palaeolithic technology is 307 chronologically not yet established in Hungary. However, the arrival of modern humans in 308 this part of Europe is evidenced as early as 41-37 ka in Peştera cu Oase Cave, Southwestern 309 Romania (Trinkaus et al. 2003, Kuzmin & Keats 2014) and 47-43 ka in Bacho Kiro Cave, 310 Central Bulgaria (Hublin et al. 2020). Although Oase 1 and 2 were found in a galery of the 311 cave without any archaeological material, Bacho Kiro individuals were associated with Initial 312 Upper Palaeolithic (IUP) industry. Palaeogenetic (Oase 1, Bacho Kiro IUP) and 313 morphological (Oase 2, Muierii) data show evidences of physical contacts (interbreeding) of 314 these modern human populations with contemporary Neanderthals (Soficaru et al. 2006, 315 Rougier et al. 2007, Fu et al. 2015, Hajdinjak et al. 2021). Cultural contacts have been 316 assumed based on similarities between pendants found in the IUP industry of Bacho Kiro 317 Cave and in the Chatelperronian layers of Grotte du Renne Cave in France made by 318 Neanderthals (Hublin et al. 2020). Unfortunately, Neanderthal human remains were not 319 discovered in this region of Southeastern Europe. The closest ones are known actually from 320 layer G₁ of Vindija Cave and layer 11 of Subalyuk Cave. As it was discussed above, Vindija 321 G₁ hominins have both Middle and Upper Palaeolithic cultural association but it is debated 322 (Ahern et al. 2013, Zilhão 2009), however Subalyuk hominins have evident Quina-type 323 324 Mousterian context. Middle Palaeolithic industries unearthed in the caves of the Southern Carpathians were often related to Quina-type Mousterian or Charentian (Gábori 1976, 325 Păunescu 1989, Mertens 1996). În the Peștera Muierii, the Mousterian industry underlying the 326 layer with modern human remains was dated to about 42 ka by conventional radiocarbon 327 328 method (Soficaru et al. 2006, Dobos et al. 2010). Actually, there are not any archaeological evidences at our disposal witnessing contacts between Late Middle Palaeolithic and Early 329 330 Upper Palaeolithic groups in the region, however it is worth to mention that an analysis using the whole assemblage behavioral indicator (WABI) method demonstrated a broad level of 331 behavioral continuity during the transitional period in terms of land-use strategies, 332 organizational flexibility and lithic technological organization (Riel-Salvatore et al 2008). 333 Therefore, future studies with chronological precision will be important to further our 334 understanding of the patterns of regional population movements, and the contribution of East 335 Central European sites to the debate regarding the peopling history of Europe during the Late 336 Middle to Early Upper Palaeolithic transition. 337

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353 **Declaration of competing interest**

- 354 The authors declare that there is no conflict of interest.
- 355
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- Figure 1. Location of Subalyuk Cave and sites mentioned in the text. 1: Subalyuk, 2:
 Görömböly-Tapolca, 3: Remete-Felső, 4: Érd, 5: Šaľa, 6: Dzeravá skala, 7: Krapina, 8:
 Vindija, 9: Peştera cu Oase, 10: Peştera Muierii, 11: Bacho Kiro.
- Figure 2. Vertebral remains of the Subalyuk adult Neanderthal specimen in the original 1932
 boxes (photo courtesy of György Pálfi).
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- Figure 3. Stratigraphic sequence of Subalyuk Cave (after Kadić 1940, modified); crosses in
 layer 11 represent the location of the hominin remains.
- Figure 4. Anterior (A) and lateral (B) view of the adult mandible (photos courtesy of Ildikó
 Pap).
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- Figure 5. Superior (A) left side (B) and right side (C) view of the subadult calvaria (photos
 courtesy of György Pálfi (A) and Ildikó Pap (B and C)).
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- Figure 6. Reconstruction of the location of the hominin bones in layer 11 at Subalyuk Cave;
- the circle represents the remains of the child; the squares show the adult bones. A: projection
- to the transversal section at line 0; B: projection to the longitudinal section (after Mester 2004,
- 717 Figs 4 and 5).
- 718

Table

Table 1. Data of the radiocarbon analyses. Lab. code = laboratory code; ¹⁴C age = conventional date; BP = before present; cal. = calibrated date; $1\sigma = 1$ standard deviation (68.2% probability); $2\sigma = 2$ standard deviations (95.4% probability). The given δ^{13} C values from measuring with AMS

are not comparable with data from isotope ratio mass spectrometry (IRMS).

Sample	Lab. code.	Material	¹⁴ C age (BP)	δ ¹³ 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























