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1 **Neanderthal plant use and stone tool function investigated through non-**
2 **pollen palynomorphs analyses and pollen washes in the Abri du Maras,**
3 **South-East France.**

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39

40 **Abstract**

41 This pioneering research performed at the Abri du Maras (Ardèche, South-East
42 France) explores the potential of non-pollen palynomorphs (NPP) to provide new
43 insights into the relationships between Neanderthals and plant resources.
44 Remains of endophytic fungi found during the analysis are key indicators of the
45 local presence of plants, which could have potentially been used by Neanderthal
46 groups. The recording of high concentrations of *Chaetomium*-type (HdV-7A) in
47 archaeological contexts from localized areas within the shelter suggests the local
48 presence of decayed plants near an *in situ* fireplace. This could point to the use
49 of grasses or other types of plants from aquatic or marshy areas such as reed
50 and rushes for a surface preparation (bedding?) near the fireplace. Our research
51 has also applied for the first time a combined study of archaeological sediments
52 and pollen washes of artefacts following a microspatial approach in the study of
53 Middle Palaeolithic archaeological contexts. One artefact (1079), identified as a
54 sidescrapper, provided positive results, with the recording of high concentrations
55 of *Diporotheca webbiae*-type (HdV-143). We could identify the host plant of the
56 fungal signature documented on the tool surface as alder roots by comparing
57 archaeobotanical results with NPP analyses in modern surface samples. Following
58 this, we have proposed the use of this Middle Palaeolithic sidescrapper for
59 processing this plant by Neanderthal groups. Marsh and riparian ecosystems
60 were thus attractive for Neanderthals occupying the Abri du Maras. This study
61 clearly shows that NPP must be considered as key taphonomical, environmental
62 and cultural indicators in archaeobotanical analyses. It also underlines the
63 contribution of combined studies of archaeological sediments and pollen washes
64 of artefacts following a microspatial approach to a better understanding of Middle
65 Palaeolithic lithic tools and plant use relationships.

66

67 **Keywords**

68 Non-pollen palynomorphs; *Diporotheca webbiae*; *Chaetomium*; Pollen washes;
69 Stone tool; Plant use; Neanderthals

70

71 **1. Introduction**

72 Different studies performed in the last 15 years have demonstrated that the
73 contribution of plants in the Neanderthal diet and culture has been undervalued.
74 In this sense, Shipley and Kindscher (2016) report a large number of plants,
75 which are involved in a wide range of activities or uses: diet (e.g. Lev et al.,
76 2005), technical and fire-making activities (e.g. Hardy, B. et al., 2020; Mazza et
77 al., 2006; Vallverdú et al., 2010; Vidal-Matutano et al., 2015), or medicinal uses
78 (e.g. Hardy, K. et al., 2013). Varied subsistence strategies were already in place
79 with early Neanderthals (Hardy and Moncel, 2011; Hardy, B. et al., 2013).

80 Nevertheless, plant remains are less likely to survive than animal remains in
81 archaeological sites especially in temperate environments where freeze-thaw and
82 moisture promote plant decay. Inferring the presence of plants and their uses by
83 Neanderthal groups requires approaches based on the analysis of a large set of
84 complementary macro- and microfossils. In addition to conventional indicators
85 (botanical macroremains, pollen and phytoliths), starch remains and residues
86 combined to lithic use-wear are nowadays frequently analysed (e.g. Hardy, B.,
87 2004; Venditti et al., 2019) as well as the exploration of new archaeological
88 materials (e.g. dental calculus, Power et al., 2018) or the development of new
89 tools like biomolecular markers (Sistiaga et al., 2014).

90 In the past decade, palynological investigations performed in lakes or mires
91 systematically associate Non-Pollen Palynomorphs (NPP) to the study of pollen in
92 order to obtain refined palaeoenvironmental reconstructions (e.g. Miras et al.,
93 2015; Luelmo-Lautenschlaeger et al., 2018). NPP correspond to different types of
94 resistance or dissemination elements produced by organisms belonging to the 5
95 kingdoms of life (van Geel, 1978). They mainly correspond to fungal spores and
96 phyto- and zooplankton remains. Nevertheless, systematic studies of NPP in
97 archaeological sites are very scarce and often concern protohistorical and
98 historical periods (e.g. Diot, 1991; Florenzano et al., 2019; Nicolas et al., 2012;
99 Revelles et al., 2016; van Geel et al., 2003). The even rarer NPP analyses carried
100 out in Palaeolithic sites (Medeanic and Sapozhnikov, 2008; Expósito et al., 2017;
101 Vinogradova and Burjachs Casas, 2018; Liu et al., 2018) demonstrate the
102 preservation of NPP in older archaeological contexts. The aim of the research
103 presented here and performed on materials from the Middle Palaeolithic site of
104 the Abri du Maras (Ardèche, France) is to explore the potential of these
105 microfossils to investigate plant use by Neanderthals. We will focus on the
106 analysis of endophytic fungi, which develop close relationships with plants as
107 they live within the host tissues and are liberated during host senescence (Abdel-
108 Azeem, 2020). Moreover, the cell walls of fungal spores are mainly composed of
109 chitin and glucans (Deacon, 2006), which makes them particularly resistant to
110 corrosion and oxidation - often more than pollen and peridiphyte spores (van
111 Geel, 1986). In consequence, endophyte fungal spores in archaeological layers
112 could thus provide direct evidence of the local presence of plant remains, which
113 may not have been otherwise preserved.

114 In addition to the study of fungal spores in the Abri du Maras, we present the
115 first application in a Palaeolithic site of the pollen washes technique. Geib and
116 Smith (2008) developed this technique in order to recover botanical microfossils
117 embedded in the porous surface of archaeological artefacts through a series of
118 chemical washes. The purposes are to investigate past plant usage and
119 consumption and to characterize the functionality of artefacts related to plant
120 processing, gathering and storage. Recent improvements of the technique (Miras
121 et al., 2018) allow a more thorough, deeper and precise washing method, which
122 permits the study of smoother and smaller lithic artefacts, such as Middle
123 Palaeolithic stone tools originating from the Abri du Maras in a level dated to 90
124 thousand years. In this paper, we aim to:

- 125 1) validate NPP as useful bioarchaeological microfossils, especially in
126 Palaeolithic contexts;
- 127 2) explore the potential of the pollen washes technique to assess plant use
128 and stone tool function for the Palaeolithic period;
- 129 3) gain an improved understanding of which plant resources Neanderthals
130 used and for doing what;
- 131 4) obtain fresh insights on subsistence activities and behaviour of
132 Neanderthal groups.

133

134 **2. Site background**

135 The Abri du Maras (44° 31' 20 " ; 4° 56' 28"E) is located in a small valley less than 1
136 km from the Ardèche River, a tributary of the Rhône River, and close to the
137 Rhône Valley. Its elevation is 170 m a.s.l. and 70 m above the Ardèche River
138 (Fig. 1). Recent excavations (Moncel et al., 2014) revealed three discontinuous
139 sedimentary layers, which result from successive infillings. The current research
140 concerns layer 5, corresponding to a Neanderthal occupation, which took place
141 under a large cave roof that collapsed over time. Based on ESR-U/Th dating
142 (Richard, 2012), layer 5 is dated to the end of the MIS 5/beginning of MIS 4 at c.
143 90 thousand years. A rich assemblage of lithic remains and fireplaces found in
144 the more than 52 m² of excavated surface suggest that the Abri du Maras was
145 recurrently occupied during the deposition of layer 5.

146 Layer 5 corresponds to an organic brown level with a sandy-silty matrix,
147 overlying the limestone substratum and covering in part the older layer 6 deposit
148 (Puaud et al., 2015). Layer 5 is composed of two sub-units (upper level 5 and
149 lower level 5, a more stony deposit). Layer 5 is truncated at the front of the site
150 by erosion, and is covered by a sterile level, in discontinuity with disturbed
151 sediments of the overlying layer 4.2 (Moncel et al., 2015). Layer 5 was probably
152 deposited under a large shelter now completely collapsed, before incision during
153 the Holocene. During the deposition of layer 5, the shelter covered both sides of
154 the small valley, whereas now it only covers the right side of this valley. From a
155 palaeoclimatic point of view, these geological data suggests temperate and
156 humid conditions. This is indeed corroborated by ongoing faunal studies.
157 Although reindeer dominates the faunal assemblage, there is an increasing
158 presence of temperate species, which prefer forested conditions such as red
159 deer, roe deer and wild boar (Daujeard et al., 2017). Taphonomical analysis in
160 progress indicates that faunal assemblages were the result of Neanderthal's
161 activities (Marin *in* Moncel, 2019).

162 2000 well-preserved artefacts have been recovered so far in layer 5 and their
163 vertical distribution shows three main occupations phases (Moncel, 2019). The
164 main density of these artefacts is located in the central and eastern part of the
165 site, under the thick layer of limestone blocks, which originated from the main
166 roof collapse. These blocks were removed during excavations performed between
167 2017 and 2019 (Fig. 1). Lithic studies are still in progress. Nevertheless,
168 numerous small flint flakes and cores, entire pebbles of various stones and flake-

169 tools (including scrapers) compose the lithic Middle Palaeolithic assemblage
170 (Moncel and Chacón Navarro *in* Moncel, 2019).

171

172 **3. Material and methods**

173

174 **3.1. Studied artefacts, sampling and application of the pollen** 175 **washes technique**

176 Eight stone tools distributed throughout layer 5 were examined and processed
177 using the pollen washes technique (Table 1, Fig. 2). These flints measure
178 between 50 and 70 mm-long and are amongst the largest stone tools of the
179 assemblage. Sediment samples from area immediately surrounding each artefact
180 were collected for NPP analysis. This multiple sample strategy allows us to obtain
181 a study of layer 5 at a high spatial resolution. No disturbances of the sediment
182 (e.g. burrow, den) were noted during excavations. Layer 5 was well-preserved
183 and protected over time by the overlying thick layer of blocks that completely
184 covered the deposit. These blocks were removed just before the excavation and
185 the collection of the stone tools. To reduce the possibility of modern
186 contamination, the artefacts were immediately placed unwashed after excavation
187 in a zip-style plastic bag until the realisation of the pollen washes. The latter took
188 place in the University of Bretagne Sud (Geosciences Ocean, UMR 6538-CNRS,
189 Vannes, France) following methods detailed in Miras et al., (2018). Sediment
190 adhered to the artefact surface – called “sticking sediment” – was carefully
191 collected (Fig. 2) and analysed separately. In order to retrieve biological
192 microfossils embedded in the artefact surface’s pores and vesicles, stone tools
193 were subsequently entirely washed using a high-pressure (between 3 and 4 bar)
194 turbine spray gun machine (Fig. 2). This was filled with a cleaning solution based
195 on hot distilled water and 5% dimethyl sulphoxide, a solvent and penetrant. A
196 total of 24 samples comprising sediment samples from layer 5 in the vicinity of
197 the artefacts, sticking sediments samples, and pollen washes samples were
198 collected and correspond to the “archaeological sample assemblage” (see full
199 description in Table 1).

200 Twelve modern control samples were also collected outside the shelter to
201 monitor possible natural deposition of fungal spores in the shelter and to better
202 identify fungal spore’s plant hosts. They correspond to the “modern control
203 samples assemblage” (see detailed description in Table 2). Different contexts
204 were selected for the modern control sample, including:

- 205 - mosses collected in the immediate vicinity of the shelter to monitor
206 potential fungal aerial deposition/inputs to the site,
- 207 - soil surfaces in the immediate area surrounding the shelter to evaluate
208 potential fungal contamination of the site by run-off processes,
- 209 - samples resulting both from a combination of soil samples and plant
210 roots/rhizome and from exclusively roots/rhizome fragments to investigate
211 possible plant host of the fungi evidenced in the shelter. Alder (*Alnus*)
212 carrs (waterlogged wooded terrains populated with alder tress) were
213 specifically sampled as *Diporotheca webbiae* D. Hawksworth., B. van Geel

214 et P. Wiltshire (NPP-type: HdV-143, van Geel et al., 1989; Hawksworth et
215 al., 2016) were observed in fossil samples restricted to pollen zones
216 interpreted as alder carr in previous research (Barthelmes et al., 2006;
217 van der Wiel, 1982). Populations of *Thelypteris palustris* Schott. were also
218 sampled as this fern is suspected to be the host of *Diporothea webbiae*
219 (Hawksworth et al., 2016). In the latter case, sampling was carried out in
220 2 of the 7 remaining populations of marsh fern situated in Ardèche.

221 The comparison between the archaeological and control samples allows the
222 detection of microfossil enrichment, which could indicate potential anthropogenic
223 botanical microfossils deposition related to plant use in specific archaeological
224 microcontexts (Riera et al., 2018).

225

226 **3.2. Non-pollen palynomorphs analysis**

227 Modern control and archaeological samples were processed following a modified
228 standard palynological procedure (Faegri and Iversen, 1989) at the GEOLAB UMR
229 6042 CNRS laboratory in Clermont-Ferrand, France). Samples were treated with
230 hydrochloric and hydrofluoric acids and then sieved through a 0.20mm mesh and
231 centrifuged. Samples were subsequently treated with heavy liquid separation
232 using zinc chloride. Acetolysis was not conducted to avoid potential deterioration
233 of fungal material, as demonstrated by recent experimental studies (Perrotti and
234 van Asperen, 2019). A drop of safranin was added to stain the microfossils.
235 *Lycopodium* tablets were added to allow the calculation of microfossils
236 concentrations (Stockmarr, 1971). After processing, samples were suspended in
237 glycerine jelly prior to being mounted on slides.

238 Fungal spore quantification was undertaken at the HNHP (UMR 7194 CNRS,
239 Muséum national d'Histoire naturelle, Paris) using a light ZEISS microscope at
240 $\times 600$ and $\times 1000$ magnification). Mean values of 350 *Lycopodium* spores were
241 counted, which is sufficient to calculate significant concentrations of fungal
242 spores (Etienne and Jouffroy-Bapicot, 2014). Fungal spores were identified using
243 morphological keys and atlas (e.g., Cugny, 2011; van Geel, 1989). Results are
244 expressed in number of elements.g⁻¹. Following Geib and Smith (2008), we also
245 expressed the results of pollen washes samples as pollen concentrations per unit
246 of artefact-surface area (denoted as elements.cm⁻²).

247

248 **4. Results**

249 **4.1. General results**

250 *Concentration and preservation* - Amongst the eight studied stone tools, only
251 object n°1079 (square N6) gave significant positive results. This confirms the
252 poor preservation of botanical microfossils in the Abri du Maras (Table 1).
253 Concentrations of pollen and pteridophyte spores recovered from the
254 archaeological samples are negligible in samples S13, S14 and S15 (median
255 values around 60 elements.g⁻¹), and almost nil for the other samples originating
256 from layer 5. This poor preservation can probably be explained by the sandy-silty
257 composition of the deposit. The preponderance of coarse sediment may have

258 indeed enhanced oxidation of pollen and spores (Faegri and Iversen, 1989). A
259 similar poor preservation was previously observed for the overlying layer 4 in the
260 Abri du Maras (Moncel et al., 2015). By contrast, fungal spores have been more
261 regularly observed in archaeological samples, ratifying their higher ability to be
262 preserved than pollen in archaeological sediments (van Geel, 1986).
263 Nevertheless, only object n°1079 (S14 and S15) and its surrounding sediment
264 (S13) yielded statistically significant fungal assemblages with specific
265 morphotypes (Table 1 and Fig. 3 and 4). This could be explained by a local
266 accumulation of organic matter in this area. It is noteworthy that a fireplace was
267 found very close (1 m distant) to the stone tool (square N7, x=37, y=72,
268 z=414), which supports better organic preservation in this sector (Fig. 1). The
269 record of 2 specific fungal morphotypes in this area seems to argue against a
270 background fungal signature in the whole shelter, allowing us to associate the
271 fungal features obtained on object 1079 and its nearby sediment sample to their
272 microarchaeological context.

273 Pollen, spore and fungi preservation are generally good in the modern control
274 samples except in those corresponding to roots or rhizomes fragments: S32,
275 S34, S36. Despite low fungal concentration, the latter nevertheless provide
276 interesting qualitative information (Table 2, Fig. 5 and 6). The other control
277 samples are mainly characterized by high pollen concentration with mean and
278 median values of 334136 and 53710 elements.g⁻¹, respectively. Undifferentiated
279 fungal spores also show high abundances (mean and median concentrations of
280 42656 and 27055 elements.g⁻¹, respectively).

281 *Diversity and prevalent morphotypes* – 7 different morphotypes have been
282 evidenced in the archaeological samples from object 1079 while 36 morphotypes
283 characterized modern control samples. In the archaeological samples, NPP
284 assemblages are largely dominated by fungi, and specifically by *Chaetomium*-
285 type (HdV-7A) and *Diporotheca webbiae*-type (HdV-143). Some hyaline
286 microfossils have also been punctually recorded at low values. HdV-984 is similar
287 to zygospores of *Euastrum*-t (Carrión and van Geel, 1999), corresponding to the
288 green algae *Euastrum* Ehrenberg ex Ralfs 1848, Desmidiaceae. HdV-989 is of
289 unknown origin (Carrión and van Geel, 1999). In the control samples, fungi also
290 largely prevail in the NPP assemblage. The number of fungal taxa is high and
291 have different ecological affinities. The predominant taxa are first saprobic or
292 parasitic fungi such as *Brachydesmiella*-type HdV-1005, *Glomus*-type HdV-207,
293 *Microthyrium* Desm-type HdV-8B, *Gaeumannomyces*-type HdV-126, *Diporotheca*
294 *webbiae*-type HdV-143, *Dictyosporium*-type TM-4093 and *Triposporium elegans*-
295 type TM-M1. According to the classification of Perrotti and van Asperen (2019),
296 other taxa observed are coprophilous fungi among which the most represented
297 are *Sporormiella*-type (HdV-113), *Delitschia*-type (TM-23), *Sordaria*-type (HdV-
298 55), *Arnium*-type (HdV-261) and *Cercophora*-type (HdV-112). Other abundant
299 registered fungal taxa such as *Curvularia*-type HdV-1029, Phragmoconidies or
300 TM-030 are more ubiquitous. Finally, low concentrations of algal spores such as
301 *Spirogyra*-type HdV-315 and Pseudoschizaea-type, faunal remains such as
302 Turbellaria, *Assulina*-type HdV-32, *Arcella*-type HdV-352 and *Macrobotus*
303 *hufelandi*-type, as well as and Bryophyta spores are also present.

304

305 **4.2. Spatial dimension: site vs off-site samples**

306 Through the application of the pollen washes technique, we obtained a
307 microtransect sampling going from the sediment immediately surrounding the
308 artefact (S13) until to the artefact itself (S14 and S15). This microtransect allows
309 us to discriminate 2 different dominant taxa of the fungal spectrum between the
310 stratigraphic unit and the tool (Fig. 3). A decreasing trend in *Chaetomium*-type
311 (HdV-7A) concentrations is evidenced along this transect. High concentrations of
312 *Chaetomium*-type characterized the stratigraphic unit (S13: c. 2000 elements.g⁻¹),
313 while only rare occurrences were encountered in the sticking sediment (S14:
314 43 elements.g⁻¹). The abundance of this fungus is not observed after the gun
315 wash of the artefact (S15). *Chaetomium*-type appears thus to be directly related
316 to the sediment of the archaeological layer 5. Conversely, values of *Diporothea*
317 *webbiae*-type (HdV-143) present an increasing trend from low values in the
318 stratigraphic unit (S13: 341 elements.g⁻¹) to high concentrations in the tools
319 samples (S14: 9361 elements.g⁻¹; S15: 2704 elements.g⁻¹). The area
320 immediately surrounding a stone tool generally offers good preservation at the
321 microscopic fragments, which can be associated with the artefact (Hardy, B. et
322 al., 2020). This could explain the small amounts of *Diporothea webbiae*-type
323 recorded in the archaeological layer. Moreover, samples from artefact 1079
324 register noticeable concentrations of aggregates of *Diporothea webbiae*-type,
325 with increasing values between the sticking sediment (S14: 280 elements.g⁻¹)
326 and the artefact itself (S15: 375 elements.g⁻¹). The largest aggregates (between
327 5 and 15 ascospores stuck together) come from the stone tool washes (S15). All
328 this suggest that *Diporothea webbiae*-type is directly related to the lithic object.
329 Values expressed in concentration per unit of artefact-surface confirm that the
330 stone tool n°1079 is strictly defined by high amounts of *Diporothea webbiae*-
331 type, both in ascospores – 283 and 56 elements.cm⁻² - and aggregates – around
332 8 elements.cm⁻² in samples S14 and S15, respectively, Fig. 4). The object
333 constitutes thus the archaeological microcontext of this fungus.

334 In the control samples (Fig. 5 and 6), *Chaetomium*-type and *Diporothea*
335 *webbiae*-type were only found at negligible values in respectively one of the 2
336 sampling locations situated just outside the shelter (*Chaetomium*-type, S25: 62
337 elements.g⁻¹, *Diporothea webbiae*-type, S26: 24 elements.g⁻¹). NPP
338 assemblages are moreover very different in the sediment samples inside (S13)
339 and outside the archaeological site (S25, S26). In the control soil-surface
340 samples, the composition of NPP is very diverse and mainly dominated by
341 morphotypes which were not evidenced in the archaeological layer (S25
342 dominant taxa- spores of Bryophyta: 17760, Pseudoschizaea: 1603,
343 Phragmoconidies: 1480 elements.g⁻¹, *Microthyrium* Desm-type HdV-8B: 493;
344 S26 dominant taxa- *Triposporium elegans*-type TM-M1: 1243, *Dictyosporium*-
345 type TM-4093: 853, *Gaeumannomyces*-type HdV-126: 755, *Microthyrium* Desm-
346 type HdV-8B: 585, *Assulina*-type HdV-32: 390, *Sphaeroides* cf. *fimicola*-type TM-
347 20: 366, Pseudoschizaea: 317 elements.g⁻¹) or at lower frequencies (*Glomus*-
348 type HdV-207- S13: 214, S14: 151, S15: 19, S25: 3761, S26: 731 elements.g⁻¹).
349 Similar discrepancies are also evidenced between the archaeological samples

350 and the moss samples which are mainly characterized by taxa unregistered at
351 the site: S27- Phragmoconidies: 7785, *Arcella*-type HdV-352: 4933; S28-
352 Phragmoconidies: 89712, *Triposporium elegans*-type TM-M1: 906, *Cercophora*-
353 type HdV-112: 906, Sordariaceae: 453 elements.g⁻¹. The lack of both
354 *Chaetomium*-type and *Diporothea webbiae*-type in the control samples rules out
355 natural inputs of both fungal spores into the shelter due to run-off processes or
356 by wind. Once again, sampling in the shelter was carried out immediately after
357 the removal of the collapsed stone slabs covering layer 5 during the excavations
358 performed between 2017 and 2019. All this strengthens the local presence of
359 these 2 fungi inside the archaeological site.

360 It is noteworthy that substantial quantities of *Diporothea webbiae*-type were
361 observed in the samples concerning litter and roots from of an *Alnus glutinosa*
362 (black alder) population located on a wet habitat of the Ardèche riverbank (S29
363 with 4406 elements.g⁻¹ and S30 with 9666 elements.g⁻¹). These concentrations
364 are similar to the values obtained in the stone tool samples (S14 and S15).
365 Moreover, sample S30 also contains some juvenile ascospores of *Diporothea*
366 *webbiae*-type (Fig. 7), described by Hawksworth et al. (2016). The absence of
367 *Diporothea webbiae*-type ascospores in samples S31 and S32, which also
368 correspond to alder litter and roots may be explained by drier conditions of these
369 locations in comparison to sample S29. This is supported by higher rates of
370 *Brachydesmiella*-type HdV-1005 documented in S31 (7833 elements.g⁻¹) than in
371 S29 (110 elements.g⁻¹). *Brachydesmiella*-type is indeed a saprobe fungus on
372 dead and decaying leaves and wood, sometimes partially submerged (Gelorini et
373 al., 2011). Secondly, this is coherent with higher rates of *Glomus*-type HdV-207
374 in S31 (2843 elements.g⁻¹) than in S29 (330 elements.g⁻¹). *Glomus*-type –
375 probably *Glomus cf. fasciculatum* – is a mycorrhizal fungus in association with
376 different plants, and especially Cyperaceae (sedges) (Pals et al., 1980), which
377 prefer humid to seasonally flooded areas. All this suggests that *Diporothea*
378 *webbiae*-type is more common in more permanently submerged parasitized alder
379 roots. Finally, only low concentrations of ascospores of *Diporothea webbiae*-type
380 were found in sample S35 (401 elements.g⁻¹), originating from populations of
381 marsh fern (*Thelypteris palustris*). Zero or trace concentrations were evidenced
382 in rhizome samples S34 and 36.

383

384 **5. Discussion**

385 **5.1. Assessing Neanderthal plant-related activities in the Abri du** 386 **Maras**

387 Our data, combined with the few existing studies of Palaeolithic Non-Pollen-
388 Palynomorphs (NPP) (Medeanic and Sapozhnikov, 2008; Expósito et al., 2017;
389 Vinogradova and Burjachs Casas, 2018; Liu et al., 2018), validate their potential
390 for identifying organic matter accumulations both in Pleistocene sediments and in
391 Palaeolithic archaeological sites. The better preservation of NPP, mainly fungal
392 spores, compared to pollen and fern spores, urges the systematic study of NPP in
393 archaeological deposits. These pioneering studies explored the contribution of
394 these microfossils to a better knowledge of the different processes (geological,
395 biological, physical and chemical) that resulted in the archaeological deposits,

396 and successfully laid the groundwork for their use as environmental indicators.
397 Our research is more focused on exploring the potential use of NPP, especially
398 endophyte fungal spores, as a means of detecting and better understanding the
399 presence of plants in Neanderthal sites and their possible uses. In this sense, the
400 data discussed here aim thus to validate these palynomorphs as cultural
401 indicators thanks to the microsampling method and the pollen washes technique.

402 High contents of *Chaetomium*-type (HdV-7A) were recorded in the square N6 of
403 layer 5, in the immediate vicinity of stone tool n° 1079 (sample S13, Fig. 3 and
404 7). Chaetomiaceae G. Winter is a family of saprobic or parasitic fungi, growing on
405 plant debris, dung, soils and different other substrates (Maharahchikumbura et
406 al., 2016). *Chaetomium*-type is thus a cosmopolitan fungus, which can also be
407 found in soils and in the air and that could be naturally transported into the
408 shelter through airborne or erosive inputs. Nevertheless, the near absence of
409 *Chaetomium*-type in the area immediately surrounding the Abri du Maras
410 (samples S25 to S28, Fig. 5) and its confined observation at high values in a
411 specific sector of layer 5 lead us to suggest that it indicates the local presence of
412 decayed plant materials in that sector. Following this, *Chaetomium* species are
413 mainly non-clavicipitaceous endophytes, found in the tissues of bryophytes,
414 ferns, gymnosperms and angiosperms (Abdel-Azeem, 2020). They are cellulose
415 decomposing fungi and occur wherever the substrate, most particularly plant
416 remains like damp straw, is abundant (van Geel, 2001). The *Chaetomium*-type
417 (HdV-7A) observed in the Abri du Maras is a lemon-shaped dark-brown spore
418 with dimensions close to *Chaetomium globosum*-type. According to Chivers
419 (1915), this is a very common species, which often occurs on dead stalks and
420 leaves, especially from plants in damp wet places. In this sense, van Geel et al.,
421 (1989) and Sánchez Márquez et al. (2010) recorded many *Chaetomium*-type
422 spores in samples from an initial sedge fen and leaves of *Holcus lanatus*, a grass
423 that grows in humid soils in temperate zones. Moreover, *Chaetomium*-type
424 seems to prefer decomposing aerial plant components and does not colonize
425 roots of aquatic plant species (Fisher et al., 1991; Sánchez Márquez et al.,
426 2010). This makes very unlikely that the observed *Chaetomium*-type is due to
427 post-depositional developments from roots infiltrations. A local presence of
428 decayed aerial plant materials possibly originating from wet places may explain
429 this high amount of fungal spores in the archaeological sediments. An
430 anthropogenic cause could also explain the localised presence of these spores in
431 the shelter. In the Abri du Maras, *Chaetomium*-type spores were found nearby a
432 fireplace *in situ* probably corresponding to the same occupation of the shelter
433 (Moncel, 2019, Fig. 1). A close spatial co-occurrence between hearths and
434 preparation of the living floor has been previously reported from some Middle
435 Palaeolithic sites (Cabanès et al., 2010; Henry et al., 2004; Vallverdú et al.,
436 2010; Wroth et al., 2019). It is thus probable that this area in the Abri du Maras
437 had surface preparation such as bedding using grasses or other types of plants,
438 possibly from nearby wet areas such as reed and rushes. It is noteworthy that
439 analyses of residues carried out in the Abri du Maras show that Neanderthals
440 exploited a wide range of plant species for diverse activities in the shelter,
441 including the manufacture of string and cordage during MIS 3 (layer 4, Hardy, B.
442 et al., 2013 and 2020). Some of the fibres discovered likely derive from reeds,
443 rushes, or similar plants (Hardy, B. et al., 2013). Neanderthal groups from the

444 Abri du Maras may have had a special interest in plants from damp places
445 between the end of MIS 5 and the beginning of the MIS 4.

446 Another possible hypothesis explaining these high amounts of *Chaetomium*-type
447 is the local presence of dung. *Chaetomium* is not a strict coprophilous but rather
448 a fimiculous fungi, for which dung is only one of the suitable substrates where
449 they can develop (Abdel-Azeem, 2020). The proximity of dung to the hearth
450 could indicate the use of animal dung as fuel but this practice remains uncertain
451 for Neanderthal groups (Henry, 2007). Moreover, the presence of other
452 coprophilous fungi may have been expected in S13 if dung was locally present in
453 the area, which is not the case. All this makes unlikely that the presence of
454 *Chaetomium*-type is related to dung.

455

456 **5.2. New insights into the characterization of a potential plant-** 457 **related Neanderthal stone tool**

458 Neanderthals collected plants for different purposes, such as food, fuel, bedding
459 and other constructive or technical activities (Riehl et al., 2015). The contribution
460 of plants in Neanderthal behaviour and subsistence is a pressing question, which
461 can be addressed by analysing stone tools. Botanical microfossils adhered and
462 embedded into the artefact surface can indeed be sensitive indicators of plant
463 past use. By analysing the pollen and – in the case of the Abri du Maras study,
464 the non-pollen palynomorphs (NPP) - embedded in the porous surface of
465 archaeological artefacts (microporosity in the case of flint tools), the pollen
466 washes technique can contribute to identify lithic artefacts associated with plant
467 processing (Miras et al., 2018). This initial application of the pollen washes
468 technique on Middle Palaeolithic lithic materials gave only one positive result
469 from eight objects, but did yield positive results even with the small sample size.

470 A striking NPP signature has been evidenced in the analysis of the object n°1079.
471 This artefact is a backed flake with a scraper on the cutting edge opposite to the
472 back. It is a small tool measuring 72 mm long, 66 mm wide and 27 mm thick
473 (Fig. 8). The fact that high concentrations of *Diporothea webbiae*-type (HdV-
474 143, samples S14 and S15, Fig. 3 and 7) are almost exclusively found in the
475 tool's surface sticking sediment (S14) and in the washes sample (S15) suggests
476 direct exposure of the tool with this fungus. Moreover, the fact that substantial
477 values of aggregates of this ascospores are documented in these two samples,
478 together with both increased concentrations of clumps and larger clumps in S15,
479 obtained after the gun wash of the tool surface, confirm that ascospores were
480 embedded in the fine-grained structure of the tool. Ascospores of many fungi
481 tend to stick together during their formation in the perithecia or when they are
482 released from the fruit-body (van Asperen et al., 2016). Large aggregates are
483 heavy and have a lower dispersal ability than single spores. Moreover, the near
484 absence of *Diporothea webbiae*-type in the modern control samples (S25 to
485 S28, Fig. 5) allows us to dismiss a natural aerial or water source of these
486 ascospores. Finally, artefacts were immediately collected and bagged from layer
487 5 just after the removal of the stone slabs, which rules out modern
488 contamination. All these data imply that the stone tool was in direct contact with

489 the fruit body of *Diporothea webbiae*-type. Diporotheceae, a family of
490 Ascomycetes described in 1995 by Mibey and Hawksworth (1995), are root
491 colonizers or parasites of different vascular plants. As perithecia develops within
492 and on the plant roots surface, only repeated and direct contact of the tool with
493 the infected plant parts can explain the embedded presence of this fungus in the
494 tool surface.

495 The ecology of *Diporothea webbiae* (Hawksworth et al., 2016) is unfortunately
496 poorly known, but this fungus especially occurs in mosses, soils and sediment
497 from peat deposits or alder carrs (Barthelmes et al., 2006), where *Thelypteris*
498 *palustris* is abundant. This led previous authors to consider this marsh fern as
499 the plant host (van Geel et al., 1986). Control samples S29, 30, 33 and 35 (Fig.
500 6) clearly show that alder is a better candidate host plant. Samples recovered
501 from *Alnus glutinosa* litter and roots show high concentrations of *Diporothea*
502 *webbiae*-type, which resemble those obtained by the stone tool wash
503 (concentrations above several thousand elements.g⁻¹ in any case). Fungal
504 assemblages also include immature ascospores of *Diporothea webbiae*-type,
505 which indicate the presence of perithecia on the infected roots (Fig. 7). It is
506 noteworthy that Hillbrand et al. (2012) found a positive correlation between
507 *Diporothea webbiae*-type and *Alnus* macrofossils in the palaeoenvironmental
508 sequence of Lake Nussbaumersee, in Switzerland. Conversely, low
509 concentrations of the ascospore retrieved from fern samples (S33 and S35)
510 tends to dismiss the marsh fern as the main plant host. Based on the results
511 obtained in the modern control samples, the striking NPP feature in the tool
512 samples is the fungal imprint of the contact between the stone tool and infected
513 alder roots.

514 Before exploring several hypotheses to explain the contact of alder roots with the
515 tool, modern contaminations need to be ruled out. The fact that alder is the host
516 plant dismisses any possible modern contamination, as present-day dry
517 environmental conditions do not allow any development of alder populations in
518 the immediate vicinity of the shelter. A riparian or marsh vegetation including
519 alder stands could have existed or developed in the surrounding of the site after
520 the tool deposition. In this case, infected roots could have naturally enriched the
521 artefact. Without being ignored, this assumption seems unlikely. If this was the
522 case, high concentrations of *Diporothea webbiae*-type may also be expected in
523 the sediment sample from the microenvironmental context of the tool (S13).
524 However, the bioarchaeological microsampling method followed with the pollen
525 washes technique clearly shows that the archaeological sediment sampled in the
526 vicinity of the stone tool (S13) only contains low values of *Diporothea webbiae*-
527 type which are between ten- and thirty-fold lower than those obtained in the
528 tool's surface sticking sediment (S14). This low amount of *Diporothea webbiae*-
529 type in the immediate surrounding of the tool is consistent with the observation
530 that the microenvironment of an artefact generally preserves microscopic
531 elements related to it (Hardy, B. et al., 2020). A natural preferential
532 accumulation of fungal spores near or beneath the tool as a result of taphonomic
533 processes can also be dismissed as no significant increases of undifferentiated
534 fungi are evidenced between the stratigraphic unit (S13) and the tool (S14 and
535 15) samples, and other fungi such as *Chaetomium*-type or *Glomus*-type

536 noticeably decline. Moreover, the multiple samples in layer 5 and the observed
537 absence of *Diporotheca webbiae*-type in the sediment samples collected allows
538 us to certify that no background signature of this NPP exists in this layer. The
539 potential infiltration of infected alder roots in the proximity of the tool after the
540 artefact was deposited due to the development of alder populations in the vicinity
541 of the shelter, would have resulted in a more uniform dispersion of *Diporotheca*
542 *webbiae*-type within layer 5. Results obtained from samples in direct contact with
543 the artefact surface (S14 and 15) clearly associate high concentrations of
544 *Diporotheca webbiae*-type with the tool, which suggests that the fungal signature
545 may result from the use of the tool. Processing alder roots implies repeated and
546 long-lasting contacts with the tool, which could explain the important recovery of
547 Diporotheceae in the embedded artefact surface (S14 and S15).

548

549 **5.3. Uses of alder roots and attractiveness of damp environments**

550 As documented in the ethnographic and historical literature, alder roots have
551 been widely used by past societies, and could indeed have been a targeted plant
552 resource by Neanderthal groups. Alder is a well-known medicinal plant and
553 different parts of the plant were employed: leaves to treat fever as an alternative
554 of using cinchona (Ratier, 1827), common alder (*Alnus glutinosa*) bark to treat
555 swelling, inflammation and rheumatism (Sati et al., 2011) and roots. For
556 instance, a mixture of common alder roots with fennel and burdock was
557 traditionally recommended for the treatment of tremors (Buchoz, 1764), and
558 roots of *Alnus nepalensis* are prescribed in the present-day to treat diarrhoea
559 (Sati et al., 2011). A mixture of grey alder (*Alnus incana*) roots was used until
560 recently in the northern Midwestern United States by the Chippewa women to
561 facilitate difficult childbirth (Nesom, 2003). Alder roots are also rich in tannins
562 extracted for dyeing. Technological purposes can also be possible as
563 ethnographic studies show that Californian native groups (Mason, 1988) used red
564 alder (*Alnus rubra* Bong. 1832) in baskets. Furthermore, roots of many trees,
565 including alder and various conifers can be used for making cordage (Hurcombe,
566 2014). This is of particular interest as residue analyses in the Abri du Maras
567 demonstrate that Neanderthal groups manufactured string and cordage (Hardy,
568 B. et al., 2020) during MIS 3. Some artifacts exhibited fibers, which likely derive
569 from reeds, rushes, or similar plants (Hardy, B. et al., 2013). These plants share
570 similar habitats with alder, as birch (*Betula*) charcoals fragments documented in
571 layer 5 (square M8). It is noteworthy that riverside wood is not frequently
572 recorded among firewood remains when other more suitable and abundant
573 woods like pine were available (Allué et al., 2017). If all these data are
574 considered altogether, it appears that marsh and riparian ecosystems were
575 attractive for Neanderthal groups occupying the shelter. Our results are in good
576 agreement with those obtained by Hardy, B. et al., 2013, and confirm that
577 Neanderthal groups of the Abri du Maras had precise knowledge of their
578 surrounding environment and located appropriate plants for specific purposes. It
579 is noteworthy to mention that alder roots developed nodules - a symbiotic
580 relationship with nitrogen-fixing bacteria, mainly the genus *Frankia* (Pojar and
581 Mackinnon, 1994). These nodules accumulate starch and soluble sugars (Wheeler

582 et al., 1983), which could enhance the potential interest of alder roots by
583 Palaeolithic groups. In the Abric Romani Middle Palaeolithic site in the Iberian
584 Peninsula, a similar interest for riverside forests was evidenced (Burjachs et al.,
585 2012). If we refer to anthracological studies in Middle Palaeolithic caves and
586 shelters, it appears that firewood was recollected from nearby sources (Allué et
587 al., 2017; Vidal Matutano et al., 2015). It could be thus hypothesized that
588 riparian forest or marsh/damp environments were established not far from the
589 shelter. This could also reveal the proximity of the Ardèche River. These
590 interpretations are consistent with sporadic records in layer 5 (squares L9, M6,
591 M10 and N6) of *Microtus cf. agrestis*, a rodent with a preference for fresh
592 meadows and riparian forests (Desclaux in Moncel, dir., 2019). The existence of
593 forested areas around the Abri du Maras is further suggested by the
594 predominance of *Cervus elaphus* as well as by observations of *Sus scrofa* and
595 *Dama dama* in the macrofaunal assemblages (J. Marin in Moncel, 2019), which
596 agree with more temperate climatic conditions prevailing at the end of MIS 5
597 (Moncel et al., 2018).

598

599 **Conclusion**

600 In this pioneering research, we have explored for the first time the potential of
601 non-pollen palynomorphs (NPP) to provide new insights into an improved
602 understanding of the relationships between Neanderthals and plant resources.
603 Though rarely studied in Palaeolithic sites, NPP, and particularly fungal spores,
604 have better preservation than pollen and fern spores. This encourages to
605 systematic NPP studies in archaeological deposits. Endophytic fungi, which
606 develop close relationships with plants by living within the host tissues and can
607 be liberated during host senescence, can serve as key indicators of the local
608 presence of plants, which could potentially have been used by Neanderthal
609 groups. This study clearly shows that NPP must be considered as key
610 taphonomical, environmental and cultural indicators in archaeobotanical
611 analyses. Our research has also applied for the first time the combined study of
612 archaeological sediments and pollen washes of artefacts following a microspatial
613 approach in the study of Middle Palaeolithic archaeological contexts.

614 The positive result obtained from tool 1079 of the Abri du Maras provides a
615 significant contribution to our understanding of plant-related tool use. With the
616 comparison of archaeobotanical results with NPP analyses in modern surface
617 samples, we could determine the host plant of the fungal signature documented
618 in the tool surface as alder roots and propose the use of the lithic tool for
619 processing this plant by Neanderthal groups. Alder roots have multiple potential
620 uses for both medicine and technology (cordage or basketry).

621 Plants are generally ignored or underrepresented at Palaeolithic sites due to a
622 lack of preservation. Archaeobotanical analyses including the application of the
623 pollen washes technique must be pursued in Middle Palaeolithic sites as the
624 function of Neanderthal tools is always difficult to identify and to correlate to
625 plant processing or use (e.g. soil surface preparation). By scrutinizing particular
626 pollen, spore and NPP signatures, embedded in the porous or irregular surface of

627 archaeological artefacts, and consequently related to the tool use, this technique,
628 in combination with the study of other microfossils (phytoliths, residues etc.),
629 allows better assessing Neanderthal plant uses that is otherwise invisible
630 archaeologically. Our research provided conclusive evidences that NPP can
631 provide meaningful cultural information. Their systematic tracking and mapping
632 on the different living floors will constitute the next step of their analysis in the
633 Abri du Maras and will provide new information to our understanding of
634 Neanderthal plant use and site spatial organization.

635

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645

646 **References**

- 647 Abdel-Azeem, A.M. (dir.), 2020. Recent developments on genus *Chaetomium*,
648 Springer Nature Switzerland. <https://doi.org/10.1007/978-3-030-31612-9>
- 649 Allué, E., Solé, A., Burguet-Coca, A., 2017. Fuel exploitation among Neanderthals
650 based on the anthracological record from Abric Romaní (Capellades, NE Spain).
651 Quatern. Intern. 431, 6-15. <http://dx.doi.org/10.1016/j.quaint.2015.12.046>
- 652 Barthelmes, A., Prager, A., Joosten, H., 2006. Palaeoecological analysis of *Alnus*
653 wood peats with special attention to non-pollen palynomorphs. Rev. Palaeobot.
654 Palynol. 141, 33-49. <http://dx.doi.org/10.1016/j.revpalbo.2006.04.002>
- 655 Buchoz, P.J., 1764. De l'Aulnée. Traité historique des plantes qui croissent dans
656 la Lorraine et les 3 évêchés contenant leur description, leur figure, leur nom,
657 l'endroit où elles croissent, leur culture, leur analyse et leurs propriétés, Claude-
658 Sigisbert Lamord, Paris.
- 659 Burjachs, F., López-García, J.M., Allué E., Blain, H.A., Rivals, F., Bennàsar, M.,
660 Expósito, I., 2012. Palaeoecology of Neanderthals during Dansgaard-Oeschger
661 cycles in northeastern Iberia (Abric Romaní): from regional to global scale.
662 Quatern. Intern. 247, 26-37. <http://dx.doi.org/10.1016/j.quaint.2011.01.035>
- 663 Cabanes, D., Mallol, C., Expósito, I., Baena J., 2010. Phytolith evidence for
664 hearths and beds in the late Mousterian occupations of Esquilieu cave (Cantabria,
665 Spain). J. Archaeol. Sci. 37, 2947-2957.
666 <http://dx.doi.org/10.1016/j.jas.2010.07.010>

667 Carrión, J.S., van Geel, B., 1999. Fine-resolution Upper Weichselian and
668 Holocene palynological record from Navarre's (Valencia, Spain) and a discussion
669 about factors of Mediterranean forest succession. *Rev. Palaeobot. Palynol.* 106,
670 209-236. [https://doi.org/10.1016/S0034-6667\(99\)00009-3](https://doi.org/10.1016/S0034-6667(99)00009-3)

671 Chivers, A.H., 1915. A monograph of the genera *Chaetomium* and *Ascotricha*.
672 *Memoirs of the Torrey Botanical Club. Torrey Botanical Society.* 14, 3, 155-240

673 Cugny, C., 2011. Apports des microfossiles non-polliniques à l'histoire du
674 pastoralisme sur le versant nord Pyrénéen : entre référentiels actuels et
675 reconstitution du passé. PhD, Toulouse-le-Mirail University.

676 Daujeard, C., Vettese, D., Britton, K., Béarez, P., Boulbes, N., Crégut-Bonnoure,
677 E., Desclaux, E., Lateur, N., Pike-Tay, A., Rivals, F., Allué, E., Chacón, M.G.,
678 Puaud, S., Richard, M., Courty, M.A., Gallotti, R., Hardy, B., Bahain, J.J.,
679 Falguères, C., Pons-Branchu, E., Valladas, H., Moncel, M.H., 2017. Neanderthal
680 selective hunting of reindeer? The case study of Abri du Maras (south-eastern
681 France). *Archaeol. Anthropol. Sci.* 11, 985-1011.
682 <https://doi.org/10.1007/s12520-017-0580-8>

683 Deacon, J., 2006. *Fungal biology.* Blackwell Publishing, Malden.

684 Diot, M.F., 1991. Le palynofaciès en archéologie: intérêt de son étude. *Revue*
685 *d'Archéométrie* 15, 54-62.

686 Etienne, D., Jouffroy-Bapicot, I., 2014. Optimal counting limit for fungal spore
687 abundance estimation using *Sporormiella* as a case-study. *Veget. Hist.*
688 *Archaeobot.* 23, 743-749. <http://dx.doi.org/10.1007/s00334-014-0439-1>

689 Expósito, I., Burjachs, F., Allué E., 2017. Filling in the gaps: The contribution of
690 non-pollen palynomorphs to knowledge about the local environment of the Sierra
691 de Atapuerca caves during the Pleistocene. *Quatern. Intern.* 433, 224-242.
692 <http://dx.doi.org/10.1016/j.quaint.2015.09.016>

693 Faegri, K., Iversen, J., 1989. *Textbook of pollen analysis.* Wiley, New York.

694 Fisher, P.J., Petrini, O., Webster, J., 1991. Aquatic hyphomycetes and other fungi
695 in living aquatic and terrestrial roots of *Alnus glutinosa*. *Mycol. Res.* 95, 5, 543-
696 547. [https://doi.org/10.1016/S0953-7562\(09\)80066-X](https://doi.org/10.1016/S0953-7562(09)80066-X)

697 Florenzano, A., 2019. The history of pastoral activities in S. Italy inferred from
698 palynology: a long-term perspective to support biodiversity awareness.
699 *Sustainability* 11, 404. <http://dx.doi.org/10.3390/su11020404>

700 Geib, P.R., Smith, S. J., 2008. Palynology and archaeological inference: bridging
701 the gap between pollen washes and past behaviour. *J. Archaeol. Sci.* 35, 2085-
702 101. <http://dx.doi.org/10.1016/j.jas.2008.01.011>

703 Gelorini, V., Verbeken, A., van Geel, B., Cocquyt, C., Verschuren, D., 2011.
704 Modern non-pollen palynomorphs from East African lake sediments. *Rev.*
705 *Palaeobot. Palynol.* 164, 143-173.
706 <http://dx.doi.org/10.1016/j.revpalbo.2010.12.002>

707 Hardy, B.L., 2004. Neanderthal behaviour and stone tool function at the Middle
708 Palaeolithic site of La Quina, France. *Antiquity* 78, 301, 547-565.
709 <https://doi.org/10.1017/S0003598X00113213>

710 Hardy, B.L., Moncel, M.H., 2011. Neanderthal use of fish, mammals, birds,
711 starchy plants and wood 125-250,000 Years Ago. *PLoS ONE*. 6, 8, e23768.
712 <http://dx.doi.org/10.1371/journal.pone.0023768>

713 Hardy, B.L., Moncel, M.H., Daujeard, C., Fernandes, P., Béarez, P., Desclaux, E.,
714 Chacón, M.G., Puaud, S., Gallottu, R., 2013. Impossible Neanderthals? Making
715 string, throwing projectiles and catching small game during Marine Isotope Stage
716 4 (Abri du Maras, France). *Quatern. Sci. Rev.* 82, 23-40.
717 <http://dx.doi.org/10.1016/j.quascirev.2013.09.028>

718 Hardy, B.,L., Moncel, M.H., Kerfant, C., Lebon, M., Bellot-Gurlet, L., Mélard, N.,
719 2020. Direct evidence of Neanderthal fibre technology and its cognitive and
720 behavioral implications. *Scientific Reports* 10, 4889.
721 <https://doi.org/10.1038/s41598-020-61839-w>

722 Hardy, K., Buckley, S., Huffman, M., 2013. Neanderthal self-medication in
723 context. *Antiquity* 87, 873-878. <https://doi.org/10.1017/S0003598X00049528>

724 Hawksworth, D.L., van Geel, B., Wiltshire, P.E.J., 2016. The enigma of the
725 *Diporotheca* palynomorph. *Rev. Palaeobot. Palynol.* 235, 94-98.
726 <http://dx.doi.org/10.1016/j.revpalbo.2016.09.010>

727 Henry, A.G., 2007. Neanderthal cooking and the costs of fire. *Current*
728 *Anthropology*. 58, 16, 329-336. <http://dx.doi.org/10.1086/692095>

729 Henry, D.O., Hietala, H.J., Rosen, A.M., Demidenko, Y.E., Usik, V.I., Armagan,
730 T.L., 2004. Human behavioral organization in the Middle Paleolithic: were
731 Neanderthals different? *American Anthropologist* 106, 1, 17-31.
732 <http://dx.doi.org/10.1525/aa.2004.106.1.17>

733 Hillbrand, M., Hadorn, P., Cugny, C., Hasenfratz, A., Galop, D., Haas, J.N., 2012.
734 The palaeoecological value of *Diporotheca rhizophila* ascospores
735 (Diporotheceae, Ascomycota) found in Holocene sediments from Lake
736 Nussbaumersee, Switzerland. *Rev. Palaeobot. Palynol.* 186, 62-68.
737 <https://doi.org/10.1016/j.revpalbo.2012.06.009>

738 Hurcombe, L.M., 2014. *Perishable material culture in prehistory: investigating*
739 *the missing majority*. Routledge, Taylor & Francis Ltd, United Kingdom.

740 Lev, E., Kislev, M.E., Bar-Yosef, O., 2005. Mousterian vegetal food in Kebara
741 Cave, Mt. Carmel. *Journ. Archaeol. Sci.* 32, 3, 475-484.
742 <https://doi.org/1016/j.jas.2004.11.006>

743 Liu, L., Levi, J.M., Bonomo, M.F., Wang, J., Shi, J., Chen, X., Han, J., Song, Y.,
744 2018. Harvesting and processing wild cereals in the Upper Palaeolithic Yellow
745 River Valley, China. *Antiquity* 92, 363, 603-619.
746 <https://doi.org/10.15184/aqy.2018.36>

747 Luermo-Lautenschlaeger, R., Pérez-Díaz, S., Alba-Sánchez, F., Abel-Schaad, D.,
748 López-Sáez, J.A., 2018. Vegetation history in the Toledo Mountains (Central
749 Iberia): human impact during the last 1300 years. *Sustainability* 10, 7, 25-75.
750 <https://doi.org/10.3390/su10072575>

751 Maharachchikumbura, S.S.N., Al-Sadi, A.M., Al-Kharousi, M., Al Saady, N.A.,
752 Hyde, K.D., 2016. A checklist of fungi in Oman. *Phytotaxa* 273, 4, 219–261.
753 <https://doi.org/10.11646/phytotaxa.273.4.1>

754 Mason, O., T., 1988. *American Indian Basketry*, Dover Publications, Inc, New
755 York.

756 Mazza, P.P.A., Martini, F., Sala, B., Magi, M., Colombini, M.P., Giachi, G.,
757 Landucci, F., Lemorini, C., Modugno, F., Ribechini, E., 2006. A new Palaeolithic
758 discovery: tar-hafted stone tools in a European Mid-Pleistocene bone-bearing
759 bed. *J. Archaeol. Sci.* 33, 9, 1310–1318.
760 <http://dx.doi.org/10.1016/j.jas.2006.01.006>

761 Medeanic, S., Sapozhnikov, I., 2008. Preliminary data on fungal palynomorphs
762 from the late Paleolithic Bolshaya Akkarzha archaeological site. *Proceedings of*
763 *the Institute of Geological Sciences of the NAS of Ukraine*, Kyiv 2008, pp. 343-
764 551.

765 Mibey, R.K., Hawksworth, D.L., 1995. Diporotheceae, a new family of
766 ascomycetes, and the term "hyphopodium". *Syst. Ascom.* 14, 25–31.

767 Miras, Y., Beauger, A., Lavrieux, M., Berthon, V., Serieyssol, K., Andrieu-Ponel,
768 V., Ledger, P., 2015. Tracking long-term human impacts on landscape, vegetal
769 biodiversity and water quality in the lake Aydat (Auvergne, France) using pollen,
770 non-pollen palynomorphs and diatom assemblages. *Palaeogeogr., Palaeohydrog.,*
771 *Palaeoecol.* 424, 76-90. <http://dx.doi.org/10.1016/j.palaeo.2015.02.016>

772 Miras, Y., Ejarque, A., Barbier-Pain, D., Corbineau, R., Ledger, P.M., Riera Mora,
773 S., Garreau, A., Voldoire, O., Allain, E., Mangado Llach, X., Sánchez de la Torre,
774 M., Martínez Grau, H., Bergada Zapata, M., Smith, S.J., 2018. Advancing the
775 analysis of past human/plant relationships: methodological improvements of
776 artifact pollen washes. *Archaeometry* 60, 5, 1106-1121.
777 <http://dx.doi.org/10.1111/arcm.12375>

778 Moncel, M.H., (Dir.), 2019. *Abri du Maras (Saint-Martin d'Ardèche, Ardèche).*
779 *Rapports de fouilles programmées.* Service Régional d'Archéologie d'Ardèche,
780 DRAC, 229 p.

781 Moncel, M.H., Chacón, M.G., La Porta, A., Fernandes, P., Hardy, B., Gallotti, R.,
782 2014. Fragmented reduction processes: Middle Palaeolithic technical behaviour in
783 the Abri du Maras shelter, southeastern France. *Quatern. Intern.* 350, 180-204.
784 <https://doi.org/10.1016/j.quaint.2014.05.013>

785 Moncel, M.H., Allué, E., Bailon, S., Barshay-Szmidt, C., Béarez, P., Crégut, E.,
786 Daujeard, C., Desclaux, E., Debard, E., Lartigot-Campin, A.S., Puaud, S., Roger,
787 T., 2015. Evaluating the integrity of palaeoenvironmental and archaeological
788 records in MIS 5 to 3 karst sequences from southeastern France. *Quatern.*
789 *Intern.* 378, 22-39. <http://dx.doi.org/10.1016/j.quaint.2013.12.009>

790 Moncel, M.H., Navarro Chacón, M.G., Vettese, D., Fernandes, P., Hardy, B.,
791 Puaud, S., Richard, M., Allué, E., Bearez, P., Boulbes, N., Britton, K., Courty,
792 M.A., Crégut-Bonnouere, E., Desclaux, E., Gallotti, R., Joannes-Boyau, R., Kerfan,
793 C., Lateur, N., La Porta, A., Limondin-Louzouet, N., Marin, J., Pike-Tay, A.,
794 Rivals, F., Roger, F., Roger, T., Bahain, J.J., Falguères, C., 2018. L'Abri du Maras
795 à Saint-Martin d'Ardèche, des habitats néandertaliens du début du dernier
796 glaciaire. *Ardèche Archéologie* 35, 3-11.

797 Nesom, G., 2003. Speckled alder *Alnus incana* (L.) Moench ssp rugose (Du Roi)
798 Clausen. Plant Guide, USDA / NRCS, USA.

799 Nicolas, V., Surmely, F., Miras, Y., 2012. L'évolution des paysages et des
800 architectures sur la planèze sud du Plomb du Cantal du 11^e au 19^e siècles. Apport
801 des données archéologiques, archivistiques et paléoenvironnementales, in
802 Guillere C. (Ed), *Le Paysage rural au Moyen Age*, Editions du CTHS, Paris, pp. 79-
803 105.

804 Pals, J. P., van Geel B., Delfos, A., 1980. Paleoecological studies in the
805 Klokkeweel bog near Hoogkarspel (prov. of Noord Holland). *Rev. Palaeobot.*
806 *Palynol.* 30, 371-418. [https://doi.org/10.1016/0034-6667\(80\)90020-2](https://doi.org/10.1016/0034-6667(80)90020-2)

807 Perrotti, A.G., van Asperen, E., 2019. Dung fungi as a proxy for megaherbivores:
808 opportunities and limitations for archaeological applications. *Veget. Hist.*
809 *Archaeobot.* 28, 1, 93-104. <https://doi.org/10.1007/s00334-018-0686-7>

810 Pojar, J., MacKinnon, A., 1994. *Plants of the Pacific Northwest coast:*
811 *Washington, Oregon, British Columbia, and Alaska.* Lone Pine Publishing,
812 Redmond, Washington.

813 Power, R.C., Salazar-García, D.C., Rubini, M., Darlas, A., Havarki, K., Walker, M.,
814 Hublin, J.J., Henry, A.G., 2018. Dental calculus indicates widespread plant use
815 within the stable Neanderthal dietary niche. *J. Hum. Evol.* 119, 27-41.
816 <https://doi.org/10.1016/j.jhevol.2018.02.009>

817 Puaud, S., Nowak, M., Pont, S., Moncel, M.H., 2015. Minéraux volcaniques et
818 alpins à l'abri du Maras (Ardèche, France) : témoins de vents catabatiques dans
819 la vallée du Rhône au Pléistocène supérieur. *C R Palevol.* 14, 331-341.
820 <https://doi.org/10.1016/j.crpv.2015.02.007>

821 Ratier, F.S., 1827. *Pharmacopée française ou code des médicaments.* J.-B.
822 Baillière, Paris.

823 Revelles, J., Burjachs, F., van Geel, B., 2016. Pollen and non-pollen
824 palynomorphs from the Early Neolithic settlement of La Draga (Girona, Spain).
825 *Rev. Palaeobot. Palynol.* 225, 1-20.

826 Richard, M., 2012. *Datations par les méthodes combinées ESR-U/Th et*
827 *caractérisation d'émail dentaire de sites du Paléolithique Moyen d'Ardèche.*
828 *Master 2. Museum national d'Histoire naturelle (unpublished).*

829 Riera, S., Servera Vives, G., Picornell Gelabert, Ll., Cabanis, M., Boi, M., Miras,
830 Y., 2018. Pollen signatures of a ritual process in the collective burial cave of Cova
831 des Pas (Late Bronze Age, Minorca, Balearic Islands), in: Livarda, A., Madgwick,

- 832 R., Riera, S., (Eds), The bioarchaeology of ritual and religion. Oxbow Books,
833 Oxford and Philadelphia, pp. 28–43.
- 834 Riehl, S., Marinova, E., Deckers, K., Malina, M., Conard, N.J., 2015. Plant use
835 and local vegetation patterns during the second half of the Late Pleistocene in
836 southwestern Germany. *Archaeol. Anthropol. Sci.* 7, 151-167.
837 <https://doi.org/10.1007/s12520-014-0182-7>
- 838 Sánchez Márquez, S., Bills, G.F., Domínguez Acuña, L., Zabalgoeazcoa, I., 2010.
839 Endophytic mycobiota of leaves and roots of the grass *Holcus lanatus*. *Fungal*
840 *Diversity* 41, 115-123. <http://dx.doi.org/10.1007/s13225-009-0015-7>
- 841 Sati, S.C., Sati, N., Sati, O.P., 2011. Bioactive constituents and medicinal
842 importance of genus *Alnus*. *Pharmacogn. Rev.* 5, 10, 174-183.
843 <http://dx.doi.org/10.4103/0973-7847.91115>.
- 844 Shipley, G.P., Kindscher, K., 2016. Evidence for the paleoethnobotany of the
845 Neanderthal: a review of the literature. *Scientifica* 1-12.
846 <http://dx.doi.org/10.1155/2016/8927654>
- 847 Sistiaga, A., Mallol, C., Galván B., Summons, R.E., 2014. The Neanderthal meal:
848 a new perspective using faecal biomarkers. *PLOS ONE* 9(6): e101045.
849 <http://dx.doi.org/10.1371/journal.pone.0101045>
- 850 Stockmarr, J., 1971. Tablets with spores used in absolute pollen analysis. *Pollen*
851 *et Spores.* 13, 615–21.
- 852 van Asperen, E.N., Kirby, J.R., Hunt, C.O., 2016. The effect of preparation
853 methods on dung fungal spores: implications for recognition of megafaunal
854 populations. *Rev. Palaeobot. Palynol.* 229, 1-8.
855 <http://dx.doi.org/10.1016/j.revpalbo.2016.02.004>
- 856 van der Wiel, A.M., 1982. A palaeoecological study of a section from the foot of
857 the hazendonk (zuid-holland, the netherlands), based on the analysis of pollen,
858 spores and macroscopic plant remains. *Rev. Palaeobot. Palynol.* 38, 35-90.
859 [https://doi.org/10.1016/0034-6667\(82\)90049-5](https://doi.org/10.1016/0034-6667(82)90049-5)
- 860 van Geel, B., 1978. A palaeoecological study of Holocene peat bog sections in
861 Germany and the Netherlands. *Rev. Palaeobot. Palynol.* 25, 1-120.
862 [https://doi.org/10.1016/0034-6667\(78\)90040-4](https://doi.org/10.1016/0034-6667(78)90040-4)
- 863 van Geel, B., 1986. Application of fungal and algal remains and other microfossils
864 in palynological analyses, in: Berglund, B.E. (Eds.), *Handbook of Holocene*
865 *Palaeoecology and Palaeohydrology*. Wiley, Chichester, pp. 497–505.
- 866 Van Geel, B., 2001. Non-pollen palynomorphs, in: Smol, J.P., Birks, H.J.B., Last,
867 W.M. (Eds.), *Tracking Environmental Change Using Lake Sediments. Terrestrial,*
868 *Algal and Silicaceous Indicators III*. Kluwer Academic Publishers, Dordrecht, pp.
869 99–119.
- 870 van Geel, B., Coope, G.R., van der Hammen, T., 1989. Palaeoecology and
871 stratigraphy of the Lateglacial type section at Usselo (the Netherlands). *Rev.*
872 *Palaeobot. Palynol.* 60, 25-129. [https://doi.org/10.1016/0034-6667\(89\)90072-9](https://doi.org/10.1016/0034-6667(89)90072-9)

873 van Geel, B., Buurman, J., Brinkkemper, O., Schelvis, J., Aptroot, A., van
874 Reenen, G., Hakbijl, T., 2003. Environmental reconstruction of a Roman period
875 settlement site in Uitgeest (The Netherlands), with special reference to
876 coprophilous fungi. *J. Archaeol. Sci.* 30, 873–883.
877 [https://doi.org/10.1016/S0305-4403\(02\)00265-0](https://doi.org/10.1016/S0305-4403(02)00265-0)

878 Venditti, F., Nunziante-Cesaro, S., Parush, Y., Gopher, A., Barkai, R., 2019.
879 Recycling for a purpose in the late Lower Paleolithic Levant: use-wear and
880 residue analyses of small sharp flint items indicate a planned and integrated
881 subsistence behavior at Qesem Cave (Israel). *J. Hum. Evol.* 131, 109-128.
882 <https://doi.org/10.1016/j.jhevol.2019.03.016>

883 Vidal-Matutano, P., Hernández, C.M., Galván, B., Mallol, C., 2015. Neanderthal
884 firewood management: evidence from Stratigraphic Unit IV of Abric del Pastor
885 (Eastern Iberia). *Quat. Sci. Rev.* 111, 81-93.
886 <http://dx.doi.org/10.1016/j.quascirev.2015.01.010>

887 Vallverdú, J., Vaquero, M., Cáceres, I., Allué, E., Rosell, J., Saladié, P., Chacón,
888 G., Ollé, A., Canals, A., Sala, R., Courty, M. A., 2010. Sleeping activity area
889 within the site structure of archaic human groups: evidence from Abric Romaní
890 level N combustion activity areas. *Current Anthropology* 51, 1, 137-145.
891 <http://dx.doi.org/10.1086/649499>

892 Vinogradova, O., Burjachs Casas, F., 2018. Palynological analysis of coupled
893 sediment-control sample: the pollinic taphonomy from the Middle Paleolithic
894 level M of Abric Romaní (Capellades, Spain). *Емінак* 3, 3, 35-48.

895 Wheeler, C.T., Watts, S.H., Hillman, J.R., 1983. Changes in carbohydrates and
896 nitrogenase compounds in the root nodules of *Alnus glutinosa* in relation to
897 dormancy. *New Phytol.* 95, 209-218. [https://doi.org/10.1111/j.1469-](https://doi.org/10.1111/j.1469-8137.1983.tb03486.x)
898 [8137.1983.tb03486.x](https://doi.org/10.1111/j.1469-8137.1983.tb03486.x)

899 Wroth, K., Cabanes, D., Marston, J.M., Aldeias, V., Sandgathe, D., Turq, A.,
900 Goldberg, P., Dibble, H.L., 2019. Neanderthal plant use and pyrotechnology:
901 phytolith analysis from Roc de Marsal, France. *Archaeol. Anthropol. Sci.* 11,
902 4325-4346. <https://doi.org/10.1007/s12520-019-00793-9>

903

904

905

906 Table 1. Description of the archaeological samples. Samples with statistically
 907 significant fungi concentrations are marked in grey.

908

year of excavation	number	square	x	y	z	sample code and description
2017	947	K6	94	50	382	S1 : Stratigraphic Unit S2 : Sticking Sediment S3: Stone Wash
2017	1015	K6	43	57	388	S4: Stratigraphic Unit S5: Sticking Sediment S6: Stone Wash
2017	1306	M6	89	72	401	S7: Stratigraphic Unit S8: Sticking Sediment S9: Stone Wash
2017	252	N6	46	92	378	S10: Stratigraphic unit S11: Sticking Sediment S12: Stone Wash
2017	1079	N6	21	67	408	S13: Stratigraphic Unit S14: Sticking Sediment S15: Stone Wash
2018	765	M10	87	27	541	S16: Stratigraphic Unit S17: Sticking Sediment S18: Stone Wash
2018	1918	L6	21	30	420	S19: Stratigraphic Unit S20: Sticking Sediment S21: Stone Wash
2018	1227	L6	38	35	381	S22: Stratigraphic Unit S23: Sticking Sediment S24: Stone Wash

909

910 Table 2. Description of the modern control samples. Samples with statistically
 911 significant fungi concentrations are marked in grey.

912

sample Code	sample description
S25	Soil surface sampled in the upper and eastern immediate surrounding of the shelter
S26	Soil surface sampled in the lower and eastern immediate surrounding of the shelter
S27	Mosses collected from a tree located in the immediate vicinity of the shelter
S28	Mosses collected from a rock located in the immediate vicinity of the shelter
S29	Combination of litter and roots of <i>Alnus glutinosa</i> (L.) Gaertn. The population of <i>Alnus glutinosa</i> is located on the Ardèche riverbank (ca 70m away from the shelter)
S30	Roots of <i>Alnus glutinosa</i> (L.) Gaertn. (same location as S29)
S31	Combination of litter and roots of <i>Alnus glutinosa</i> (L.) Gaertn. The population of <i>Alnus glutinosa</i> is located in the slope between the river and the shelter (ca 40 m away from the shelter)
S32	Roots of <i>Alnus glutinosa</i> (L.) Gaertn. (same location as S31)
S33	Combination of litter and rhizome of <i>Thelypteris palustris</i> (spot 1: Sagnet in Saint-Paul-le-Jeune, Ardèche)
S34	Rhizome of <i>Thelypteris palustris</i> (same location as S33)
S35	Combination of litter and rhizome of <i>Thelypteris palustris</i> (spot 2: Ribes, Ardèche)
S36	Rhizome of <i>Thelypteris palustris</i> (same location as S35)

913

914

915 **Captions**

916

917 Fig. 1. Situation and site background.

918 1: location of the Abri du Maras and other major Palaeolithic sites (CAD S.
919 Puaud, in Moncel et al., 2018); 2: view of the present-day shelter; 3: stone slabs
920 recovering the layer 5; 4: top of the layer after the removal of the stone slabs;
921 5: hearth. Credits: M.H. Moncel.

922

923 Fig. 2. Studied stone tools and process of the pollen washes technique.

924 1: unwashed studied stone tools; 2: washed studied stone tools; 3: removal of
925 the sticking sediment; 4: gun wash of object n°1079; 5: both sides of object
926 n°1079 after wash.

927

928 Fig. 3. Concentrations of non-pollen palynomorphs of the archaeological samples
929 (results expressed in number of elements per gram).

930

931 Fig. 4. Concentrations of non-pollen palynomorphs of the archaeological samples
932 (results expressed in number of elements per cm²).

933

934 Fig. 5. Concentrations of non-pollen palynomorphs of the control samples
935 (results expressed in number of elements per gram): soil surfaces and mosses.

936 S25: Soil surface sampled in the upper and eastern immediate surrounding of
937 the shelter; S26: Soil surface sampled in the lower and eastern immediate
938 surrounding of the shelter; S27: Mosses collected from a tree located in the
939 immediate vicinity of the shelter; S28: Mosses collected from a rock located in
940 the immediate vicinity of the shelter.

941

942 Fig. 6. Concentrations of non-pollen palynomorphs of the control samples
943 (results expressed in number of elements per gram): litters, roots and rhizomes.

944 S29: Combination of litter and roots of *Alnus glutinosa* (L.) Gaertn. The
945 population of *Alnus glutinosa* is located on the Ardèche riverbank (ca 70m away
946 from the shelter); S30: Roots of *Alnus glutinosa* (L.) Gaertn. (same location as
947 S29); S31: Combination of litter and roots of *Alnus glutinosa* (L.) Gaertn. The
948 population of *Alnus glutinosa* is located in the slope between the river and the
949 shelter (ca 40 m away from the shelter); S33: Combination of litter and rhizome
950 of *Thelypteris palustris* (spot 1: Sagnet in Saint-Paul-le-Jeune); S35:
951 Combination of litter and rhizome of *Thelypteris palustris* (spot 2: Ribes).

952

953 Fig. 7. Major non-pollen palynomorphs (NPP) evidenced in the Abri du Maras
954 (Saint-Marcel-d'Ardèche, Ardèche).

955 1: spore of *Chaetomium*-type HdV-71, sample S13; 2: ascospore of *Diporothea*
956 *webbiae*-type HdV-143, sample S14; 3 and 4: aggregates of ascospores of
957 *Diporothea webbiae*-type HdV-143, sample S15; 5: ascospore of *Diporothea*
958 *webbiae*-type HdV-143, sample 29; 6: immature ascospore of *Diporothea*
959 *webbiae*-type HdV-143, sample 30.

960

961 Fig. 8. Sidescraper on a backed flake, n°1079, level 5 upper.

962

963

964 Table 1. Description of the archaeological samples. Samples with statistically
965 significant fungi concentrations are marked in grey.

966 Table 2. Description of the modern control samples. Samples with statistically
967 significant fungi concentrations are marked in grey.

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970