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

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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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## 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 m<sup>2</sup> 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<sup>-1</sup>. 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<sup>-2</sup>).

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<sup>-1</sup>), 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<sup>-1</sup>, respectively. Undifferentiated  
279 fungal spores also show high abundances (mean and median concentrations of  
280 42656 and 27055 elements.g<sup>-1</sup>, 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<sup>-1</sup>),  
313 while only rare occurrences were encountered in the sticking sediment (S14:  
314 43 elements.g<sup>-1</sup>). 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 *Diporotheca*  
317 *webbiae*-type (HdV-143) present an increasing trend from low values in the  
318 stratigraphic unit (S13: 341 elements.g<sup>-1</sup>) to high concentrations in the tools  
319 samples (S14: 9361 elements.g<sup>-1</sup>; S15: 2704 elements.g<sup>-1</sup>). 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 *Diporotheca webbiae*-type  
323 recorded in the archaeological layer. Moreover, samples from artefact 1079  
324 register noticeable concentrations of aggregates of *Diporotheca webbiae*-type,  
325 with increasing values between the sticking sediment (S14: 280 elements.g<sup>-1</sup>)  
326 and the artefact itself (S15: 375 elements.g<sup>-1</sup>). The largest aggregates (between  
327 5 and 15 ascospores stuck together) come from the stone tool washes (S15). All  
328 this suggest that *Diporotheca 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 *Diporotheca webbiae*-  
331 type, both in ascospores – 283 and 56 elements.cm<sup>-2</sup> - and aggregates – around  
332 8 elements.cm<sup>-2</sup> 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 *Diporotheca*  
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<sup>-1</sup>, *Diporotheca webbiae*-type, S26: 24 elements.g<sup>-1</sup>). 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<sup>-1</sup>, *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<sup>-1</sup>) or at lower frequencies (*Glomus*-  
348 type HdV-207- S13: 214, S14: 151, S15: 19, S25: 3761, S26: 731 elements.g<sup>-1</sup>).  
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<sup>-1</sup>. 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<sup>-1</sup> and S30 with 9666 elements.g<sup>-1</sup>). 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<sup>-1</sup>) than in  
371 S29 (110 elements.g<sup>-1</sup>). *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<sup>-1</sup>) than in S29 (330 elements.g<sup>-1</sup>). *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<sup>-1</sup>), 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 *Diporotheca webbiae*-type. Diporothecaceae, 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 *Diporotheca 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 *Diporotheca*  
502 *webbiae*-type, which resemble those obtained by the stone tool wash  
503 (concentrations above several thousand elements.g<sup>-1</sup> in any case). Fungal  
504 assemblages also include immature ascospores of *Diporotheca 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 *Diporotheca 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 *Diporotheca 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 *Diporotheca 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 *Diporotheca 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

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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 cm<sup>2</sup>).

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.

968

969

970