Wild cereal grain consumption among Early Holocene foragers of the Balkans predates the arrival of agriculture

Authors

E. Cristiani^{1*}, A. Radini^{1,2}, A. Zupancich¹, A. Gismondi³, A. D'Agostino³, C. Ottoni¹, M. Carra¹, S. Vukojičić⁴, M. Constantinescu⁵, D. Antonović⁶, T. Douglas Price⁷, D. Borić^{8,9,10*}

Affiliations

¹ DANTE – Diet and ANcient TEchnology Laboratory, Department of Oral and Maxillo-Facial Sciences, Sapienza University of Rome, Via Caserta 6, Rome 00161, Italy.

² Department of Archaeology, University of York, UK.

³ Laboratory of General Botany, Department of Biology, University of Rome “Tor Vergata,” Via della Ricerca Scientifica 1, 00133 Rome, Italy.

⁴ University of Belgrade, Faculty of Biology, Institute of Botany and Botanical Garden “Jevremovac”, Takovska 43, 11000 Belgrade, Serbia.

⁵ Romanian Academy, Institute for Anthropological Research “Francisc I. Rainer,” Bucharest, Romania.

⁶ Institute of Archaeology, Knez Mihailova 35/IV, 11000 Belgrade, Serbia.

⁷ Department of Anthropology, University of Wisconsin, 1180 Observatory Drive, WI 53706, Madison, USA.

⁸ The Italian Academy for Advanced Studies in America, Columbia University, 1161 Amsterdam Avenue, New York, NY 10024, USA.

⁹ Department of Environmental Biology, Sapienza University of Rome, P.le A. Moro 5, Rome 00185, Italy.

¹⁰ Department of Anthropology, New York University, 25 Waverly Place, 10003 New York, NY, USA.

* Corresponding authors

Abstract

Forager focus on wild cereal plants has been documented in the core zone of domestication in southwestern Asia, while evidence for forager use of wild grass grains remains sporadic elsewhere. In this paper, we present starch grain and phytolith analyses of dental calculus from 60 Mesolithic and Early Neolithic individuals from five sites in the Danube Gorges of the central Balkans. This zone was inhabited by likely complex Holocene foragers for several millennia before the appearance of the first farmers ~6200 cal BC. We also analyzed forager ground stone tools for evidence of plant processing. Our results based on the study of dental calculus show that certain species of Poaceae (species of the genus *Aegilops*) were used since the Early Mesolithic, while ground stone tools exhibit traces of a developed grass grain processing technology. The adoption of domesticated plants in this region after ~6500 cal BC might have been eased by the existing familiarity with wild cereals.

Introduction

46 Forager knowledge and consistent use of wild cereals are still debated and poorly documented
47 outside of the assumed centers of domestication in Southwestern Asia (Kotsakis, 2003). For
48 some time, it has been claimed that in the Balkans some forms of intense gathering or incipient
49 human management of local plant and animal species might have occurred before the full-blown
50 transition to the Neolithic (Clarke, 1978; Halstead, 1996; Kotsakis, 2003; Kotzamani and
51 Livarda, 2014; Srejović, 1988; y'Edynak and Fleisch, 1983), partly due to the region's
52 geographical proximity to the Near East. However, the hypothesis of a systematic use of wild
53 grasses of the Poaceae family (e.g., *Aegilops* spp.; *Hordeum* spp.) during the Mesolithic remains
54 to be verified in this region.

55

56 In Southeastern Europe, specifically in its Mediterranean zone, where one would expect a
57 greater spectrum of small seeded grasses, fruits, and nuts, forager consumption of wild cereals is
58 well documented only at Franchthi Cave in Greece. Here, wild barley (*Hordeum* sp.) appears in
59 the archaeobotanical record starting in the Late Upper Palaeolithic and throughout the
60 Mesolithic, along with oat (*Avena* sp.), pulses (*Lens* sp. Mill.), bitter vetch (*Vicia ervilia* (L.)
61 Willd.), almond (*Prunus amygdalus* Batsch), and terebinth (*Pistacia* cf. *lentiscus* L.) (Hansen,
62 1991; Van Andel et al., 1987). More recently, at Vlakno Cave in Croatia, starch granules of a
63 wild species of barley (*Hordeum* spp.), along with those of oat (*Avena* spp.), were found in the
64 dental calculus of a Mesolithic forager individual, dating to the late eight millennium cal BC
65 burial (Cristiani et al., 2018).

66

67 Besides this type of evidence, data about the increase of cereal-type pollen in the Late
68 Mesolithic come from palynological spectra from across Europe. Although the exclusive
69 reliance on pollen evidence for inferring cultivation can be problematic, consistent evidence for
70 interventions in the forest canopy, marked as disturbances in pollen spectra, might suggest
71 anthropogenic activity. Due to low dispersal rates of cereal-type pollen grains as well as
72 Cerealia-type pollens, their very presence in pollen spectra could be highly indicative of
73 anthropic origin of disturbance phases (Edwards, 1989), and could be interpreted as forest
74 clearances.

75 Recent methodological advances in our ability to analyse micro-residues in the form of micro-
76 remains along with surface modifications and micro-residues on ground stone tools (henceforth
77 GST) (Barton et al., 2018; Dubreuil and Nadel, 2015; Radini et al., 2017) have the potential to
78 contribute to this old debate about Balkan and other prehistoric foragers' familiarity with plant
79 species. Moreover, far from seeing foragers as passive recipients of novelties arriving from
80 Neolithic groups at the time of agricultural transitions, there is now growing evidence of the
81 active role of hunter-gatherers in shaping their landscape ecologies, including plant
82 management, and manipulation of ecosystems through niche constructing (Lombardo et al.,
83 2020; Rowley-Conwy and Layton, 2011; Smith, 2011).

84

85 We examine these pertinent issues in hunter-gatherer research by studying dental remains and
86 GSTs found at Mesolithic and Neolithic sites in the Danube Gorges area of the north-central
87 Balkans between present-day Serbia and Romania (Figs. 1,2,3). This is one of the best
88 researched areas of Europe regarding the Mesolithic-Neolithic transition period with more than

20 sites spanning the duration of the Epipalaeolithic through to the Mesolithic and Early Neolithic (~13,000–5500 cal BC) (Bonsall, 2008; Borić, 2011, 2016; Radovanović, 1996; Srejšović, 1972). Open-air sites began appearing in the archaeological record with the start of the Holocene warming on river terrace promontories in the vicinity of strong whirlpools, narrows, and rapids of the Danube, which facilitated intense fishing operations (Borić, 2011). The Early and Middle Mesolithic (~9600–7300 cal BC) deposits at many sites are damaged by later Mesolithic and Neolithic intrusions, but a number of burials have directly been AMS-dated to these early phases. From the Early Mesolithic onwards, these sites became places for a continuous interment of the dead (Borić, 2016; Borić et al., 2014; Radovanović, 1996), thus creating a substantial mortuary record, which is in the excess of 500 individuals. Osteological collections allowed for a host of bioarchaeological analyses to be applied on this material (Bonsall et al., 1997; Borić et al., 2004; Borić and Price, 2013; Mathieson et al., 2018). Fishing seems to have remained one of the main subsistence foci throughout the Holocene, with a possible intensification during the Late Mesolithic (~7300–6200 cal BC), the period that saw an intense inhabitation of the area, with recognizable features in the archaeological record, such as stone-lined rectangular hearths and abundant primary burials placed as extended inhumations parallel to the Danube River. Between ~6200 and 5900 cal BC, there are clearest indications based on both material culture associations and isotope and genomic data (Borić and Price, 2013; Mathieson et al., 2018) that the local Mesolithic foragers came into contact with the first Neolithic groups appearing in this region, and who likely founded several new sites in this area, especially in the downstream part of the region. These documented encounters of two different cultural groups are most clearly observed at the site of Lepenski Vir (Borić, 2016; Borić et al., 2018). After ~5900 cal BC, it seems that the forager cultural specificity was lost and that various sites remained to be used as typical Early Neolithic Starčevo culture villages up until ~5500 cal BC, when most of the previously used locales were abandoned.

While sources of animal protein in the diet of Mesolithic-Neolithic inhabitants of the area are well understood by now, the significance of plant foods in this region has remained less well known. Non-flaked tools such as pestles, grinders, crushers, and anvils have recently been associated with fruit, seed, and nut processing in early prehistoric and ethnographic contexts (de Beaune, 2004; Dubreuil and Nadel, 2015; Hamon et al., 2021; Pardoe et al., 2019; Wright, 1994). However, this category of artefacts is primarily documented from the Late Mesolithic onwards and only sporadically associated with earlier periods in the region of the Danube Gorges (Antonović et al., 2006; Borić et al., 2014; Srejšović and Letica, 1978).

Such a lack of evidence about the role of plant foods in Mesolithic stems from very limited attempts to recover macro-botanical remains through intense sediment flotation, which has only been applied at two more recently excavated sites in this region—Schela Cladovei (Mason et al., 1996) and Vlasac (Borić et al., 2014; Mason et al., 1996). Despite a generally poor preservation of plant remains due to taphonomic issues, recent carpological analyses indicated a relatively wide spectrum of wild resources available to the local Mesolithic foragers. These included drupes, fruits, and berries (Marinova et al., 2013), among which cornelian cherry (*Cornus mas* L.), hazelnut (*Corylus avellana* L.), and elderberry (*Sambucus nigra* L.) were the most frequent taxa (Filipović et al., 2010; Marinova et al., 2013). Molecular record of *C. avellana* and *S. nigra*

133 was also found preserved in the dental calculus of two Late Mesolithic individuals from Vlasac,
 134 which underwent metagenomic analysis (Ottoni et al., 2021). Moreover, in the study region of
 135 the Danube Gorges, at the site of Vlasac, presumed human palaeofeces contained pollen of
 136 *Amaranthaceae* and *Cerealia* (Cârciumaru, 1978). Evidence from the Mesolithic levels at the site
 137 of Icoana, located in the same region, has suggested local cereal cultivation (Cârciumaru, 1973).
 138 Pollen provides only indirect evidence for consumption and cultivation and, unfortunately, the
 139 1960–70s excavations of the sites in the Danube Gorges did not involve any flotation of
 140 contextual units associated with burning in domestic contexts. While the extensive program of
 141 flotation at the site of Vlasac in the course of more recent work (2006–2009) has not led to the
 142 discovery of macro-botanical remains of wild or domesticated cereal grains, it should also be
 143 emphasized that the new excavations at this site have taken place in a marginal, upslope part of
 144 the site with little or no evidence of domestic features associated with burning that might have
 145 preserved macro-botanical remains (Borić et al., 2014). More recently, starch granules identified
 146 in dental calculus within a sample of 12 individuals provided evidence for the consumption of
 147 domesticated cereals at the site of Vlasac during the Late Mesolithic (Cristiani et al., 2016).
 148

149 Hence, plant debris recovered in human dental calculus constitute the most reliable line of
 150 evidence to unveil the role of plants in the local forager diets. Our previous pilot study has
 151 provided the first evidence of domesticated cereal grains and plant food consumption in the Late
 152 Mesolithic from the analyses of dental calculus (Cristiani et al., 2016). Based on a more robust
 153 sample of human dental calculus, which now also involves numerous Early Mesolithic
 154 individuals not included in our previous study, and complementary functional evidence from the
 155 most conspicuous assemblage of Mesolithic GSTs from the Danube Gorges, the present study
 156 details forager use of certain species of the *Triticeae* tribe and other plant foods in the region
 157 already since ~9500 cal BC.
 158
 159

160 **Figure 1.** Sites in the central Balkans investigated in the article, which provided dental calculus
 161 and ground stone tools. EM = Early Mesolithic; LM = Late Mesolithic; M/N=
 162 Mesolithic/Neolithic; N = Neolithic; BA = Bronze Age; MA = Medieval.
 163
 164

165 **Figure 2.** Studied teeth photographed under the microscope before dental calculus sampling.

Figure 3. Late Mesolithic GSTs from the site of Vlasac featuring use-wear traces and residues related to plant food processing.

170
171
172
173
174
175
176
177
178
179
180
181
182
183
184

Results

Dental calculus

Starch granules were almost ubiquitous in the analyzed individuals and many of them were found still in part associated with dental calculus remains. Six morphotypes have been retrieved in this study (Tables 1,2). We have not attempted the identification of starch granules less than 5 μm to avoid misinterpretation of transitory and small storage starch granules (Haslam, 2004).

Table 1. Details of dental calculus sampled for the study (n=60). * no stable isotope values are currently available for this individual in order to correct the obtained radiocarbon date for the reservoir effect, and the calibrated range should probably be considered too old for its actual age, likely being 200–500 years younger. All calibrated ranges have end points rounded outwards to 5 years. The dates were individually calibrated using OxCal 4.4 and IntCal 20 (Reimer et al., 2020).

Site	Burial no.	Period attribution	AMS dates				Calculus location		
			<i>Lab Code and Source</i>	<i>¹⁴C age (BP)</i>	<i>Reservoir effect corrected age (BP)</i>	<i>95.4% confidence, cal BC</i>	<i>Tooth</i>	<i>Surface</i>	<i>Weight (mg)</i>
Padina	PAD20	Early Meso					17	buccal	9.6
Padina	PAD25	Early Meso					38	buccal	9.59
Padina	PAD15	Early Meso	OxA-17145 (Borić, 2011)	9310±44	8870±63	8240–7770	38	lingual	9.58
Padina	PAD16 a	Early Meso	PSU-2407 (Mathieson et al., 2018)	9340±35	8907±66	8275–7815	34	buccal	9.62
Padina	PAD18 b	Early Meso	PSU-2376 (Mathieson et al., 2018)	9715±40	9424±55	9115–8550	48	lingual	9.67
Padina	PAD9	Early Meso	AA-57771 (Borić, 2011)	9920±100	9480±110	9225–8495	42, 46	lingual	9.59
Padina	PAD11	Early Meso	OxA-16938 (Borić, 2011)	9665±54	9225±70	8620–8290	27	lingual	9.57
Padina	PAD12	Early Meso	BM-1146 (Borić, 2011)	9331±58	–	8750–8350	27	lingual	9.76
Padina	PAD17	Early Meso	PSU-2375 (Mathieson et al., 2018)	9505±35	9105±62	8540–8230	25	buccal	9.64
Lepenski Vir	LV50	Early Meso	BA-10651 (Borić et al., 2018)	9455±38	9082±62	8540–8020	35	buccal	9.99
Lepenski Vir	LV20	Early Meso	OxA-39629 (this paper)	10,268±38	9928±58	9740–9270	48	lingual	9.73
Padina	PAD26	Early Meso					14	buccal	9.58
Padina	PAD6	Early Meso					47	lingual	9.65
Padina	PAD2	Late Meso	BM-1143 (Borić, 2011)	7738±51	–	6650–6465	36	lingual	9.68
Hajdučka Vodenica	HV25/2 6	Late Meso					44	buccal	9.60
Hajdučka Vodenica	HV29	Late Meso	AA-57774 (Borić, 2011)	8151±60	7711±75	6690–6425	48	lingual	10.72
Hajdučka Vodenica	HV8	Late Meso	OxA-13613 (Borić, 2011)	8456±37	8016±58	7075–6695	48	buccal	9.61
Hajdučka Vodenica	HV11	Late Meso					48	buccal	9.71
Hajdučka Vodenica	HV profil A	Late Meso					27	buccal	9.70
Hajdučka Vodenica	HV30	Late Meso					27	buccal	9.56
Vlasac	VL82c	Late Meso	BRAMS-2588 (Jovanović et al., 2021)	8035±28	7595±53	6590–6270	42	buccal	9.68
Vlasac	VL2	Late Meso					14	buccal	9.54
Vlasac	VL80a	Late Meso					26	lingual	9.84
Vlasac	VL55	Late Meso	BRAMS-2583 (Jovanović et al., 2021)	8377±29	7837±63	7035–6500	33	lingual	9.64
Vlasac	VL74	Late Meso	BRAMS-2587 (Jovanović et al., 2021)	8149±28	*	7315–7055*	28	lingual	9.70
Vlasac	VL83	Late Meso	OxA-5826 (Borić, 2011)	8200±90	7760±100	7030–6420	24	lingual	9.62
Vlasac	VL43	Late Meso					27	lingual	
Vlasac	VL31	Late Meso	AA-57777 (Borić, 2011)	8196±69	7756±82	6900–6430	26	buccal	9.58
Vlasac	VL45	Late Meso	AA-57778 (Borić et al., 2008)	8117±62	7677±77	6655–6400	38	buccal	9.50
Vlasac	VL70	Late Meso					17	buccal	10.42
Vlasac	VL79	Late Meso	BRAMS-2448 (Jovanović et al., 2021)	8005±29	7565±54	6565–6250	16	buccal	9.60
Vlasac	U44	Late Meso					27	buccal	9.96
Vlasac	H232	Late Meso	OxA-20702 (Borić, 2011)	7725±40		6640–6470	28	lingual	9.92
Vlasac	H317	Late Meso	PSU-2381 (Mathieson et al., 2018)	8110±35	7625±71	6645–6270	26, 36	lingual	9.73
Vlasac	U115	Late Meso					28	buccal	9.95
Vlasac	U326	Late Meso	PSU-2382 (Mathieson et al., 2018)	8045±30	7728±51	6645–6465	17	buccal	9.94
Vlasac	U326	Late Meso	PSU-2382 (Mathieson et al., 2018)	8045±30	7728±51	6650–6460	1, 2	buccal	9.1
Vlasac	U64 x.11/H8 l	Late Meso	OxA-20762 (Borić, 2011)	8125±45	7685±64	6645–6430	20, 26, 27, 29, 30, 31	lingual	9.92
Vlasac	H341	Late Meso					1	buccal	10.12
Vlasac	VL48	Late Meso					34	lingual	10.06
Vlasac	U222 x.18	Late Meso					2	buccal	9.54
Lepenski	LV28	Meso-Neo				–	43	buccal	9.58

Vir									
Lepenski Vir	LV79a	Meso-Neo	OxA-25091 (Bonsall et al., 2015)	7605±38	7119±74	6220–5805	33	buccal	9.69
Hajdučka Vodenica	HV16	Meso-Neo					36	lingual	9.54
Hajdučka Vodenica	HV19	Meso-Neo					37	buccal	9.58
Hajdučka Vodenica	HV13	Meso-Neo	AA-57773 (Borić, 2011)	7435±70	6995±83	6020–5720	17	lingual	9.56
Padina	PAD4	Meso-Neo	AA-57769 (Ottoni et al., 2021)	7518±72	7078±85	6080–5745	48	buccal	9.73
Padina	PAD5	Meso-Neo	AA-57770 (Borić, 2011)	7598±72	7158±85	6230–5845	15	buccal	8.10
Vlasac	U24 x.30	Meso-Neo					32	lingual	9.97
Vlasac	H53	Meso-Neo	OxA-16544 (Borić et al., 2014)	7035±40	–	6015–5805	3, 28, 29	lingual	10.04
Lepenski Vir	LV4	E. Neolithic					33	buccal	9.64
Lepenski Vir	LV73	E. Neolithic	BA-10652 (Borić et al., 2018)	7265±30	6973±48	5980–5735	34	buccal	9.69
Lepenski Vir	LV8	E. Neolithic	AA-58319 OxA-25207 (Borić et al., 2018)	6825±51 7097±36	6690±54 6984±39	5715–5520 5985–5750	44	lingual	9.69
Lepenski Vir	LV32A	E. Neolithic	OxA-5828 (Bonsall et al., 1997)	7270±90	7032±95	6065–5730	42, 43, 36	buccal	9.77
Lepenski Vir	LV17	E. Neolithic	AA-58320 (Bonsall et al., 2015)	7007±48	6787±53	5775–5565	15	lingual	9.10
Padina	PAD30	Bronze Age	PSU-2379 (Lazaridis et al., in press)			2140–1765	47	buccal	9.69
Velesnica	2A	Neo	OxA-19191 (Bonsall et al., 2015)	7409±38	7196±47	6220–5930	8	lingual	9.74
Velesnica	2D	E. Neolithic	OxA-19210 (Bonsall et al., 2015)	7327±38	7183±42	6215–5925	9	lingual	7.2
Girlestj		E. Neolithic					2	lingual	8.22
Lepenski Vir	LV30	Medieval	OxA-25218 (Bonsall et al., 2015)	427±23		AD1440–1490	16	lingual	9.67

185

186

187

188

189

190

191

192

193

194

195

196

197

198

199

200

201

202

Type I. Size, shape, morphology and bimodal distribution that characterize granules of this type are encountered in Europe only in the members of the plant tribe Triticeae (Poaceae family) and considered diagnostic features for taxonomic identification (Henry and Piperno, 2008; Stoddard, 1999; Yang and Perry, 2013). Such distribution involves the presence of large granules (A-Type), mostly with a clear, round to sub-oval in 2D shape, ranging between 21.1 and 62.7 µm in maximum dimensions (mean size of 41.9 µm), lenticular 3D shape with equatorial groove always visible, a central hilum and high density of deep lamellae concentrated in the mesial part; and small granules (B-Type) with round/sub-oval shapes, a central hilum, generally smaller than 10 µm (Geera et al., 2006; Stoddard, 1999; Yang and Perry, 2013). A-Type granules possess diagnostic features while smaller B-Type granules are rarely diagnostic to taxa (Yang and Perry, 2013). However, in our archaeological population, variability in the proportion and dimension of small B-type granules has been noticed, resulting in a unimodal granule size distribution without a clear distinction between A and B granules in some cases. Several studies (Howard et al., 2011; Stoddard and Sarker, 2000) suggested that this characteristic is common in the species of the genus *Aegilops* of the Triticeae tribe and can be attributed to both environment (Blumenthal et al., 1995, 1994) and genetics (Stoddard and Sarker, 2000). A unimodal starch granule size distribution characterized by normal A-type granules and a lack/reduced quantity of

203 B-type granules was also evident in our modern reference collection of local *Aegilops* species
204 (Fig. 6). Based on these observations, Type I category was further divided into two subtypes (Ia
205 and Ib). In subtype Ia, B-Type granules are small, dimensionally uniform (up to 12 μ m) and
206 round in shape (fig.6). Conversely, subtype Ib is characterized by a high variation in starch
207 granule size not allowing for a distinction between A and B-type granule, resulting in a
208 unimodal distribution (Fig.9).

209
210 Type I (Ia and Ib) is very common in the analyzed samples (Table 2), as already emphasized in
211 our earlier study albeit in different quantities (24). These starch granules were documented,
212 often lodged in the amyloplast, in most of the analyzed Mesolithic individuals (5 for EM, 16 for
213 LM, 5 for M/N), and in five EN individuals of our population (Table 2). A-Type granules
214 recovered in EM and most of the LM individuals were very large, mostly with a clear, round
215 shape, central *hilum*, and high density of deep lamellae mainly concentrated in the mesial part of
216 the granules. Based on literature (Henry et al., 2011; Yang and Perry, 2013) and our extensive
217 experimental and statistical results on modern botanical collection (Tables 4,5; Figs. 6, 7, 9), we
218 confirm that these characteristics are consistent with A-Type granules of most species of the
219 Triticeae tribe.

220
221 *Subtype Ia.* A few LM and M/N individuals (for example, HV11 and 16, H53, 64.x11, H327,
222 H232) yielded a combination of oval A-Type granules and uniformly small, round B-Type
223 granules (Fig. 4m). Our previous claims that this pattern is a recognizable feature of the
224 domestic species of the tribe Triticeae (e.g., *Triticum* spp./*Hordeum* spp.) (Figs. 6,9) (Cristiani
225 et al., 2016) are now further supported by a new morphometric analysis of both domestic and
226 wild Triticeae species (Fig.9). Moreover, in the same individuals, A-Type granules could show
227 cratered appearance (Fig. 4y). Similarly, in the EN individuals, lenticular and oval/sub-oval A-
228 Type granules with equatorial groove and, an often visible, cratered surface are always
229 associated with very small and uniformly shaped B-Type granules. Type A granules appear
230 damaged in few EN individuals, which may be linked to enzymatic digestion (salivary amylase)
231 although plant food processing could also result in starch damage based on experimental results
232 (Ma et al. 2019; Zupancich et al. 2019)

233
234 *Subtype Ib.* Significant unevenness in granule dimensions and shape was recorded in the EM
235 and most of the LM individuals (e.g., PAD9 and VL45). Granules in this subtype are
236 dimensionally variable and their shapes can range from round to oval (Fig. 4b). The well-known
237 limitations in the inclusion, preservation, and recovery of plant debris in dental calculus (Radini
238 et al., 2017) might be responsible for not recognizing this subtype previously.

Figure 4. Starch granules from Mesolithic and Neolithic dental calculus. *Early Mesolithic:* (a) Type Ib (PAD11); (b) Type Ib (PAD9); (c) Type Ib (PAD11); (d) Type V (PAD12); (e) Type III (PAD11); (f) Type Ib (PAD15); *Late Mesolithic:* (g) Type II (VL82c); (h) Type IV (VL31); (i) Type VI (VL70); (j, k) Multicellular structures of long cells embedded in dental calculus (HV25/26, VL70); (l) Type Ia (HV11); *Mesolithic-Neolithic:* (m) Type Ia (HV16). *Neolithic:* (n) Type III (LV32a); (o-v) Damaged Type I granules (A-Type granules) (VEL-2D); (w) Type I (A-Type granule) (VEL-2D); (x) Single dendritic cell (Gârlești); (y) Type I (A-Type granule) (VEL-2D) (VEL-2A).

Figure 5. Other dietary and non-dietary debris found in Mesolithic dental calculus from the Danube Gorges. *Early Mesolithic*: (a) Type V (PAD11); (b,c) Type III (PAD12); (d) Type I (A-Type granule) (VEL-2D) (PAD12); (e) Type I (A-Type granule) (PAD12); (f) Smoke particle (LV50); (g, h) Plant fiber embedded in calculus (PAD16); (i) Type Ib (PAD9); (j) Feather barbule embedded in calculus (PAD9); *Late Mesolithic*: (k) Type II (PAD2); (l) Polylobate phytolith (US64 x.11); (m) Phytoliths (VL79); (n-p) Type VI (VL70,VL83); (q) Feather barbules embedded in calculus (HV25/26); (r) Feather barbule embedded in calculus (VL80a); (s) Echininate pollen grain in calculus (VL83); (t) Plant tissue (LV79a); (u) Type II (VL43); (v)

259 Type Ia (HV11); *Mesolithic/Neolithic*: (w) Type I (HV16); (x) Wood particle (PAD4); (y)
 260 Phytoliths (LV28); (z) Feather barbule (PAD4).
 261

Figure 6. Starch granule morphological variability within the species of the genus *Aegilops* and domestic species of the Triticeae tribe. **a)** *Aegilops cylindrica*; **b)** *A. neglecta*; **c)** *A. speltoides tauschii*; **d)** *A. caudata*; **e)** *A. triuncialis*; **f)** *A. comosa*; **g)** *A. uniaristata*; **h)** *A. ventricosa*; **i)** *A. geniculata*; **j)** *A. crassa*; **k)** *A. peregrina*; **l)** *Elymus caninus*; **m)** *Bromus tectorum*; **n)** *Agropyron pungens*; **o)** *A. farctus*; **p)** *Dasypyron villosum*; **q)** *Triticum monococcum*; **r)** *Hordeum vulgare*; **s)** *T. dicoccum*; **t)** *T. aestivum*.

Figure 7. Experimental reference for starch granules identified in the dental calculus and GSTs. **a)** *Aegilops triuncialis*; **b)** *A. crassa*; **c,d)** *Avena strigosa*; **e,f)** *Setaria italica*; **g)** *Vicia cracca*; **h)** *V. sylvatica*; **i)** *Quercus pubescens*; **j)** *Q. robur*; **k)** *Q. colurna*; **l)** *Cornus mas*.

Type II. Starch granules attributed to this type consist of large aggregates as well as clustered polyhedral/irregular granules (main axis ranging from 5 to 15 µm). They were retrieved from 10 individuals (2 EM, 11 LM, 2 M/N, and 3 EN) (Table 2) (Fig. 4g). The identification of archaeological specimens is based on published records (Lippi et al., 2015) and our experimental reference (*Avena barbata* L., *A. strigosa* Schreb., *A. fatua* L.) (Fig. 7). Granules of this morphotype were grouped in the tribe Aveneae/Poeae based on the fact that such large aggregates are found mostly in the genus *Avena* L. (oat), which is very common in the region.

Type III. Starch granules attributed to this type are characterized by a polyhedral to sub-polyhedral 3D morphology, a central hilum, and fine cracks. They were recovered in 16 individuals (5 for EM, 16 for LM, 2 for M/N, and 1 for EN) (Table 2) (Fig. 4e, Fig. 5b and c). These features are consistent with starch granules of the tribe Paniceae of the grass family Poaceae and very well known in ancient starch research (Madella et al., 2016). In our sample, starch granules assigned to type III reach 21 µm of maximum width, which falls within the size range found in several species of *Setaria* spp., *Panicum* spp., and *Echinochloa* spp. (Lucarini et al., 2016) (Fig. 7). Small granules characterized by a round to sub-polyhedral 3D morphology, and a central open hilum have been attributed to the tribe Andropogoneae and are here described under the general group of “millets” as is common practice (Madella et al., 2016).

Type IV. Starch granules of this type are identified in 10 individuals (2 EM, 8 LM, 1 M/N, and 2 EN) and are recovered above 6 granules per specimen, with the exception of the only EN

individual (Table 2). Diagnostic morphological characteristics for type IV granules are known in ancient starch research and include a reniform shape in 3D, a collapsed/sunken hilum forming a deep fissure along almost the entire granule, and a size ranging between 12 to 35 μm (Henry et al., 2011). Small cracks were observed departing from such hilum and were very evident under cross-polarized light. In most cases the extinction cross was very bright and showed several lateral arms diverging from the hilum in correspondence with the cracks (Fig. 4H). Moreover, lamellae were visible towards the outer part of the granules. All these features are very peculiar and diagnostic of starch granules included in the species of the plant family Fabaceae (Henry et al., 2011), which is mostly known for its several edible domesticated species of legumes (e.g. *Lens culinaris* Medikus, *Vicia faba* L., and *Pisum sativum* L.), but also has a number of wild edible such as vetches (*Vicia* spp.). While many edible species of the family Fabaceae grow in the Balkans (e.g. *Vicia sativa* L., *V. cracca* L., *V. hirsuta*, *V. ervilia*, *Lathyrus pratensis* L., *L. sylvestris* L.), an identification at species or genus was not possible due to overlaps in shape and size of starch granules at tribe level, which were observed in our modern reference collection (Fig. 7).

Type V. Few starch granules attributed to this type have been identified in 8 individuals (2 EM, 5LM, 1MN) (Fig. 4d, 5a and Table 2). Starch granules reach 23 μm in length and are mostly triangular with round corners and/or have an irregular oval shape (Fig. 5a). Overall, lamellae can rarely be visible. The granules show a linear fissure in the center and sometimes the hilum appears as a wide depression. Under polarized light, the hilum is mostly centric while the extinction cross has bent arms. This type was found to have a very close visual match with the starch found in acorns of oaks (*Quercus* spp.), a Fagaceae member and well known in ancient starch research (Liu et al., 2010) (Fig. 7i,j).

Type VI. Granules ascribed to this type have been identified in two individuals (1 LM, 1 M/N) (Table 2). They are characterized by a round 3D morphology and a central hilum, which appears as a wide depression, and no lamellae or facets (Fig. 4i, Fig. 5n-p). Zarrillo and Kooyman (2006) consider these morphological features diagnostic of some species of drupes and berries. In our sample, starch granules of this morphotype can reach 12 μm of maximum width, which is beyond species of berries and drupes in the Rosaceae family known in literature (Zarrillo and Kooyman 2006) and in our modern reference (e.g. *Prunus spinosa* L.). Based on our experimental record, we assign type VI to species of the family Cornaceae (e.g. *Cornus mas*) (Fig. 7), the remains of which are documented at Vlasac (Filipović et al. 2010).

In addition to starch granules, 42 phytoliths were retrieved in 24 individuals (EM=4; LM=13; MN=2; N=5). Mostly, short cells, commonly produced in leaves, stems and inflorescences, were identified (14) and attributed to Pooid grasses. Multicellular structures of long cells were identified in Mesolithic individuals (HV25/26, VL70, VL79, U222) (Fig. 4j,k; Fig. 5m). Of particular relevance is the recovery of multicellular phytoliths with dendritic appearance. It was observed at least in one case, still embedded in the dental calculus (Fig.4k). Single or multicellular dendritic structures were also identified in Neolithic individuals (VEL-2D and Gîrlestj) (Figs. 4w,x) (Fig. 4w). A single polylobate cell was found in one Late Mesolithic individual (US64 x.11). With the exception of dendritic structures, characterizing grass

inflorescences, different non-dietary reasons may be suggested for the inclusion of phytoliths in dental calculus (i.e., accidental ingestion, inhalation, dust in the environment generated by the use of grasses in a variety of activities and uses, such as flooring, kindling etc.) (Norström et al., 2019).

Table 2. Details of the micro-debris (starch granules and other micro-remains) found in the archaeological dental calculus samples (PO=Pollen; W=Wood; Ch= Microcharcoal/burnt debris; Gr=Grit; P=Phytoliths; FE=Feathers; FI=Fibers; FU=Fungi; S=Smoke) (n=51).

	Site	Burial label	Chrono-cultural attribution	Type I Tritic eae	Type II Aveneae	Type III Paniceae	Type IV Fabeae	Type V Fagaceae	Type VI Cornaceae	Indet.	Other
1	Padina	PAD20	Early Meso			7	4			3	1P/10FI/2FE/2W/1Ch/Gr
2	Padina	PAD25	Early Meso			1					1P/1Ch/Gr
3	Padina	PAD15	Early Meso	>100	4		6				1P/4PO/1W/1Ch/Gr
4	Padina	PAD16a	Early Meso			20				3	1P/10FI/8Ch/Gr
5	Padina	PAD9	Early Meso	>200							2FI/2FE
6	Padina	PAD11	Early Meso	>100		8		1			
7	Padina	PAD12	Early Meso	36		12		1		1	
8	Lepenski Vir	LV50	Early Meso		1					1	1FI;S
9	Lepenski Vir	LV20	Early Meso	4						1	
10	Padina	PAD2	Late Meso	13	1	7	1				1PO/1FI/2FE/2W/1Ch/Gr
11	Hajdučka Vodenica	HV25/26	Late Meso	5		15				1	2P/1PO/2FI/3FE/1Ch/3FU/Gr
12	Hajdučka Vodenica	HV29	Late Meso		5		3			5	3P/1PO/1FI/1FE/13W/1FU/Gr
13	Hajdučka Vodenica	HV8	Late Meso		1						
14	Hajdučka Vodenica	HV11	Late Meso	>100	8	1					
15	Hajdučka Vodenica	HV profil A	Late Meso			14				1	3PO/1FI/2FE/3W/1Ch/1FU/Gr
16	Hajdučka Vodenica	HV30	Late Meso			1					
17	Vlasac	U222 x.18	Late Meso				2				1P
18	Vlasac	U326	Late Meso	>60						1	1P
19	Vlasac	VL82c	Late Meso	4	23	7	2			5	1P/3PO/1FE/1W/1Ch/Gr
20	Vlasac	VL2	Late Meso	2	12						2P/1PO/2FI/1FE/2FU/Gr
21	Vlasac	VL80a	Late Meso	3	15	5	5	1			1P/4FE/1W/1Ch/1FU/Gr
22	Vlasac	VL55	Late Meso			6				1	1P/1PO/1FI/1W/1FU/Gr
23	Vlasac	VL74	Late Meso			1				1	1P/3PO/17FI/1Ch/Gr
24	Vlasac	VL83	Late Meso	6		8	1				1P/1PO/

											1FE/2W/ 5Ch/Gr
25	Vlasac	VL43	Late Meso	>200	12	1		1		2	2FE/1W/ 2Ch/1F U/Gr
26	Vlasac	VL31	Late Meso			18	3			3	4PO/5F E/1Ch/2 FU/Gr
27	Vlasac	VL45	Late Meso	23	8	20		1		14	1PO/2F E/2Ch
28	Vlasac	VL70	Late Meso	3		3		1	14		4P/1FI/7 Ch
29	Vlasac	VL79	Late Meso								1P/2FI
30	Vlasac	U44	Late Meso	3			2				
31	Vlasac	H232	Late Meso	<100	4	1					1PO/1F E
32	Vlasac	U115	Late Meso					1			
33	Vlasac	U64 x.11	Late Meso	>200	10	32				4	2P/4FI/2 FE/3Ch/ 1FU
34	Vlasac	H341	Late Meso	1							
35	Lepenski Vir	LV28	Meso-Neo	4		3	1			6	2P/2PO/ 1FE/2W/ 4Ch/Gr
36	Hajdučka Vodenica	HV16	Meso-Neo	>200							1FU
37	Hajdučka Vodenica	HV19	Meso-Neo	1							1FE
38	Hajdučka Vodenica	HV13	Meso-Neo		1						
39	Padina	PAD4	Meso-Neo					1		7	2PO/1FI /3FE/4W /2Ch/1F U/Gr
40	Padina	PAD5	Meso/Neo	6							
41	Vlasac	U24 x.30	Meso-Neo						10		1P/2Ch
42	Vlasac	H53	Meso-Neo	22	>200	5					1FE/1W
43	Lepenski Vir	LV4	Neo	1	3					1	
44	Lepenski Vir	LV73	Neo	12	9					1	7P/2PO/ 17FI/1F E/3FU/G r
45	Lepenski Vir	LV8	Neo	11			4				1W
46	Lepenski Vir	LV32A	Neo		8	>200					1P/2FE
47	Lepenski Vir	LV17	Neo	14			5				
48	Velesnica	2A	Neo								4FU
49	Velesnica	2D	Neo	12							2P/2FU
50	Gârlești		Neo	1							1P/1Ch
51	Lepenski Vir	LV30	Medieval			12	4				1P/1PO/ 4Ch/1F U/Gr
	Total			>1446	324	>409	43	8	24		284

Ground stone tools

Diagnostic use-wear and residues are identified on 44 GSTs from the site of Vlasac. Analyzed tools included functional categories such as handstones (e.g., grinders and crushers) as well as passive bases (anvils) (Table 3). All of the tools are made of sandstone, characterized grains ranging in size between 0.2 and 1 mm densely distributed within the matrix. The combination of different functional modifications (i.e., flattened surfaces, pitted areas, rounding, etc.) on the single specimens suggests the long and complex life-histories of the artefacts, often used in different activities. Within the tools displaying diagnostic use wear, a total of 17 GSTs have

361 surfaces bearing functional areas positively associated with plant food processing (Table 3 and
 362 Fig. 3). The analysis conducted at low magnification on these tools revealed macro-traces
 363 resulting in levelled surface crystal grains, sometimes covered by spots of yellowish organic
 364 film (sometimes striated) and white compacted powder (Fig. 4Z, Aa). At a high magnification,
 365 high and low micro topographies of the GST surfaces are affected by a smooth domed, and
 366 sometimes striated, micro polish (Fig. 4Bb, Cc). The aforementioned combination of use-wear
 367 and macro residues are commonly associated with GSTs used as handstones for crushing and
 368 grinding grass grains and/or fruits, such as hazelnuts and/or acorns in our experimental record
 369 (Cristiani and Zupancich, 2020) (Fig. 8).
 370

371
 372
 373 **Figure 8.** Experimental macro residues and micro polish associated with grass grains
 374 processing compared to macro residue and micro polish identified on archaeological GSTs from

the site of Vlasac; **a-e**) yellowish organic film covering the crystal grains on experimental GSTs used to process oat (**a**), downy brome (**b**), wild grass grains, (**c**) and millet (**d**); smooth domed and flat micro polish developing over the high and low micro topographies associated with oat (*Avena barbata*) grinding; **f**) smooth flat and domed micro polish developing over the surface high and low micro topographies and characterized by narrow micro striations associated with grinding downy brome (*Bromus tectorum* L.); **g**) smooth flat micro polish developed over the high and low micro topographies characterized by sporadic narrow striations associated with grinding wild grass grains (*Aegilops ventricosa* Tausch); **h**) smooth domed polish developed over the high and low micro topographies associated with the grinding of foxtail millet (*Setaria italica* (L.) P. Beauvois); **i-l**) spots of organic film, yellowish in color covering the crystal grains across the surface of archaeological GSTs; **m,p**) smooth domed micro polish identified on archaeological GSTs developing over the high and low surface micro topographies and associated with micro striations (**m,n,p**). **q-w** Starch granules identified on archaeological GSTs. (**q**) Type I (GST no. INV80); (**r**) Type I (GST no. INV146); (**S**) Type III (GST no. INV 28); (**t**) Type VI (GST no. INV.67); (**u**) Type VI (GST no. INV 10); (**v**) Type VI (GST no. INV146); (**w**) Type I (GST no. INV.71).

A total of 137 starch granules have been retrieved from the surfaces of the GSTs characterized by plant-related functional microscopic features. The optical and morphological properties of the starch granules support their attribution to morphotypes already documented in dental calculus from the Danube Gorges: type I assigned to caryopses of the tribe Triticeae (76) (Fig.4 Dd, Ee, Ff); type IV, assigned to the Fabaceae family (13) (Fig.4 Ii); type III assigned to the tribe Paniceae of the grass family Poaceae (16) (Fig.4 Gg); and type VI, assigned to berries of the family Cornaceae (32) (Fig.4Hh;Jj).

In sum, several hundreds of starch granules and phytoliths of grass grains of the Triticeae tribe have been identified in the analyzed dental calculus of the Mesolithic population in the Danube Gorges. In addition, residues and use-wear identified on GSTs from Late Mesolithic Vlasac show the existence of a plant food processing technology during this period aimed at preparing a coarse-grained flour through a combination of pounding and grinding gestures (Table 3 and Figs. 3, 9). Grit particles, often retrieved in the analyzed dental deposit (Table 2), further confirm the use of sandstone GSTs in food processing. The conclusion about the consumption of partially processed grains is corroborated by the presence of starch granules still lodged in their amyloplast on Mesolithic GSTs and dental calculus, as suggested in our previous study (Cristiani et al., 2016). Interestingly, A-Type granules in EN dental calculus are generally retrieved singularly and exhibit a damage pattern observed when producing fine-grained flour experimentally only through prolonged bidirectional grinding (Dietrich et al., 2019). The pattern of bidirectional grinding is not documented on the examined Late Mesolithic GST from Vlasac, suggesting the existence of two different grain processing modalities typical of respective Mesolithic and Neolithic cultural traditions.

Table 3. Late Mesolithic GSTs from the site of Vlasac.

Inv. no.	Archaeological context	Shape	Tool type	Length(cm)	Width(cm)	Thickness(cm)	Weight (gr)	Volume(cm3)	State of preservation	PDM	Micro polish description	Micro polish location	Micro striation description	Micro striation orientation	Crystal grain modification	Gesture
10	F KB 0,1/III	subangular	Handstone/Gri nder	12.7	10.5	7.88	1542	645	preserved	light soil concretion	smooth and domed	high micro topographies	short narrow with a matt bottom	unidirec tional	Y	mixed
13	a1-VIII	round	Handstone/Gri nder	11	8.16	5.68	680	287	preserved	none	smooth and domed with sporadic pits	high and low micro topographies	NA	NA	N	longitudinal
23	BV/C/IV-X	subangular	Indeterminable	11.7	8.79	8.76	823	367	preserved	light soil concretion	rough to smooth with domed and flat spots	high and low micro topographies	NA	NA	N	longitudinal
28	BIII-C/V	oval	Passive base	13.3	11.8	7.18	1283	499	fractured	none	smooth	high micro topographies	NA	NA	Y	longitudinal
56	A/II-XIII	round	Passive base	15.9	14.8	7.7	1038	368	preserved	heavy surface concretion on one surface	smooth domed and flat	high micro topographies	NA	NA	Y	Mixed
63	b/17-XV	round	Handstone/Gri nder	8.4	6.6	4.47	403	141	preserved	light surface abrasion	rough to smooth with reticulated and flat spots	high and low micro topographies	NA	NA	N	longitudinal
65	C/I-VI	round	Passive base	100	84.3	55.5	680	298	broken	fractures	smooth domed and reticulated	high micro topographies	narrow with a matt bottom	mixed	N	longitudinal
66	C/I II/V	round	Indeterminable	9.5	8.5	7.6	1170	437	preserved	none	smooth domed and cratered	high and low topographies	NA	NA	Y	mixed
67	C/I-C/II-III	subangular	Passive base	10.8	8.4	5.91	633	253	broken	light soil concretion and surface abrasion	smooth and reticulated	high micro topographies	short and deep with a matt bottom	unidirec tional	N	longitudinal
71	C/I-V	round	Handstone/Gri nder	72.1	57.9	45.9	309	119	preserved	none	smooth domed to flat	high micro topographies	long and shallow with a polished bottom	mixed	Y	longitudinal
75	b/18-V	subangular	Handstone/Gra nder	5.53	5.29	3.45	137	57	broken	fractures	smooth and domed	high and low micro topographies	short narrow with a polished bottom	unidirec tional	N	longitudinal
80	C/II-II/6	ovate	Passive base	9,85	8,35	3,72	547	225	broken	none	smooth domed	high micro topographies	short and narrow with a matt bottom	unidirec tional	Y	longitudinal
134	b/V3-XII	subangular	Indeterminable	12.2	9.57	8.13	1433	565	preserved	none	smooth domed	high and low micro topographies	short deep with a matt bottom	unidirec tional	Y	longitudinal
141	B/I/0-8.9	round	Handstone/Gri nder	10.8	9.92	9.22	370	NA	preserved	soil concretion	smooth domed and flat	high micro topographies	NA	NA	Y	longitudinal
146	B/I-ISPOD 1.9	round	Handstone/Gri nder	6.65	5.7	4.66	275	106	preserved	light soil concretion	smooth domed and reticulated	high micro topographies	short narrow with a matt bottom	unidirec tional	N	longitudinal
162	A/16-X	round	Handstone/Gri nder	10.6	9.3	7.52	1143	424	preserved	none	smooth domed	high and low micro topographies	shirt narrow with a matt bottom	unidirec tional	Y	longitudinal
167	a/15-VII	round	Indeerminalbe	8.94	8.82	5.65	611	241	broken	light surface abrasion	rough granular and domed	high and low topographies	NA	NA	Y	orthogonal

423 For some time now, there has been a recognition of the importance of plant foods in forager
424 diets, based on both archaeological and ethnographic evidence (Clarke, 1978; Lee and DeVore,
425 2017). Research on mineralized dental plaque has significantly advanced our awareness about
426 ancient pre-agrarian food choices in Europe, Asia, and Africa, thanks to the dental plaque's
427 potential to preserve plant micro-remains (Buckley et al., 2014; Cristiani et al., 2018, 2016;
428 Cummings et al., 2018; Nava et al., 2021; Norström et al., 2019). However, in many
429 archaeological case studies dating to early prehistory, preservation or recovery biases render
430 plant food evidence invisible. In exceptional cases, good preservation has allowed for the
431 remains of plant macro-remains to be found, such as wild cereals at the Epipaleolithic site of
432 Ohalo II in Israel, dating to 23 kya (Nadel et al., 2012; Piperno et al., 2004), or parenchyma
433 remains at the Gravettian site of Dolní Věstonice in the Czech Republic (Pryor et al., 2013). On
434 the other hand, micro-remains of oat caryopses have been detected on GST found at the
435 Gravettian site of Paglicci cave in Italy (Lippi et al., 2015). In a seminal synthesis about plant
436 foods in the European Mesolithic, Zvelebil (1994) reviews macro- and micro-botanical,
437 palynological, artefactual (antler hoes, mattocks, GST), and human osteological (dental size and
438 presence of caries) evidence for the consumption of nuts and fruits by European Holocene
439 foragers, arguing for a form of niche constructing in temperate woodlands by means of
440 deliberate forest clearance in order “to increase the productivity of nut and fruit trees and shrubs,
441 wetland plants, and possibly native grasses” (Zvelebil, 1994). The emphasis is on the existence
442 of some form of husbandry of wild plant species, which did not necessarily lead to
443 domestication. Furthermore, between 200 and 450 indigenous European edible plants (grass
444 seeds, nuts, fruits, roots, tubers, pulses) are found concentrated in wetland (coastal, lacustrine,
445 and riparian) habitats (Clarke, 1978). Despite preservation and recovery problems, hundreds of
446 Mesolithic sites across Europe have yielded the remains of hazelnuts, acorns, water-chestnuts,
447 and other remains (Zvelebil, 1994).

448
449 In this paper, two complementary lines of evidence that we examined provide the first
450 unambiguous and direct support for the consumption and processing of Poaceae grains among
451 other types of edible plants by the Early Holocene foragers in the Danube Gorges area. The
452 chronological framework of the analyzed sample suggests that this interest in and familiarity
453 with various species of wild grasses of the Triticeae tribe (namely grass grains of the genus
454 *Aegilops*) dates back to at least ~9500 cal BC. Macrobotanical remains belonging to this genus
455 have not been recovered at Mesolithic and Early Neolithic sites in the central Balkans (Cristiani
456 et al., 2016: 10301). However, such absence in the archaeobotanical record could be the result
457 of a host of taphonomic and recovery problems and should not be used to exclude the use of this
458 genus during the Mesolithic (contra Cristiani et al. 2016: 4). Newly obtained evidence from the
459 analysis of 61 individuals, which now also involves several EM individuals, lead us to suggest
460 that *Aegilops* species were consumed in the region since the beginning of the Holocene. The
461 mentioned difficulties associated with the recovery and preservation of botanical remains in
462 local early prehistoric forager contexts along with some voids in the extant data regarding plant
463 use by Mesolithic groups underlines the significance of our findings based on the application of
464 relatively recent advances in dental calculus and GST analyses.

465

We have previously argued that three Late Mesolithic individuals from the site of Vlasac dated to the mid-seventh millennium cal BC (H53, 64.x11, and H232), as well as two presumed Early Neolithic individuals from Lepenski Vir (8 and 20) exhibit starches consistent with domesticated cereal species, such as *Triticum monococcum* L. (einkorn wheat), *Triticum dicoccum* L. (emmer wheat), and/or *Hordeum distichon* L. (barley) (Cristiani et al., 2016). This observation was based on the bimodal pattern of starch granules distribution, commonly attributed to domestic species and absent in most of the wild species of the genus *Aegilops* (Howard et al., 2011; Stoddard, 1999). This bimodal pattern is now further retrieved in two other individuals from two different sites (H326 from Vlasac and HV16 from Hajdučka Vodenica) dating to the Late Mesolithic and thus pre-dating the arrival of full-blown agriculture in the region. However, burial 20 from Lepenski Vir, previously published as dating to the Early Neolithic, has recently been directly AMS-dated to the Early Mesolithic (Table 1). This new chronological attribution does not correspond with our expectations that domesticated grains were introduced in the Danube Gorges only in the Late Mesolithic. At the face of the current evidence, we explain this inconsistency in our results by arguing that the admittedly small number of starch granules found in this archaeological specimen might have affected the visibility of the potential variation in A-Type vs. B-Type population. Moreover, a large variability of starch granule distributions among different species of the Triticeae tribe has been acknowledged in the literature (Henry and Piperno, 2008; Yang and Perry, 2013) and supported by our experimental reference (Fig. 9). Furthermore, fluctuations in environmental and growing conditions have also been recognised as relevant factors affecting starch granule size distribution (Stoddard, 1999; Stoddard and Sarker, 2000).

comparing the length of starch granules in wild and domesticated species; d) Interquartile Range (IQR) ranges of wild and domestic species. IQR corresponds to the difference in the medians of the lower and upper half of the data.

Figure 9-source data 1. Starch granule length in modern wild and domestic cereal species.

540

541 In addition to starch granules, other micro-remains, such as phytoliths and burnt debris, were
542 recovered in the dental calculi of the analyzed Mesolithic population (Fig. 5L,M,Y). The paucity
543 of archaeological phytoliths calls for caution when interpreting their dietary origin. Yet, the
544 presence of few dendritic phytoliths in local forager dental calculus is likely related to plant
545 consumption, as such micro-remains have experimentally been associated with mechanical
546 destruction of husks and culms of Pooids by grinding (Portillo and Albert, 2014). In the
547 investigated population, phytoliths could potentially provide means of understanding the use of
548 plants as kindling and exposure to potential respiratory irritants generated during daily life
549 activities, but their pathways are too many to narrow them down, and further work is required
550 to better understand the origin of burnt material in dental calculus (Radini et al., 2019, 2017;
551 Scott and Damblon, 2010). The retrieval of phytoliths from herbaceous plants that appear burnt
552 could suggest that plant materials, potentially harvested, were used in a diverse range of
553 activities, including kindling and roofing. Phytoliths of such plants might have also been
554 naturally present in the environment, water, and soil (Norström et al., 2019). Such burnt debris
555 may have reached the mouth by accidental ingestion through food and/or breathing. Other
556 micro-debris, such as nettle and wood fibers, might have also been linked to textile. Pathways to
557 wood inclusion in calculus vary from the use of a toothpick to crafting activities (Radini et al.,
558 2016) and the production and maintenance of weapons, such as arrowheads.

559

560 For the moment, it remains unclear to what extent plant foods, and species of the Poaceae
561 family, contributed to the diet of the Danube Gorges foragers, and it is equally difficult to be
562 more specific about the range of activities involved in their acquisition prior to processing and
563 consumption – from sporadic collecting of wild grasses to forest clearances, or some form of
564 indigenous system of plant management. Yet, it seems clear from our data that this specific
565 subsistence practice was passed over generations in this regional context up to the first contacts
566 of these foragers with Neolithic, farming groups in the second half of the seventh millennium
567 BC. Previously, we suggested that some sort of exchange between Late Mesolithic foragers and
568 first Neolithic groups in the southern Balkans might have allowed for the introduction of the
569 domesticated species of Triticeae in the Danube Gorges area ~6500 cal BC (Cristiani et al.,
570 2016). Now, our extended study seems to suggest that this introduction of domesticated cereals,
571 i.e. more productive cereal strains from Southwestern Asia, was preceded by several millennia
572 of collecting and consumption of native grass grains. Adoption of previously unknown plant
573 foods is often facilitated by those local foods that in shape and taste resemble the new arrivals
574 (Livarda, 2011). Incipient management practices on certain wild plant taxa have been
575 documented among non-agricultural societies for environmental and/or cultural reasons, for
576 protecting or promoting the relative abundance of a species, or for reducing the energy involved
577 in its harvesting (Fuller et al., 2011; Smith, 2011).

578

579 Another recent study of dental calculus from the Danube Gorges area has reached a conclusion
580 that domesticated cereals started to be used in this region only with the start of the Neolithic
581 (Jovanović et al., 2021). In the same study, the individuals dated to the Early Mesolithic exhibit
582 a high occurrence of starch granules, which we have shown to be compatible with a variety of
583 wild species of the Triticeae tribe (e.g., genus *Aegilops*). Jovanović et al. (2021:10) disregard the

584 evidence of *Aegilops* consumption during the Early Mesolithic as an “implausible pattern”.
585 However, our results, based on the combination of a robust sample of analyzed individuals,
586 GSTs, and experimental data are in opposition to the conclusions of the mentioned study.

587
588 Most of prehistoric forager groups might have had regular access to plant nutrients and some
589 sort of dependency on specific plants (Fuller et al., 2011). Accordingly, in our analysis of dental
590 calculus and GSTs, we have shown that besides wild grasses, local foragers consumed oat,
591 legumes, minor millet species of the genus *Echinochloa* and/or *Setaria* known as “forgotten
592 millets” (cfr Madella et al., 2016; Weber and Fuller, 2008), acorns, and Cornelian cherries (Fig.
593 4; Tables 1,2). Even if secure identification to species or genus level was not possible in every
594 case (cfr. Soto et al., 2019), the morphological characteristics of starch granules systematically
595 encountered in our archaeological samples, and the data available for the analysis of material
596 culture, clearly show a contribution to the diet from these plant taxa.

597
598 Several starch granules of the tribe Aveneae have been identified in dental calculus, especially
599 during the Late Mesolithic. Very abundant in temperate ecosystems, oat caryopses have been
600 processed as foodstuff already during the Upper Palaeolithic at Paglicci Cave, in the south of
601 Italy (Lippi et al., 2015). They have also been documented in the dental calculus of the
602 aforementioned Late Mesolithic individual from Vlakno Cave in the Eastern Adriatic region
603 (Cristiani et al., 2018). Overall, starch granules of this tribe were remarkably well preserved in
604 our dental calculus samples and large aggregates characterizing Aveneae were abundant.
605 Interestingly, starches of this tribe recorded on archaeological GSTs, and associated with the
606 production of flour, consist of abundant single sparse polyhedral granules (Lippi et al., 2015). In
607 our case study, exceptionally well-preserved aggregates of Aveneae have been identified in
608 dental calculus only. The concentration of semi-open aggregates (Figs. 4G, 5K,U) sustains the
609 hypothesis of a coarse processing of the seeds during the Mesolithic, already suggested for other
610 grass grain taxa.

611
612 Small starch granules from grasses of the Poaceae family have been attributed to the
613 Andropogoneae and Paniceae tribes (Fig. 5B,C) (Madella et al., 2016). Our results confirm
614 previous conclusions about the use of grasses of the tribe Paniceae by the Late Mesolithic
615 foragers (Cristiani et al., 2016), while extending the consumption of this general types of millets
616 to Early Mesolithic foragers too. However, no evidence of this food has been ascertained on the
617 basis of stable isotope analysis (Borić et al., 2004). This pattern could mean that their
618 consumption was not predominant in dietary practices of these Mesolithic foragers. We stress
619 that a great variety of species of C₄ plants belonging of the tribe Paniceae and the tribe
620 Andropogoneae (e.g., species of plants of the genera *Setaria* Beauv. and *Echinochloa* P. Beauv.)
621 grow well nearby water environments and slow-flowing waters, and it is very likely that a
622 mixture of species from such genera might have contributed to the Mesolithic diet. Furthermore,
623 they often grow in association with each other. The presence of Paniceae and the
624 Andropogoneae tribes, combined with the evidence of several feather barbule fragments from
625 aquatic birds, clearly point to a familiarity with resources from riverine environments other than
626 fish.

627

Species of the family Fabaceae are well represented in the Early Mesolithic and Late Mesolithic individuals from the Danube Gorges area. While a secure identification to species or genus was not possible in our samples, we know that wild pulses (*Lens* sp. Mill.) and bitter vetch (*Vicia ervilia* (L.) Willd.) were used as foodstuffs for the Mesolithic inhabitants of Franchthi Cave (Asouti et al., 2018; Van Andel et al., 1987). Further evidence for a pre-Neolithic consumption of the species of the tribe Fabeae comes from Uzzo Cave, Italy, where wild legumes (*Lathyrus* sp. L., *Pisum* sp. L.) are well represented along with other arboreal fruits (*Arbutus unedo* L.), acorns (*Quercus* sp. L.), and wild grapes (*Vitis vinifera* subsp. *sylvestris* L.) (Costantini, 1989), as well as from the site of Barma Abeurador in southern France (Vaquer et al., 1986). In addition to the evidence from dental calculus, indirect evidence for the consumption of species of the family Fabaceae has also been retrieved from one GST (Fig. 4Ii).

Species of the Fagaceae family (cfr. *Quercus ilex* L., *Quercus* sp. L.) were also a significant food resource for the Danube Gorges foragers (Fig. 5A). Fragments of acorns were found at several Mesolithic sites across Europe (Holden et al., 1995; Kubiak-Martens, 1999) and in the investigated region (Mason, 1995).

Evidence for the consumption of Cornelian cherries (*C. mas* L.) has been retrieved in dental calculus belonging to Late Mesolithic and Mesolithic/Neolithic individuals from Vlasac (Fig. 5N-P) and also on eight GSTs from the same site. The results based on the analyses of GSTs not only corroborate the evidence for the use of these fruits derived from the calculus analysis, but also support the role of such plants in Mesolithic daily life. Cornelian cherries are the most recurrent macro-remains at Vlasac and are documented across Europe as a Mesolithic source of food and medicine (Divišová and Šída, 2015; Filipović et al., 2010). Ethnographically, various fruits commonly referred to as “cherries” and/or “berries” are particularly well documented among Native American groups (Siegfried, 1994; Zarrillo and Kooyman, 2006). Throughout much of North America several species of the Cornaceae and Rosaceae plant families were processed using unmodified pounding stone tools to add to pemmican or to dry as cake. Interestingly, Woodland Cree people used to mix berries and cherries with fish eggs (Siegfried, 1994) and meat (Lowie, 1922).

We conclude that the long-lasting interactions with edible grains (but also wild pulses), documented in the Balkans since the end of the Pleistocene might have allowed enough time for specific eating habits, tastes, and “cultural valuation” (Hastorf and Foxhall, 2017) to develop. Such a shared knowledge about specific plant resources effectively predates the introduction of agriculture in Europe, and might have eventually eased the introduction of domesticated species starting from the second half of the seventh millennium BC. Our results call for more systematic and interdisciplinary research in order to reconstruct plant food traditions and cultural tastes before the introduction of agriculture.

Materials and Methods

The examined collection of the teeth previously studied for strontium isotopes (Borić and Price, 2013) from five sites in the Danube Gorges area and the site of Gârlești from the region of

672 Oltenia in Romania and additionally collected teeth from the sites of the Velesnica and the
673 2006–2009 excavations at Vlasac contained a total of 155 specimens. Of these, a total of 60
674 individuals had sufficiently preserved calculi for further analyses (Table 1): 13 individuals date
675 to the Early Mesolithic (EM), 29 to the Late Mesolithic (LM), 9 to the Mesolithic-Neolithic
676 transition phase (M/N), and 8 to the Early Neolithic (EN). In addition, two later period burials
677 were also included in the analysis as a methodological comparison (Table 1). In order to
678 corroborate data obtained through dental calculus analysis, we also analyzed 101 sandstone
679 GSTs of the 131 implements found at the site of Vlasac during the 1970–71 excavations and
680 chronologically attributed to the Late Mesolithic (Borić et al., 2014; Srejović and Letica, 1978).
681 While GSTs are well documented during the Mesolithic-Neolithic transition at the site of
682 Lepenski Vir (Antonović, 2006), earlier evidence for their use is available only from the site of
683 Vlasac. This site yielded the richest Mesolithic assemblage of non-flaked stone tools recovered
684 so far in the region (Antonović et al., 2006; Borić et al., 2014; Srejović and Letica, 1978). GSTs
685 underwent a functional study aimed at verifying their function and potential involvement in
686 plant food processing (Table 3 and Fig. 3).

687

688 *Dental calculus – sampling, extraction, decontamination and examination procedures*

689 All the sampling was conducted under the stereoscope, as can be seen in Fig. 2 (for more details
690 see below), and following strict protocols systematized by Sabil and Fellow Yates (Sabin and
691 Fellow Yates, 2020) with some variation (disposable blades were changed after each sample
692 extraction). Deposits of dental calculus were judiciously left on the teeth for future research.
693 Whenever possible, sampled dental calculus was further subdivided for metagenomic analysis
694 aimed at reconstructing aDNA of oral bacteria (Ottoni et al., 2021).

695

696 Decontamination and the extraction procedures for micro-debris were conducted in dedicated
697 clean spaces not connected to modern botanical work and under strict environmental monitoring
698 of the DANTE laboratory of Sapienza University of Rome (IT), the BioArch laboratory at
699 University of York (UK), and the aDNA facility of the University of Vienna (Austria). In all of
700 these facilities, strict contamination rules were followed. Cleaning is carried out daily and no
701 food is allowed in order to prevent any type of modern contamination. Bench space surfaces
702 were cleaned prior to the analysis of each sample, using soap and ethanol, followed by covering
703 of the surfaces by aluminium foil, and using of clean starch-free nitrile gloves at all times.
704 Calculus cleaning was carried out under the stereomicroscope, on a Petri dish previously washed
705 and immersed in hot ultrapure water, with magnifications up to 100x. The removal of the
706 mineralized soil adhering on the surface of the calculus was meticulously carried out using
707 sterile tweezers to hold the sample and a fine acupuncture needle to gently scrape off the soil
708 attached to the external layer of the mineralized plaque. The procedure was performed using
709 drops of 0.05 M Hydrochloric (HCl) acid to dissolve the mineralized flecks of soil and ultrapure
710 water to block the demineralization, as well as to wash and remove the contaminants. Once the
711 calculus surface was cleaned, the contaminated soil was checked for possible cross
712 contamination and the clean samples were washed in ultrapure water up to three times in order
713 to remove any trace of sediment. The clean calculus was then dissolved in a solution of 0.5 M
714 HCl and subsequently mounted on slides using a solution of 50:50 glycerol and ultrapure water.
715 Furthermore, control samples from the clean working tables and dust-traps were collected and

analyzed for comparative purposes in order to prevent any type of modern contamination in these laboratories – this is a practice routinely done in our laboratories, even at times where no archaeological analysis occur, to allow a better understanding of the flow of contaminations through seasons. Our results based on this procedure show that synthetic and plant fibers and hairs, fungal spores and hyphae, palm and conifer pollens, insects' debris; maize starch granules were detected twice while unidentified small starch granules were very rare; phytoliths and starch granules belonging to species of the Triticeae tribe were never recovered (Fig. 10). We did not retrieve any debris morphologically similar to any of the remains in the environmental control samples. Furthermore, starch granules amounted to a neglectable fraction of the laboratory “dust” – suggesting it is extremely unlikely that an event of contamination of starch granules would occur in the lab, where no other remains from dust, way more common, were not found.

The examination of micro-debris embedded in the calculus matrix was performed at Sapienza University of Rome and at the University of York using a Zeiss Imager2 cross and an Olympus polarized microscope with magnifications ranging from 100X to 630X. A modern reference collection of 300 plants native to the Balkans, the Mediterranean region, and Europe was used as a comparison, along with published literature, for the identification of archaeological starch granules. The experimental reference collection also included species documented in the local archaeological record (Filipović et al., 2010; Marinova et al., 2013).

Ground Stone Tools functional analysis

GSTs were sampled and analyzed at the Archaeological Collection of the University of Belgrade. Strict protocols were followed for controlling modern contamination during the residue sampling and functional analysis of GSTs: bench surfaces where the work was conducted were cleaned before the analysis of each tool using ethanol, hot water, and covered by aluminium foil; starch-free gloves were used while handling the GSTs; dust samples from the storage boxes and the working tables were collected and analyzed for comparative purposes; use-wear and residue analyses were performed on the surfaces not affected by severe post-depositional modifications and free from concretions. Furthermore, starch granules were considered reliable only when in combination with use wear traces associated with plant processing.

Functional study involved the analysis of use-wear traces on the GST surfaces at low magnification (0.75x–168x) using a Zeiss Discovery V20 stereomicroscope and at high magnification (200x–500x) with a Zeiss AxioScope metallographic reflected light microscope (Cristiani and Zupancich, 2020; Dubreuil et al., 2015). At low magnification, GSTs were analyzed using a Zeiss Discovery V20 Stereomicroscope, which allowed us to assess the state of preservation of the materials and identify the residues still adhering to the surfaces. Appearance, morphological features, and spatial patterns of macro-residue distribution were considered (Langejans, 2010). Casts of the used areas were taken by means of a high-resolution polyvinylsiloxane (Provil Novo Light Fast Set), and later analyzed at high magnification (up to

760 500x) at the DANTE Laboratory at the Sapienza University of Rome. Micro-polish, abrasions,
761 and micro striations across the tools' surfaces were identified using a Zeiss AxioScope
762 metallographic microscope, and described following relevant parameters available in literature
763 (Adams et al., 2006; Dubreuil et al., 2015; Hamon and Plisson, 2009).

764
765 Micro-residues were sampled before surface casts. Ultrapure water was placed on the crevices
766 of surface and left for one minute on the artefact in order to soften the residues, then pipetted out
767 and stored in a sterile tube. Once in laboratory, the samples were centrifuged and the natant
768 mounted on microscope slides using a 50% solution of purified water and glycerol. Slides were
769 subsequently analyzed in transmitted light using Zeiss Imager2 microscope (630x) and cross-
770 polarizing filters. For archaeological residues, appearance, morphological features, and spatial
771 patterns of distribution were considered (Cristiani and Zupancich, 2020).

772
773 An experimental reference collection of used GSTs and starch granules housed at the DANTE
774 laboratory was consulted along with relevant literature and scientific databases. High-resolution
775 images of the identified use-wear and residue were taken at 630x using a Zeiss AxioCam 305
776 high definition color camera. Risk of modern contamination from the storage and sampling
777 environment was minimized following a strict cleaning procedure before and during the
778 sampling/analysis.

779

CONTROL -WORKING SURFACES

CONTROL BOXES AND WORKING SURFACES - UNIVERSITY OF BELGRADE

Figure 10. Controls for contamination. (a-w) Evidence of pollutants retrieved from clean working surfaces and dust traps located in different areas of the DANTE Laboratory at Sapienza University of Rome; (x-Ll) Dust recorded in storage boxes where groundstone tools were stored at the Faculty of Philosophy, University of Belgrade.

Testing morphological differences in experimental starch granules from Aegilops, Hordeum, and Triticum species

Methodologically, we were able to characterize the morphological variability of starch granules in ancient plant species consumed in the investigated area, hence complementing our previous work and its implications (Cristiani et al., 2016). Differences in the starch granules assigned of the tribe Triticeae in the analyzed individuals were identified on the basis of (1) the specific morphology, dimensions, and appearance of type A and B granules; and (2) the proportion between A-Type and B granules. In particular, during the EM A-Type granules preserved in calculi are very large and round in shape with deep lamellae visible only in the granules' mesial part. Additionally, B-Type granules with different sizes and shape have been recorded in all of the EM individuals and most of Late Mesolithic (LM) individuals (Fig. 4). This feature is absent in the Early Neolithic (EN) individuals analyzed in this work, displaying only identical small round B-Type granules, while A-Type granules are large, round to oval/lenticular, with lamellae less pronounced in the mesial part of the grains and well visible craters on their surfaces (Fig. 4Y). We could not match these differences in our experimental record, which includes various *Aegilops* species as well as wild species within the genera *Hordeum*, *Elymus* L., *Agropyron* Gaertn., *Dasypyron* L. growing locally, and in the literature (see Henry et al. 2010). The above-mentioned features have consistently been assigned to modern domestic Triticeae species (*Triticum* spp. and *Hordeum* spp.) (Cristiani et al., 2016; Piperno et al., 2004; Yang and Perry, 2013). Given the high variability recorded in the dimensions and distribution of starch granules within the modern, locally available, species of the genus *Aegilops* (Fig. 6A-J), further statistical work was carried out in order to interpret starch granules assigned to the tribe Triticeae in Mesolithic/Neolithic transitional contexts.

Caryopses from 11 *Aegilops* species (*A. triuncialis*, *A. comosa*, *A. crassa*, *A. cylindrica*, *A. geniculata*, *A. neglecta*, *A. speltoides tauschii*, *A. peregrina*; *A. triuncialis*, *A. uniaristata*, *A. ventricosa*), 1 *Hordeum* species (*Hordeum vulgare distichon*), and 2 *Triticum* species (*Triticum monococcum*; *T. dicoccum*) grown in the central Balkans were collected. All plant material was grounded using pestle and mortar. Starch powder (0.5 mg) was resuspended in 100 µL of sterile distilled water and vortexed for 5 minutes. After that, the sample was observed by an optic transmitted light microscopy (Fig. 6). Fifty starch granules were randomly selected (for size and shape), counted, and their length measured. Minimum and maximum lengths, mean, and median values with relative standard deviations and Interquartile ranges (IQR) were reported for each species in Table 4. Length distribution and variation of modern starches were reported in Fig. 9. Finally, length distribution of the starches from each species was compared with the other species to investigate the existence of significant differences. This statistical analysis was carried out through a Pairwise Wilcoxon test (Table 5). Results were considered significant for p-values <0.05 (<0.05; *<0.01; ***<0.001) and not significant (n.s.) for measurements >0.05.

Triticeae starches are known to possess a bimodal distribution, made up of small (B-type) and large (A-type) granules (Fig. 6). In the analyzed *Triticum* and *Hordeum* genera, B-type grains are more abundant than A-type, except for *H. secalinum* Schreb., which does not exhibit the large granules. Differently, in *Aegilops* genus, the size distribution of starches is characterized by two different trends. The first one, evidenced in *A. caudata* L., *A. cylindrica* Host, *A. comosa* Sm., and *A. speltoides tauschii* Coss., appears very similar to that of *Triticum* and *Hordeum* samples, although B-type grains are less abundant than their counterparts in wheat and barley.

832 On the other hand, the second cluster (*A. crassa* Boiss. ex Hohen., *A. geniculata* Roth, *A.*
833 *neglecta* Req. ex Bertol., *A. speltoides tauschii* Tausch, *A. triuncialis* L., *A. uniaristata* Vis., and
834 *A. ventricosa* Tausch) exhibits larger starches, determining a significant shift of the mean size
835 towards intermediate lengths. In general, the present experimental analysis revealed that
836 *Aegilops* sp. starch granules show a larger size distribution than *Hordeum* sp. and *Triticum* sp.
837 (Figs. 6,9). This evidence is also supported by the Pairwise Wilcoxon test, which highlights that
838 *Aegilops* spp. starch measurements are significantly different from those obtained for *Hordeum*
839 sp. and *Triticum* sp. counts (Table 4).

840

841 **Table 4.** Summary statistics of the length of wild grass grains and domestic cereal starch
842 granules.
843 **Table 4-source data 1.** Summary statistics of the length of wild grass grains and domestic
844 cereal starch granules.
845
846

Species	Min.	Max.	Mean	Median	StDev.	Range	IQR
<i>A. caudata</i>	5.29	59.3	21.6	16.7	15.17	5.29 – 59.33	26.55
<i>A. comosa</i>	7.95	34.5	21.5	21.7	9.78	7.95 – 34.54	20.09
<i>A. crassa</i>	13.38	53.7	35.3	33.7	11.09	13.38 – 53.69	19.08
<i>A. cylindrica</i>	8.52	54.0	24.2	23.7	13.07	8.52 – 54.05	21.6
<i>A. geniculata</i>	11.61	47.0	26.3	26.0	8.39	11.61 – 47.03	12.87
<i>A. neglecta recta</i>	10.54	62.7	35.0	36.2	14.46	10.54 – 62.71	26.5
<i>A. peregrina</i>	9.84	53.6	27.8	25.9	9.89	9.84 – 53.62	11.34
<i>A. speltoides tauschii</i>	13.25	40.0	23.5	22.2	5.93	13.25 – 39.97	8.39
<i>A. triuncialis</i>	5.60	50.1	28.2	28.2	11.24	5.60 – 50.06	15.18
<i>A. uniaristata</i>	14.35	62.4	38.2	39.3	12.87	14.35 – 62.38	22.83
<i>A. ventricosa</i>	14.10	40.0	26.3	25.7	7.44	14.10 – 40.04	12.77
<i>H. vulgare distichon</i>	5.19	29.6	19.7	22.2	8.12	5.19 – 29.59	8.32
<i>T. dicoccum</i>	6.17	41.5	16.5	12.8	8.66	6.17 – 41.55	14.07
<i>T. monococcum</i>	6.68	36.6	20.1	19.1	7.11	6.68 – 36.61	10.44

847
848
849
850
851
852
853
854
855
856
857
858
859
860
861
862
863
864
865
866
867
868

869 **Table 5.** Pairwise Wilcoxon test performed on the length distribution of modern starches from
870 *Aegilops*, *Hordeum*, and *Triticum* species (*p*-value: not significant/n.s.>0.05; *<0.05; **<0.01;
871 ***<0.001).

872 **Table 5-source data 1.** Length of modern starch granules of *Aegilops*, *Hordeum*, and *Triticum*
873 *species*

	<i>A. caudata</i>	<i>A. comosa</i>	<i>A. crassa</i>	<i>A. cylindrica</i>	<i>A. geniculata</i>	<i>A. neglecta recta</i>	<i>A. peregrina</i>	<i>A. speltoides tauschii</i>	<i>A. triuncialis</i>	<i>A. uniaristata</i>	<i>A. ventricosa</i>	<i>H. vulgare distichon</i>	<i>T. dicoccum</i>
<i>A. comosa</i>	ns	-	-	-	-	-	-	-	-	-	-	-	-
<i>A. crassa</i>	***	***	-	-	-	-	-	-	-	-	-	-	-
<i>A. cylindrica</i>	ns	ns	***	-	-	-	-	-	-	-	-	-	-
<i>A. geniculata</i>	ns	*	***	ns	-	-	-	-	-	-	-	-	-
<i>A. neglecta recta</i>	***	***	ns	***	***	-	-	-	-	-	-	-	-
<i>A. peregrina</i>	*	**	**	ns	ns	**	-	-	-	-	-	-	-
<i>A. speltoides tauschii</i>	ns	ns	***	ns	ns	***	*	-	-	-	-	-	-
<i>A. triuncialis</i>	*	**	**	ns	ns	*	ns	*	-	-	-	-	-
<i>A. uniaristata</i>	***	***	ns	***	***	ns	***	***	***	-	-	-	-
<i>A. ventricosa</i>	ns	*	***	ns	ns	***	ns	ns	ns	***	-	-	-
<i>H. vulgare distichon</i>	ns	ns	***	ns	***	***	***	*	***	***	***	-	-
<i>T. dicoccum</i>	ns	*	***	**	***	***	***	***	***	***	***	ns	-
<i>T. monococcum</i>	ns	ns	***	ns	***	***	***	*	***	***	***	ns	*

874
875
876
877 **Acknowledgments**

878 The authors wish to thank the late Živko Mikić (University of Belgrade), the late Borislav
879 Jovanović (Serbian Academy of Sciences and Arts), Duško Šljivar (National Museum in
880 Belgrade), and Jelena Rankov (National Museum, Belgrade) for permissions to sample the
881 osteological collections from the Danube Gorges. **Funding:** The research leading to these
882 results has received funding from the European Research Council (ERC) under the Horizon
883 2020 Framework Program (Starting Grant Project HIDDEN FOODS grant agreement no.
884 639286 to EC), the National Science Foundation Grant BCS-0235465 to TDP and DB, the
885 NOMIS Foundation grant to DB. Funding for excavations at Vlasac in 2006–2009 was provided
886 by the grants from the British Academy (SG-42170 and LRG-45589) and the McDonald
887 Institute for Archaeological Research, University of Cambridge to DB. This research was also in
888 part funded by the Wellcome Trust (grant number 209869_Z_17_Z to AR). For the purpose of
889 open access, the authors have applied a CC BY public copyright licence to any Author Accepted
890 Manuscript version arising from this submission. For the purpose of open access, the author has
891 applied a CC BY public copyright license to any Author Accepted Manuscript version arising
892 from this submission. **Competing interests:** The authors declare that they have no competing
893 interests. **Data and materials availability:** All data needed to evaluate the conclusions in the
894 paper are present in the paper and in the source data. Additional data related to this paper may be
895 requested from the authors.

896
897

898
899
900
901
902
903
904
905
906
907
908
909
910
911
912
913
914
915
916
917
918
919
920
921
922
923
924
925
926
927
928
929
930
931
932
933
934
935
936
937
938
939
940
941
942
943
944
945
946

References

- Adams JL, Delgado S, Dubreuil L, Hamon C, Plisson H, Risch R. 2006. Functional analysis of macro-lithic artefacts: A focus on working surfaces In: Sternke F, Eigeland L, Costa L-J, editors. BAR International Series. Presented at the Non-Flint Raw Material Use in Prehistory. Archaeopress.
- Antonović D. 2006. Stone tools from Lepenski Vir. Belgrade: Institute of Archaeology.
- Asouti E, Ntinou M, Kabukcu C. 2018. The impact of environmental change on Palaeolithic and Mesolithic plant use and the transition to agriculture at Franchthi Cave, Greece. *PLoS One* **13**:e0207805.
- Barton H, Mutri G, Hill E, Farr L, Barker G. 2018. Use of grass seed resources c.31 ka by modern humans at the Haua Fteah cave, northeast Libya. *Journal of Archaeological Science* **99**:99–111.
- Blumenthal C, Bekes F, Gras PW, Barlow EWR, Wrigley CW. 1995. Identification of wheat genotypes tolerant to the effects of heat stress on grain quality. *Cereal Chem.*
- Blumenthal C, Wrigley CW, Batey IL, Barlow EWR. 1994. The heat-shock response relevant to molecular and structural changes in wheat yield and quality. *Funct Plant Biol* **21**:901–909.
- Bonsall C. 2008. The Mesolithic of the iron gates. *Mesolithic Europe* 238–279.
- Bonsall C, Lennon R, McSweeney K, Stewart C, Harkness D, Boroneanț V, Bartosiewicz L, Payton R, Chapman J. 1997. Mesolithic and Early Neolithic in the Iron Gates: A palaeodietary perspective. *J Eur archaeol* **5**:50–92.
- Borić D. 2016. Deathways at Lepenski Vir: Patterns in Mortuary Practice. Belgrade: Serbian Archaeological Society.
- Borić D. 2011. Adaptations and transformations of the Danube Gorges foragers (c. 13,000–5500 cal. BC): an overview In: Krauß R, editor. Beginnings – New Research in the Appearance of the Neolithic between Northwest Anatolia and the Carpathian Basin. Papers of the International Workshop 8th - 9th April 2009, Istanbul. Organized by Dan Ciobotaru, Barbara Horejs Und Raiko Krauß., Menschen – Kulturen – Traditionen: Studien Aus Den Forschungsclustern Des Deutschen Archäologischen Instituts; ForschungsCluster 1. Presented at the Beginnings - new research in the appearance of the Neolithic between Northwest Anatolia and the Carpathian Basin: Papers of the international workshop. Rahden/Westf.: Verlag Marie Leidorf GmbH. p. 231.
- Borić D, French CAI, Stefanović S, Dimitrijević V, Cristiani E, Gurova M, Antonović D, Allué E, Filipović D. 2014. Late Mesolithic lifeways and deathways at Vlasac (Serbia). *J Field Archaeol* **39**:4–31.
- Borić D, Grupe G, Peters J, Mikić Ž. 2004. Is the Mesolithic-Neolithic subsistence dichotomy real? New stable isotope evidence from the Danube Gorges. *European Journal of Archaeology* **7**:221–248.
- Borić D, Higham T, Cristiani E, Dimitrijević V, Nehlich O, Griffiths S, Alexander C, Mihailović B, Filipović D, Allué E, Buckley M. 2018. High-Resolution AMS Dating of Architecture, Boulder Artworks and the Transition to Farming at Lepenski Vir. *Sci Rep* **8**:14221.
- Borić D, Price TD. 2013. Strontium isotopes document greater human mobility at the start of the Balkan Neolithic. *Proc Natl Acad Sci U S A* **110**:3298–3303.
- Buckley S, Usai D, Jakob T, Radini A, Hardy K. 2014. Dental calculus reveals unique insights into food items, cooking and plant processing in prehistoric central Sudan. *PLoS One* **9**:e100808.

- Cârciumaru M. 1978. L'analyse pollinique des coprolithes de la station archéologique de Vlasac. *Vlasac, A Mesolithic Settlement in the Iron Gates II: Geology, Biology, Anthropology Beograd: Srpska akademija nauka i umetnosti* 31–34.
- Cârciumaru M. 1973. Compte rendu de l'analyse pollinique des coprolithes d'Icoana--Portes de Fier. *Actes du VIIIe Congrès International des Sciences Préhistoriques et Protohistoriques, Beograd 9-15 septembre 1971* 172–173.
- Clarke DL. 1978. Mesolithic Europe: the economic basis. Duckworth.
- Costantini L. 1989. Plant exploitation at Grotta dell'Uzzo, Sicily: new evidence for the transition from Mesolithic to Neolithic subsistence in southern Europe In: Harris D, Hillman G, editors. *Foraging and Farming: The Evolution of Plant Exploitation*. Unwin Hyman Ltd.
- Cristiani E, Radini A, Borić D, Robson HK, Caricola I, Carra M, Mutri G, Oxilia G, Zupancich A, Šlaus M, Vujević D. 2018. Dental calculus and isotopes provide direct evidence of fish and plant consumption in Mesolithic Mediterranean. *Sci Rep* **8**:8147.
- Cristiani E, Radini A, Edinborough M, Borić D. 2016. Dental calculus reveals Mesolithic foragers in the Balkans consumed domesticated plant foods. *Proceedings of the National Academy of Sciences* **113**:10298–10303.
- Cristiani E, Zupancich A. 2020. Sandstone Ground Stone Technology: a Multi-level Use Wear and Residue Approach to Investigate the Function of Pounding and Grinding Tools. *Journal of Archaeological Method and Theory*. doi:10.1007/s10816-020-09488-1
- Cummings LS, Yost C, Sołtysiak A. 2018. Plant microfossils in human dental calculus from Nemrik 9, a Pre-Pottery Neolithic site in Northern Iraq. *Archaeol Anthropol Sci* **10**:883–891.
- de Beaune SA. 2004. The Invention of Technology: Prehistory and Cognition. *Curr Anthropol* **45**:139–162.
- Dietrich L, Meister J, Dietrich O, Notroff J, Kiep J, Heeb J, Beuger A, Schütt B. 2019. Cereal processing at Early Neolithic Göbekli Tepe, southeastern Turkey. *PLoS One* **14**:e0215214.
- Divišová M, Šída P. 2015. Plant use in the Mesolithic period. Archaeobotanical data from the Czech Republic in a European context – A review. *Interdisciplinaria Archaeologica: Natural Sciences in Archaeology* **6**:95–106.
- Dubreuil L, Nadel D. 2015. The development of plant food processing in the Levant: insights from use-wear analysis of Early Epipalaeolithic ground stone tools. *Philos Trans R Soc Lond B Biol Sci* **370**. doi:10.1098/rstb.2014.0357
- Dubreuil L, Savage D, Delgado-Raack S, Plisson H, Stephenson B, de la Torre I. 2015. Current Analytical Frameworks for Studies of Use–Wear on Ground Stone Tools In: Marreiros JM, Gibaja Bao JF, Ferreira Bicho N, editors. *Use-Wear and Residue Analysis in Archaeology*. Cham: Springer International Publishing. pp. 105–158.
- Edwards KJ. 1989. The cereal pollen record and early agriculture. *BAR International Series* 113–135.
- Filipović D, Allué EA, Borić D. 2010. Integrated carpological and antracological analysis of plant record from the Mesolithic site of Vlasac, Serbia. *Journal of the Serbian Archaeological Society* **26**:145–161.
- Fuller DQ, Willcox G, Allaby RG. 2011. Cultivation and domestication had multiple origins: arguments against the core area hypothesis for the origins of agriculture in the Near East. *World Archaeol* **43**:628–652.
- Geera BP, Nelson JE, Souza E, Huber KC. 2006. Composition and properties of A- and B-type starch granules of wild-type, partial waxy, and waxy soft wheat. *Cereal Chem* **83**:551–557.

- Halstead P. 1996. The development of agriculture and pastoralism in Greece: When, how, who and what. The origins and spread of agriculture and pastoralism in Eurasia 296–309.
- Hamon C, Cagnato C, Emery-Barbier A, Salavert A. 2021. Food practices of the first farmers of Europe: Combined use-wear and microbotanical studies of Early Neolithic grinding tools from the Paris Basin. *J Archaeol Sci Rep* **36**:102764.
- Hamon C, Plisson H. 2009. Functional analysis of grinding stones: the blind-test contribution In: Skakun N. LL, editor. Prehistoric Technology 40 Years Later: Functional Studies and the Russian Legacy. BAR International Series. pp. 29–38.
- Hansen JM. 1991. The Palaeoethnobotany of Franchthi Cave. Indiana University Press.
- Haslam M. 2004. The decomposition of starch grains in soils: implications for archaeological residue analyses. *J Archaeol Sci* **31**:1715–1734.
- Hastorf CA, Foxhall L. 2017. The social and political aspects of food surplus. *World Archaeol* **49**:26–39.
- Henry AG, Brooks AS, Piperno DR. 2011. Microfossils in calculus demonstrate consumption of plants and cooked foods in Neanderthal diets (Shanidar III, Iraq; Spy I and II, Belgium). *Proc Natl Acad Sci U S A* **108**:486–491.
- Henry AG, Piperno DR. 2008. Using plant microfossils from dental calculus to recover human diet: a case study from Tell al-Raqā'i, Syria. *J Archaeol Sci* **35**:1943–1950.
- Holden TG, Hather JG, Watson JPN. 1995. Mesolithic plant exploitation at the Roc del Migdia, Catalonia. *J Archaeol Sci* **22**:769–778.
- Howard T, Rejab NA, Griffiths S, Leigh F, Leverington-Waite M, Simmonds J, Uauy C, Trafford K. 2011. Identification of a major QTL controlling the content of B-type starch granules in *Aegilops*. *J Exp Bot* **62**:2217–2228.
- Jovanović J, Power RC, de Becdelièvre C, Goude G, Stefanović S. 2021. Microbotanical evidence for the spread of cereal use during the Mesolithic-Neolithic transition in the Southeastern Europe (Danube Gorges): Data from dental calculus analysis. *J Archaeol Sci* **125**:105288.
- Jovanović J, Blagojević T, Marković J, Novak M, Bedić Ž, Naumov G, Stojanova Kanzurova E, Los Dž, Hutinec M, Fidanoski Lj, Skelac G, Šlaus M, Stefanović S. 2021. New radiocarbon dates, stable isotope, and anthropological analysis of prehistoric human bones from the Balkans and southwestern Carpathian Basin. *Documenta Praehistorica* **48**:2–29.
- Kotsakis K. 2003. From the Neolithic side: the Mesolithic/Neolithic interface in Greece. *British School at Athens Studies* **10**:217–221.
- Kotzamani G, Livarda A. 2014. Plant resource availability and management in Palaeolithic and Mesolithic Greece In: Laffineur R, Touchais G, Rougemont F, editors. *Physis: L'environnement Naturel et La Relation Homme-Milieu Dans Le Monde Égéen Protohistorique, Aegaeum* (Annales d'archéologie Égéenne de l'Université de Liège et UT-PASP). Peeters Publishers.
- Kubiak-Martens L. 1999. The plant food component of the diet at the Late Mesolithic (Ertebølle) settlement at Tybrind Vig, Denmark. *Veg Hist Archaeobot* **8**:117–127.
- Langejans GHJ. 2010. Remains of the day-preservation of organic micro-residues on stone tools. *J Archaeol Sci* **37**:971–985.
- Lazaridis I, et al. 2021. The genetic history of the Southern Arc: A bridge between West Asia and Europe.
- Lee RB, DeVore I. 2017. *Man the Hunter*. Routledge.
- Lippi MM, Foggi B, Aranguren B, Ronchitelli A, Revedin A. 2015. Multistep food plant processing at Grotta Paglicci (Southern Italy) around 32,600 cal BP. *Proceedings of the national Academy of Sciences* **112**:12075–12080.

- Liu L, Field J, Fullagar R, Bestel S, Chen X, Ma X. 2010. What did grinding stones grind? New light on Early Neolithic subsistence economy in the Middle Yellow River Valley, China. *Antiquity* **84**:816–833.
- Livarda A. 2011. Spicing up life in northwestern Europe: exotic food plant imports in the Roman and medieval world. *Veg Hist Archaeobot* **20**:143–164.
- Lombardo U, Iriarte J, Hilbert L, Ruiz-Pérez J, Capriles JM, Veit H. 2020. Early Holocene crop cultivation and landscape modification in Amazonia. *Nature* **581**:190–193.
- Lowie RH. 1922. Material Culture of the Crow Indians. Lakota Books.
- Lucarini G, Radini A, Barton H, Barker G. 2016. The exploitation of wild plants in Neolithic North Africa. Use-wear and residue analysis on non-knapped stone tools from the Haua Fteah cave, Cyrenaica, Libya. *Quat Int* **410**:77–92.
- Madella M, Lancelotti C, García-Granero JJ. 2016. Millet microremains—an alternative approach to understand cultivation and use of critical crops in Prehistory. *Archaeol Anthropol Sci* **8**:17–28.
- Marinova E, Filipovic D, Obradović D, Allué E. 2013. Wild plant resources and land use in the Mesolithic and early Neolithic south-east Europe: Archaeobotanical evidence from the Danube catchment of Bulgaria and Serbia. *Offa* **69**:467–478.
- Mason S, Boroneanț V, Bonsall C. 1996. Plant remains from Schela Cladovei, Romania. *Mesolithic Miscellany* **17**:11–14.
- Mason SLR. 1995. Acornutopia? Determining the role of acorns in past human subsistence. *Food in antiquity* 12–24.
- Mathieson I, Alpaslan-Roodenberg S, Posth C, Szécsényi-Nagy A, Rohland N, Mallick S, Olalde I, Broomandkoshbacht N, Candilio F, Cheronet O, Fernandes D, Ferry M, Gamarra B, Fortes GG, Haak W, Harney E, Jones E, Keating D, Krause-Kyora B, Kucukkalipci I, Michel M, Mittnik A, Nägele K, Novak M, Oppenheimer J, Patterson N, Pfrengle S, Sirak K, Stewardson K, Vai S, Alexandrov S, Alt KW, Andreescu R, Antonović D, Ash A, Atanassova N, Bacvarov K, Gusztáv MB, Bocherens H, Bolus M, Boroneanț A, Boyadzhiev Y, Budnik A, Burmaz J, Chohadzhiev S, Conard NJ, Cottiaux R, Čuka M, Cupillard C, Drucker DG, Elenski N, Francken M, Galabova B, Ganetsovski G, Gély B, Hajdu T, Handzhyska V, Harvati K, Higham T, Iliev S, Janković I, Karavanić I, Kennett DJ, Komšo D, Kozak A, Labuda D, Lari M, Lazar C, Leppek M, Leshtakov K, Vetro DL, Los D, Lozanov I, Malina M, Martini F, McSweeney K, Meller H, Mendišić M, Mirea P, Moiseyev V, Petrova V, Price TD, Simalcsik A, Sineo L, Šlaus M, Slavchev V, Stanev P, Starović A, Szeniczey T, Talamo S, Teschler-Nicola M, Thevenet C, Valchev I, Valentin F, Vasilyev S, Veljanovska F, Venelinova S, Veselovskaya E, Viola B, Virag C, Zaninović J, Zäuner S, Stockhammer PW, Catalano G, Krauß R, Caramelli D, Zariņa G, Gaydarska B, Lillie M, Nikitin AG, Potekhina I, Papathanasiou A, Borić D, Bonsall C, Krause J, Pinhasi R, Reich D. 2018. The genomic history of southeastern Europe. *Nature* **555**:197–203.
- Nadel D, Piperno DR, Holst I, Snir A, Weiss E. 2012. New evidence for the processing of wild cereal grains at Ohalo II, a 23 000-year-old campsite on the shore of the Sea of Galilee, Israel. *Antiquity* **86**:990–1003.
- Nava A, Fiorin E, Zupancich A, Carra M, Ottoni C, Di Carlo G, Vozza I, Brugnoletti O, Alhaique F, Cremonesi RG, Coppa A, Bondioli L, Borić D, Cristiani E. 2021. Multipronged dental analyses reveal dietary differences in last foragers and first farmers at Grotta Continenza, central Italy (15,500–7000 BP). *Sci Rep* **11**:4261.
- Norström E, Gustavsson R, Molin F, Gummesson S. 2019. Micro-fossil analysis of Mesolithic human dental calculus, Motala, Sweden - Indications of health status and paleo-diet. *Journal of Archaeological Science: Reports* **26**:101866.

- Otoni C, Borić D, Cheronet O, Sparacello V, Dori I, Coppa A, Antonović D, Vujević D, Douglas Price T, Pinhasi R, Cristiani E. 2021. Tracking the transition to agriculture in Southern Europe through ancient DNA analysis of dental calculus. *Proc Natl Acad Sci U S A* **118**. doi:10.1073/pnas.2102116118
- Pardoe C, Fullagar R, Hayes E. 2019. Quandong stones: A specialised Australian nut-cracking tool. *PLoS One* **14**:e0222680.
- Piperno DR, Weiss E, Holst I, Nadel D. 2004. Processing of wild cereal grains in the Upper Palaeolithic revealed by starch grain analysis. *Nature* **430**:670–673.
- Portillo M, Albert RM. 2014. Microfossil evidence for grinding activities. *Revista d'arqueologia de Ponent*.
- Pryor AJE, Steele M, Jones MK, Svoboda J, Beresford-Jones DG. 2013. Plant foods in the Upper Palaeolithic at Dolní Věstonice? Parenchyma redux. *Antiquity* **87**:971–984.
- Radini A, Buckley S, Rosas A, Estalrich A, de la Rasilla M, Hardy K. 2016. Neanderthals, trees and dental calculus: new evidence from El Sidrón. *Antiquity* **90**:290–301.
- Radini A, Nikita E, Buckley S, Copeland L, Hardy K. 2017. Beyond food: The multiple pathways for inclusion of materials into ancient dental calculus. *Am J Phys Anthropol* **162**:71–83.
- Radini A, Tromp M, Beach A, Tong E, Speller C, McCormick M, Dudgeon JV, Collins MJ, Rühli F, Kröger R, Warinner C. 2019. Medieval women's early involvement in manuscript production suggested by lapis lazuli identification in dental calculus. *Sci Adv* **5**:eaau7126.
- Radovanović I. 1996. The Iron Gates Mesolithic. International Monographs in Prehistory Ann Arbor (Michigan).
- Reimer PJ, Austin WEN, Bard E, Bayliss A, Blackwell PG, Bronk Ramsey C, Butzin M, Cheng H, Edwards RL, Friedrich M, Grootes PM, Guilderson TP, Hajdas I, Heaton TJ, Hogg AG, Hughen KA, Kromer B, Manning SW, Muscheler R, Palmer JG, Pearson C, Plicht J van der, Reimer RW, Richards DA, Scott EM, Southon JR, Turney CSM, Wacker L, Adolphi F, Büntgen U, Capano M, Fahrni SM, Fogtmann-Schulz A, Friedrich R, Köhler P, Kudsk S, Miyake F, Olsen J, Reinig F, Sakamoto M, Sookdeo A, Talamo S. 2020. The IntCal20 Northern hemisphere radiocarbon age calibration curve (0–55 cal kBP). *Radiocarbon* **62**:725–757.
- Rowley-Conwy P, Layton R. 2011. Foraging and farming as niche construction: Stable and unstable adaptations. *Philos Trans R Soc Lond B Biol Sci* **366**:849–862.
- Sabin S, Fellow Yates J. 2020. Dental Calculus Field-Sampling Protocol (Sabin version) v2 (protocols.io.bqecmtaw). *protocols.io*. doi:10.17504/protocols.io.bqecmtaw
- Scott AC, Damblon F. 2010. Charcoal: Taphonomy and significance in geology, botany and archaeology. *Palaeogeogr Palaeoclimatol Palaeoecol* **291**:1–10.
- Siegfried EV. 1994. Ethnobotany of the northern Cree of Wabasca/Desmarais. University of Calgary.
- Smith BD. 2011. A cultural niche construction theory of initial domestication. *Biol Theory* **6**:260–271.
- Soto M, Inwood J, Clarke S, Crowther A, Covelli D, Favreau J, Itambu M, Larter S, Lee P, Lozano M, Maley J, Mwambwiga A, Patalano R, Sammynaiken R, Vergès JM, Zhu J, Mercader J. 2019. Structural characterization and decontamination of dental calculus for ancient starch research. *Archaeol Anthropol Sci*. doi:10.1007/s12520-019-00830-7
- Srejović D. 1988. The Neolithic of Serbia: Archaeological research 1948–1988. University of Belgrade, Fac. of Philosophy, Centre for Archaeological Research.
- Srejović D. 1972. New Discoveries at Lepenski Vir: Europe's First Monumental Sculpture. Thames and Hudson.

- Srejović D, Letica Z. 1978. Vlasac: A Mesolithic Settlement in the Iron Gates. Serbian Academy of Sciences and Arts.
- Stoddard FL. 1999. Survey of starch particle-size distribution in wheat and related species. *Cereal Chem* **76**:145–149.
- Stoddard FL, Sarker R. 2000. Characterization of Starch in Aegilops Species. *Cereal Chemistry Journal* **77**:445–447.
- Van Andel TH, Sutton SB, Vitaliano CJ. 1987. Landscape and People of the Franchthi Region. Indiana University Press.
- Vaquer J, Geddes D, Barbaza M, Erroux J. 1986. Mesolithic plant exploitation at the Balma Abeurador (France). *Oxford Journal of Archaeology* **5**:1–18.
- Weber SA, Fuller DQ. 2008. Millets and their role in early agriculture. *Pragdhara* **18**:e90.
- Wright KI. 1994. Ground-stone tools and hunter-gatherer subsistence in southwest Asia: Implications for the transition to farming. *Am Antiq* **59**:238–263.
- y'Edynak G, Fleisch S. 1983. Microevolution and biological adaptability in the transition from food-collecting to food-producing in the Iron Gates of Yugoslavia. *J Hum Evol* **12**:279–296.
- Yang X, Perry L. 2013. Identification of ancient starch grains from the tribe Triticeae in the North China Plain. *J Archaeol Sci* **40**:3170–3177.
- Zarrillo S, Kooyman B. 2006. Evidence for Berry and Maize Processing on the Canadian Plains from Starch Grain Analysis. *Am Antiq* **71**:473–499.
- Zvelebil M. 1994. Plant use in the Mesolithic and its role in the transition to farming. *Proceedings of the Prehistoric Society* **60**:35–74.

Figures and Tables

Figure 1. Sites in the central Balkans investigated in the article, which provided dental calculus and ground stone tools. EM = Early Mesolithic; LM = Late Mesolithic; M/N= Mesolithic/Neolithic; N = Neolithic; BA = Bronze Age; MA = Medieval.

Figure 2. Studied teeth photographed under the microscope before dental calculus sampling.

Figure 3. Late Mesolithic GSTs from the site of Vlasac featuring use-wear traces and residues related to plant food processing.

Figure 4. Starch granules from Mesolithic and Neolithic dental calculus. *Early Mesolithic*: (a) Type Ib (PAD11); (b) Type Ib (PAD9); (c) Type Ib (PAD11); (d) Type V (PAD12); (e) Type III (PAD11); (f) Type Ib (PAD15); *Late Mesolithic*: (g) Type II (VL82c); (h) Type IV (VL31); (i) Type VI (VL70); (j, k) Multicellular structures of long cells embedded in dental calculus (HV25/26, VL70); (l) Type Ia (HV11); *Mesolithic-Neolithic*: (m) Type Ia (HV16). *Neolithic*: (n) Type III (LV32a); (o–v) Damaged Type I granules (A-Type granules) (VEL-2D); (w) Type I (A-Type granule) (VEL-2D); (x) Single dendritic cell (Gârlești); (y) Type I (A-Type granule) (VEL-2D) (VEL-2A).

Figure 5. Other dietary and non-dietary debris found in Mesolithic dental calculus from the Danube Gorges. *Early Mesolithic*: (a) Type V (PAD11); (b,c) Type III (PAD12); (d) Type I (A-Type granule) (VEL-2D) (PAD12); (e) Type I (A-Type granule) (PAD12); (f) Smoke particle

(LV50); (g, h) Plant fiber embedded in calculus (PAD16); (i) Type Ib (PAD9); (j) Feather barbule embedded in calculus (PAD9); *Late Mesolithic*: (k) Type II (PAD2); (l) Polylobate phytolith (US64 x.11); (m) Phytoliths (VL79); (n-p) Type VI (VL70,VL83); (q) Feather barbules embedded in calculus (HV25/26); (r) Feather barbule embedded in calculus (VL80a); (s) Echinate pollen grain in calculus (VL83); (t) Plant tissue (LV79a); (u) Type II (VL43); (v) Type Ia (HV11); *Mesolithic/Neolithic*: (w) Type I (HV16); (x) Wood particle (PAD4); (y) Phytoliths (LV28); (z) Feather barbule (PAD4).

Figure 6. Starch granule morphological variability within the species of the genus *Aegilops* and domestic species of the Triticeae tribe. **a)** *Aegilops cylindrica*; **b)** *A. neglecta*; **c)** *A. speltoides tauschii*; **d)** *A. caudata*; **e)** *A. triuncialis*; **f)** *A. comosa*; **g)** *A. uniaristata*; **h)** *A. ventricosa*; **i)** *A. geniculata*; **j)** *A. crassa*; **k)** *A. peregrina*; **l)** *Elymus caninus*; **m)** *Bromus tectorum*; **n)** *Agropyron pungens*; **o)** *A. farctus*; **p)** *Dasyphyron villosum*; **q)** *Triticum monococcum*; **r)** *Hordeum vulgare*; **s)** *T. dicoccum*; **t)** *T. aestivum*.

Figure 7. Experimental reference for starch granules identified in the dental calculus and GSTs. **a)** *Aegilops triuncialis*; **b)** *A. crassa*; **c,d)** *Avena strigosa*; **e,f)** *Setaria italica*; **g)** *Vicia cracca*; **h)** *V. sylvatica*; **i)** *Quercus pubescens*; **j)** *Q. robur*; **k)** *Q. colurna*; **l)** *Cornus mas*.

Figure 8. Experimental macro residues and micro polish associated with grass grains processing compared to macro residue and micro polish identified on archaeological GSTs from the site of Vlasac; **a-e)** yellowish organic film covering the crystal grains on experimental GSTs used to process oat (**a**), downy brome (**b**), wild grass grains, (**c**) and millet (**d**); smooth domed and flat micro polish developing over the high and low micro topographies associated with oat (*Avena barbata*) grinding; **f)** smooth flat and domed micro polish developing over the surface high and low micro topographies and characterized by narrow micro striations associated with grinding downy brome (*Bromus tectorum* L.); **g)** smooth flat micro polish developed over the high and low micro topographies characterized by sporadic narrow striations associated with grinding wild grass grains (*Aegilops ventricosa* Tausch); **h)** smooth domed polish developed over the high and low micro topographies associated with the grinding of foxtail millet (*Setaria italica* (L.) P. Beauvois); **i-l)** spots of organic film, yellowish in color covering the crystal grains across the surface of archaeological GSTs; **m,p)** smooth domed micro polish identified on archaeological GSTs developing over the high and low surface micro topographies and associated with micro striations (**m,n,p**). **q-w** Starch granules identified on archaeological GSTs. **(q)** Type I (GST no. INV80); **(r)** Type I (GST no. INV146); **(s)** Type III (GST no. INV 28); **(t)** Type VI (GST no. INV.67); **(u)** Type VI (GST no. INV 10); **(v)** Type VI (GST no. INV146); **(w)** Type I (GST no. INV.71).

Figure 9. Starch granule length in modern wild and domestic cereal species. **a)** Distribution of starch granule length in wild species; **b)** distribution of domesticated species; **c)** Violin plot of comparing the length of starch granules in wild and domesticated species; **d)** Interquartile Range (IQR) ranges of wild and domestic species. IQR corresponds to the difference in the medians of the lower and upper half of the data.

Figure 10. *Controls for contamination.* (a-w) Evidence of pollutants retrieved from clean working surfaces and dust traps located in different areas of the DANTE Laboratory at Sapienza University of Rome; (x-Ll) Dust recorded in storage boxes where groundstone tools were stored at the Faculty of Philosophy, University of Belgrade.

Table 1. Analyzed individuals and results.

Table 2. Details of the micro-debris (starch granules and other micro-remains) found in the archaeological dental calculus samples (PO=Pollen; W=Wood; Ch=Charcoal; Gr=Grit; P=Phytoliths; FE=Feathers; FI=Fibers; FU=Fungi;S=Smoke) (n=51).

Table 3. Late Mesolithic GSTs from the site of Vlasac.

Table 4. Summary statistics of the length of modern starch granules of *Aegilops*, *Hordeum*, and *Triticum* species.

Table 5. Significance analysis performed on the length distribution of modern starches from *Aegilops*, *Hordeum*, and *Triticum* species (*p*-value: not significant/n.s.>0.05; *<0.05; **<0.01; ***<0.001).

Figure 1

Figure 2

Figure 3

Passive elements

Handstones - Crushers - Grinders

Indeterminable

Figure 4

Figure 5

Figure 6

Figure 7

Figure 8

CONTROL -WORKING SURFACES

CONTROL BOXES AND WORKING SURFACES - UNIVERSITY OF BELGRADE