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### Article

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1 Pollen taphonomy of cave sediments: what does the pollen record in caves tell us about  
2 external environments and how do we assess its reliability?

3

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6

7 Abstract

8 Cave sediments may contain important long-term records of past environments and human activity.  
9 Pollen provides key evidence, since it disperses widely and is relatively durable. We still know  
10 relatively little about the dispersal of pollen into caves, and its preservation within cave sediments,  
11 compared with our relatively detailed knowledge of pollen taphonomy in other sedimentary  
12 environments. Pollen taphonomy in caves is dependent on a variety of transport pathways and  
13 seems to be very contingent on local circumstance. The airfall component of cave pollen  
14 assemblages often seems comparable with airfall spectra in the landscape outside the cave, but  
15 bees, birds and bats may transport considerable quantities of pollen into caves, and the entrance-  
16 flora may also be significant. Cave sediments are rarely waterlogged and pollen within them can be  
17 subject to microbial and chemical degradation. Sedimentation in caves is often episodic, with  
18 episodes of storage and deposition, sometimes redeposition of sediment, which means that  
19 biostratigraphic, preservational, factors become very significant. Comparison with sequences outside  
20 caves is difficult because few caves are found in landscapes where there are comparable pollen  
21 records from lakes and bogs. Here we review the factors affecting cave pollen taphonomy and  
22 hence the reliability of palynological analysis of sediments from caves, with suggestions for future  
23 investigation.

24

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27

## 28 **1. Introduction**

29 Cave sediment sequences often accumulated over hundreds of thousands of years (e.g. Bouzouggar  
30 et al. 2007; Douka et al. 2014; McFarlane & Lundberg 2005). They contain important sedimentary  
31 evidence for environmental change plus archaeological and palaeobiological materials indicating  
32 cultural practises and environmental change – including lithics, animal bones, mollusc shell, eggshell,  
33 pollen, plant macro-remains such as seeds and charcoal (e.g. McBurney, 1967; Bailey & Woodward  
34 1997; Barker 2012, 2016; Bouzouggar et al. 2007). With multidisciplinary study of cave sequences,  
35 we can piece together a relatively rounded understanding of the sequence of human activity and its  
36 changing environmental context.

37 Pollen assemblages are, *in potentia*, a key line of evidence in the study of cave sequences. Pollen  
38 assemblages from non-cave depositional environments such as bogs and lakes are used widely to  
39 infer past environments (Faegri & Iversen 1975; Faegri et al. 1989; Moore et al. 1991). Pollen thus  
40 provides a potential link between the cave and its wider landscape context, because pollen grains  
41 and spores, which are produced by plants living in the landscape outside the cave, are known to  
42 disperse widely by both wind, insect and vertebrate vectors (Englund 1993; Nason et al. 1996; Hunt  
43 & Rushworth 2005; Jha et al. 2010; Šikoparija et al. 2013). This dispersal may take pollen into caves  
44 where they may be preserved by being buried in accreting sediments. Although pollen has been  
45 used in an increasing number of cave investigations (e.g. Schutrumpf 1939; Derville & Firtion 1951;  
46 Welten 1954, 1956; Van Campo & Leroi-Gourhan 1956; Anderson 1955; Donner & Kurten 1958;  
47 Martin 1961; Bryant 1974; Leroi-Gourhan 1975; Gale & Hunt 1985; Gale et al. 1993; Carrion et al.  
48 2001; Caseldine et al. 2008; Djamali et al. 2011; Festi et al. 2016; Gatta et al 2016; Hunt et al. 2016;  
49 Linstadter et al. 2016), our knowledge of the how representative of outside environments cave  
50 pollen assemblages might be is still fairly insubstantial, relative to our understanding of taphonomic  
51 processes in bogs and lakes, which are often the preferred environments for pollen research in  
52 regions where they exist. This matters because without a robust understanding of taphonomy it is  
53 not completely clear how much of the pollen signal reflects environmental events in the world  
54 outside the cave, and how much reflects taphonomic processes, in any given case. This paper  
55 therefore reviews the state of the art in cave pollen taphonomy, identifies wide-scale trends and  
56 patterns and suggests research directions for the future.

57

## 58 **2. The concept(s) of Taphonomy**

59 The term ‘taphonomy’ was coined by Efremov (1940). It is the science of the route by which living  
60 organisms become fossilised (Behrensmyer & Kidwell 1985). Pollen taphonomy can be  
61 conceptualised as the processes of necrolysis (by which organic materials such as pollen grains are  
62 generated and dispersed), biostratinomy (in which they are transported, deposited and buried) and  
63 diagenesis (in which buried materials come into equilibrium with the burial environment after  
64 deposition). Thus, pollen taphonomy includes a sequence of necrolytic processes through which  
65 pollen grains are generated in the male organs of plants, and dispersed by vectors such as insects,  
66 birds, mammals, wind and water. Then follow biostratinomic processes, firstly of transport in the  
67 environment by these and other vectors, then deposition, burial and preservation resulting from a  
68 variety of sedimentary and diagenetic processes (Fig. 1).

69

70 **FIG 1 ABOUT HERE**

71

## 72 **2. Necrolysis: Pollen dispersal**

73 In nature, plants produce pollen and disperse it to other plants (in most cases: there are a few self-  
74 pollinators) as part of their reproductive cycle. Dispersal is generally either by wind (anemophilous  
75 pollen such as pine, oak and grass) or by animal vectors such as bees, flies or beetles (entomophilous  
76 pollen such as that of the daisy family [Asteraceae]) bats and birds (zoophilous pollen such as the

77 mangrove *Sonneratia*), although a few taxa, such as the marine eel-grasses, have pollen grains  
78 without preservable exines that disperse in water.

79

### 80 **3. Biostratinomy**

81 Pollen can be dispersed into caves by the vectors utilised by the plants (wind, insects, bats and birds  
82 in particular), but it may also enter caves by indirect means, carried by secondary vectors or  
83 processes after original deposition in the landscape. A variety of transport pathways, very  
84 contingent on local circumstance, are known from studies of pollen taphonomy in caves (e.g. Van  
85 Campo & Leroi-Gourhan, 1956; Dumbleby 1985; Burney & Burney, 1993; Coles & Gilbertson, 1994;  
86 Prieto & Carrión, 1999; Navarro Camacho et al., 2000; Navarro et al., 2001; Navarro et al., 2002;  
87 Hunt & Rushworth, 2005; Simpson & Hunt, 2009; de Porras et al., 2011). These biostratinomic  
88 processes are usually regarded as a linear sequence, but pollen grains are durable enough and some  
89 cave environments sufficiently dynamic geomorphologically that recycling can occur. This means  
90 that sediments and their contained pollen can be eroded and redeposited (Hunt et al. 2015) on more  
91 than one occasion in the history of a pollen grain.

92 Biostratinomic processes include:

#### 93 *3.1 Direct fallout from the cave entrance flora.*

94 At Creswell Crags, in caves such as C7 and Dog Hole Cave, spores derived from the cave-entrance  
95 fern flora comprised between a 25 and 40% of the annual palynological fallout (Coles & Gilbertson  
96 1994). This phenomenon seems to be most marked in small humid caves subject to little human  
97 activity, with luxuriant cave-mouth vegetation. It is less marked in larger caves, and in caves where  
98 the cave-mouth flora is restricted at Creswell (Coles & Gilbertson 1994). In the wet tropical forest  
99 zone, fern spores, derived mostly from the entrance flora are between 20 and 40% of the total  
100 annual fallout in the very large cave-mouth of the Great Cave of Niah (Hunt et al. in press). The  
101 contribution of the entrance flora seems less marked or absent in arid-zone caves where the  
102 entrance flora is sparse or absent and other vectors and processes predominate (e.g. Weinstein  
103 1987; Simpson 2016).

#### 104 *3.2 By aeolian transport from more distant vegetation.*

105 This may be either from pollen dispersal by parent plants or from the resuspension and transport by  
106 wind of previously-deposited material. Airfall of pollen in caves after aeolian dispersal and transport  
107 from parent plants is very widely reported (e.g. Derville & Firtion 1954; van Campo & Leroi-Gourhan  
108 1956; Weinstein 1987; Coles & Gilbertson 1994; Navarro et al. 2001; Hunt & Rushworth 2005; de  
109 Porras et al. 2011; Fiacconi & Hunt 2015, 2016). The airfall component of cave pollen assemblages is  
110 often closely comparable with airfall spectra in the landscape close outside the cave (e.g. Coles &  
111 Gilbertson 1993; Hunt & Rushworth 2005; de Porras et al. 2011; Fiacconi & Hunt 2016). Total pollen  
112 accumulation figures from airfall, when measured, tend to be remarkably low in caves, generally at  
113 least one order of magnitude lower than accumulation rates outside the caves concerned (Table 1).  
114 In general, the proportion of anemophilous pollen as a percentage of total pollen accumulation in  
115 the entrance zone of caves is comparable with that accumulating close outside the cave (e.g. Coles &  
116 Gilbertson 1994; Hunt & Rushworth 2005; De Porras et al. 2011; Fiacconi & Hunt 2016). In many

117 sac-like caves, the percentage of anemophilous pollen generally declines away from the cave mouth,  
118 particularly in caves that are narrow for their length (van Campo & Leroi-Gourhan 1956; Coles &  
119 Gilbertson 1994; de Porrás et al. 2011; Fiacconi & Hunt 2016, Fig.2). Other patterns may occur in  
120 more geomorphologically-complex systems (van Campo & Leroi-Gourhan 1956; Fiacconi & Hunt  
121 2016) or where transport of pollen by vertebrates predominates (e.g. Navarro et al. 2001; de Porrás  
122 2011). Resuspension and aeolian transport of previously-deposited material is rarely reported,  
123 mostly from cold-stage sediments of loessic origin in what are today temperate-zone caves (e.g.  
124 Coles & Hunt 1985; Gale & Hunt 1985).

125

126 **FIG 2 ABOUT HERE**

127

128 **TABLE 1 ABOUT HERE**

129

130 *3.3 In drip water from the land surface above, and in sinking streams from more distant catchments.*

131 Drip water sometimes contains large amounts of pollen (e.g. Genty et al. 2001; Simpson 2016) but  
132 this is not always the case. No pollen was found in drip water in cave C7 at Creswell Crags (Coles and  
133 Gilbertson 1994) or in caves in mesic forest in New York State (Burney & Piggott Burney 1993), while  
134 drip waters analysed by Fiacconi & Hunt (2016) at Shanidar Cave contained very little or no pollen.  
135 There may be a filtering effect in biologically-active and relatively organic-rich epikarst zones, as at  
136 Creswell and in New York State. On the other hand, moss growing on seeps at Caf Sidar contained  
137 heterogeneous assemblages interpreted by Fiacconi & Hunt (2016) as largely generated by parent-  
138 plants growing close to the inlets to the conduits leading to these seeps. Peterson (1976)  
139 demonstrated the transport of pollen through streamways up to 0.8 km into the vadose Mammoth  
140 Cave system in Kentucky. The pollen became increasingly degraded as it passed down the  
141 streamway channel, but Peterson (1976) argued that the pollen load in the streamway reflected  
142 closely the vegetation in the catchment of the sinking stream. Lycopodium spores were used as  
143 tracers in karst groundwater before the advent of dye-tracing (e.g. Atkinson 1968) thus indicating  
144 that palynomorphs may be transported several kilometres underground in phreatic systems. It must  
145 be noted that river waters sometimes contain rather taphonomically-biased assemblages (e.g. Hunt  
146 1987) and alluvial sediments outside caves often contain assemblages showing a strong taphonomic  
147 imprint (e.g. Fall 1987; Hunt 1987), so care must be taken in interpreting pollen from waterlain  
148 sediments in caves.

149 *3.4 Within debris/mud flows and surface wash entering the cave.*

150 A considerable proportion of sediments in many caves in the temperate zone originate from mud-  
151 and debris flows and these sediments are not uncommon even in tropical caves (e.g. Gilbertson et  
152 al. 2005). To our knowledge, no-one has sampled an active mass movement within a cave for  
153 palynology. Recycled palynomorphs were found in a mudflow deposit in a Swiss cave (Welten 1954)  
154 and pollen was found in mudflow deposits in the Great Cave of Niah, where consistent assemblages  
155 within the mudflow unit suggest that materials had been homogenised by the mudflow processes

156 (Hunt et al. 2012). It is likely that mass-movement deposits elsewhere in caves will also contain  
157 pollen. Similarly, we are not aware of taphonomic studies of the pollen load in sheet-wash or rill  
158 flows entering caves. Simpson (2016) has sampled Holocene deposits resulting from these  
159 mechanisms at the Haua Fteah, Libya and they do not seem to be distinguishable palynologically  
160 from near-contemporary deposits resulting from other processes.

### 161 3.5 By vertebrates.

162 Transport by vertebrates is very locally-contingent because the spatial distribution of animal  
163 behaviour in caves appears to be very highly patterned, for instance by roosting and denning  
164 behaviour (Fig 3). Among others, Scott (1987), Carrión et al. (2001), González-Seampérez et al.  
165 (2003) and Djamali (2011) suggest that hyaena coprolites from caves contain pollen indicative of the  
166 general vegetation around the cave. A similar case has been argued for coprolites of giant ground  
167 sloths in North American caves (Martin et al. 1961; Thompson et al. 1980), rat droppings in a Libyan  
168 cave (Gale et al. 1993) and for sheep droppings (de Porrás et al. 2011). This is likely to be the case  
169 also for other taxa (e.g. Ingram 1969). Among the vertebrates, birds and bats which roost within the  
170 cave may be very significant as vectors of pollen e.g. Hunt & Rushworth (2005) recorded an influx of  
171 up to 1427 pollen grains per cm<sup>2</sup> per year below swiftlet nests at Niah. This is not always the case,  
172 however, as pigeons at Shanidar appear to import little pollen in their droppings (Fiacconi & Hunt  
173 2016). Ground-living animals such as foxes, badgers, porcupines and rodents may be significant  
174 importers of pollen (Bramwell et al. 1984, Diot 1991; Burney & Piggott Burney 1993; de Porrás et al.  
175 2015).

176

177 **FIGURE 3 ABOUT HERE**

178

179 Another source of pollen within the organic deposits is represented by rodent middens, including  
180 those made by packrats, hyrax and other species. Packrats (*Neotoma*) are small rodents, with twenty  
181 one species present in different habitats from Canada to Nicaragua (Betancourt et al., 1990). These  
182 animals collect vegetal material in an area up to 50 m from their dens, and this is cemented together  
183 by urine and preserved as a midden. Packrat middens are interesting because of their content of  
184 plant macrofossils and pollen grains and they can also be dated using the radiocarbon method. In  
185 dry caves, they can be preserved for thousands of years (Thompson and Anderson, 2000). The  
186 provenance of the plants used in construction is local but the pollen can be both from local and  
187 regional sources and the contribution of the two different sources is still poorly understood. Issues  
188 with the use of packrat middens in vegetational reconstruction are often related to the taphonomic  
189 processes of their formation and to post-depositional episodes such as erosion, rockfalls and  
190 collapse into crevices, which can produce a relocation of the middens in the stratigraphy (Wells,  
191 1976). Hall & Risking (2010) note that *Juniperus* pollen can be over-represented in packrat middens  
192 because the animals gather and eat the male cones.

193 Hyraxes (*Procavia capensis*) also produce middens. Carrión et al. (1999a) presented a palynological  
194 record from a hyrax midden from South Africa, explaining that these middens are different from the  
195 ones of other species as *Neotoma* or *Petromus typicus* (Dassie Rat) as they constitute a

196 stratigraphically coherent section. It has been demonstrated that the pollen found in these middens  
197 may not be strongly influenced by animal diet and it can produce a good representation of the  
198 surrounding vegetation as there is a close correspondence between the pollen composition in the  
199 samples and the composition of the vegetation in the area. Likewise, de Porras et al. (2015) showed  
200 that rodent middens in Chile contained pollen assemblages representative of the local vegetation.

201 A special case particularly notable in Mediterranean countries, North Africa and the Middle East are  
202 *fumier* deposits – thick, layered accumulations of dung and ash from partially-burnt dung resulting  
203 from domesticates such as sheep, goats and cattle stalled within caves. These contain pollen (e.g.  
204 Esposito & Burjachs 2016) which has been brought into the cave in gut contents (guano, dung), and  
205 on fur and feet. Pollen assemblages often reflect the vegetation where the animals have grazed,  
206 rather than that growing immediately around the cave (Fig. 4).

207

208 **FIGURE 4 ABOUT HERE**

209

### 210 *3.6 By invertebrates.*

211 Several groups of insects nest in caves – bees and wasps particularly. Bees nesting in caves are  
212 known to accumulate pollen, particularly entomophilous taxa such as Asteraceae and Lactucaea  
213 (Bottema 1975). In general, in the surface sediments of sac-shaped caves not subject to major  
214 vertebrate activity, entomophilous pollen rises in percentage terms towards the rear of the cave  
215 (Fiacconi & Hunt 2016). Solitary wasps sometimes line their nest-burrows with polleniferous mud,  
216 collected outside the cave (Hunt & Rushworth 2005).

217

### 218 *3.7 On or by people.*

219 People bring pollen into caves in numerous ways. Pollen can be introduced on feet, skin, hair and  
220 clothing. Vegetation carried into a cave for animal fodder, bedding or food may carry pollen with it  
221 and in particular inflorescences brought into the cave for food, medicine, ornament or ritual may  
222 contain pollen (e.g. Leroi-Gourhan 1975; Hunt et al. 2012). Pollen may be introduced on the fur or in  
223 the gut contents of animals brought into the cave for food (Coles et al. 1989). Caves have also been  
224 used as latrines and pollen may be contained in human coprolites (e.g. Bryant 1974; Schoenwetter  
225 1974; Rhode 2003; Dean 2006; Hunt et al. 2011). It has been noted that surface sediments of caves  
226 frequented by people may contain higher concentrations of pollen than sediments in those caves  
227 where people are rarely present (van Campo & Leroi-Gourhan 1956), but this is not always the case  
228 – the surface sediments of Shanidar Cave (which receives thousands of tourists per year) required a  
229 heavy liquid step to produce countable assemblages, but this was not required for other caves in the  
230 same region which are rarely, if ever, visited (Fiacconi & Hunt 2016).

231

### 232 *3.8 Overview*

233 The above discussion suggests that evaluation of the pattern of pollen accumulation in caves before  
234 excavation starts is a very worthwhile investment of time and resources since it is likely to identify  
235 sampling localities where pollen accumulation approximates to areas outside the cave. In general,  
236 the research cited suggests that areas close to the cave mouth are likely to provide samples with less  
237 marked taphonomic bias than those in the rear of the cave (Fig. 3). Pollen dispersed by wind is also  
238 likely to be more abundant in this entrance-zone than it will be toward the rear of the cave. Areas  
239 beneath bat and bird roosts and drips should be avoided if possible.

240

#### 241 **4. Sedimentation in caves and diagenetic factors**

242 Issues relating to pollen deterioration on archaeological sites, including caves, are discussed by  
243 Bryant & Hall (1993). Since cave sediments are rarely waterlogged, degradation of organic matter,  
244 including pollen, is likely to happen at times. The saturation of cave sediments by ammonia, which  
245 happens in some guano-rich tropical caves, seems however to lead to very well-preserved pollen, as  
246 at Niah Cave (Hunt et al. 2016). On the other hand, experimental studies and field experience both  
247 suggest that episodic wetting and drying of cave sediments and some forms of human activity such  
248 as burning both lead to extremely poor pollen preservation (Campbell 1991; Bryant & Hall 1993;  
249 Navarro et al. 2001).

250 While cave surface sediments often contain pollen assemblages very similar to those accumulating  
251 outside caves, there are reasons to suspect that some subfossil assemblages from caves have  
252 acquired a strong taphonomic imprint. In particular, pollen of durable taxa – *Lactuca*, *Pinus*, fern  
253 spores, *Tilia* are sometimes more common in cave sediments than is ecologically likely (e.g.  
254 Bramwell et al. 1984; Bottema 1975). This ‘over-representation’ is perhaps more likely to reflect  
255 preferential destruction of less durable taxa within the cave sediments rather than biostratigraphic  
256 factors. It has been known for many years (e.g. Havinga, 1984) that not all pollen grains are equally  
257 durable to decay processes. Further, it is becoming apparent that the type of degradation is also  
258 important, with microbial activity seeming to lead to different results than attack by oxidising  
259 chemicals (e.g. Hopkins 2010; Marquer et al. 2010; although see Lebreton et al. 2010). This is  
260 possible in caves where lime-rich environments are conducive to microbial activity (Bryant & Hall  
261 1993), although pollen in stalagmites is often well-preserved (Burney & Piggott Burney 1993;  
262 Caseldine et al. 2008).

263 Sedimentation in caves is often episodic (Gale & Hunt 1985) with sediment storage, erosion and  
264 redeposition sometimes very frequent but can be identified only by high resolution dating (Hunt et  
265 al. 2015). In this situation, biostratigraphic, preservational, factors become very significant since  
266 erosion and resedimentation of pollen will provide opportunities for repeated microbial and  
267 oxidative breakdown of pollen grains. Identifying the products of these biostratigraphic and  
268 preservational factors becomes critical in deciphering the pollen record. Episodes of very slow  
269 sedimentation may lead to extremely high pollen concentrations and ‘telescoped’ assemblages  
270 where whole interglacials are represented by no more than 10 cm of sediment accretion (Hunt &  
271 Gale 1986). Episodes of non-deposition can be recognised by sudden changes in pollen assemblages  
272 and displacements in age-depth curves (Hunt et al. 2015, 2016). At present, the observation of  
273 ecologically-incoherent assemblages or assemblages rich in durable taxa seem the best indicators of  
274 taphonomic complexity as a result of erosion and re-sedimentation.



275

276 **5. Paired and comparative studies**

277 Cave pollen records come from karst areas where lakes or bogs to provide comparisons are  
278 infrequent and where there may not be available well-dated sediments for comparative studies (e.g.  
279 Caseldine et al. 2008). A few studies have been done where cave sequences are located close to  
280 non-cave sites which have also been sampled for pollen, for instance the Younger Dryas and Early  
281 Holocene sequence at Kirkhead Cave, UK (Gale & Hunt 1985) shows very similar assemblages to  
282 nearby lacustrine sequences (Oldfield 1963), except that high fern spores reflect the cave-entrance  
283 flora. Similarly, there are parallels between swamp, cave and hyrax dung deposits in later Holocene  
284 deposits in the Karoo, South Africa (Scott et al. 2005). Finally, a recent article by Iriarte-Chiapusso et  
285 al. (2016) reconstructed the Cantabrian Gravettian by comparing the data recorded by caves, used  
286 so far for the palaeoenvironmental reconstruction of this period, with new data becoming available  
287 from open air sites in the region. In this case, they argued that data from open-air sites helped to  
288 improve the biased picture based on the information from caves. Further paired studies are highly  
289 desirable to demonstrate the robustness of cave pollen records.

290 Where multidisciplinary investigations have been carried out, we may evaluate the reliability of  
291 pollen assemblages through comparison with other indicators of palaeoenvironmental change.  
292 There are, of course, issues relating to what we 'see' with any given class of indicator, both in terms  
293 of resolution and reach. The resolution of pollen data can be quite fine-grained in circumstances  
294 where distinctive plant taxa are close to their ecological tolerances. Oxygen isotopes of stalagmites,  
295 may, however have finer resolution, with errors of less than a degree Celsius, but some groups, such  
296 as the mammals, generally enable recognition of only rather broad habitat categories. In terms of  
297 reach, pollen reflects vegetation usually within a few tens to hundreds of metres from a cave,  
298 sometimes closer (Weinstein 1983; Coles & Gilbertson 1994; de Porras et al. 2011) so is typically  
299 greater than, for instance molluscs, which typically occupy very small home ranges. Nevertheless, in  
300 general changes in pollen assemblages will be accompanied by changes in other indicators. This can  
301 be seen, for instance at La Riera, Spain (Strauss et al. 1981), where the beginning of the Holocene is  
302 indicated by pollen, mammals and land snails, and at Carihuela Cave (Spain) where the pollen record  
303 parallels the sediment and micromammal sequence (Carrion et al. 1999).

304

305 **6. Conclusions**

306 Pollen in cave sediments can provide important evidence for the palaeoecology of karst regions  
307 where other types of site may be very sparse. The pollen record in caves is particularly important  
308 because of the great chronological depth of many cave sequences, and because the pollen record in  
309 caves may be closely related to archaeological evidence for human activity and to evidence provided  
310 by other palaeoecological and sedimentary indicators. Pollen may provide direct evidence for some  
311 patterns of human behaviour, such as the import of inflorescences into caves but is most important  
312 in providing high-resolution palaeoenvironmental reconstruction.

313 Reliability is perhaps difficult to quantify with certainty, but studies in a variety of biomes in caves  
314 with simple morphology have shown that in general the pollen and spores reaching floors of cave

315 entrances are representative of vegetation in the immediate environs of the cave. The  
316 representation of anemophilous taxa then declines towards the rear of simple caves in a fairly  
317 predictable way. There are exceptions to these patterns in more geomorphologically-complex caves  
318 and where vertebrates (including people) using the cave as a latrine or activity area are eating or  
319 gathering vegetation some distance away from the cave. Guano and similar materials will generally  
320 be visible to sedimentological or geochemical investigations, however, so the pollen associated with  
321 materials of this sort can be treated as potentially unrepresentative of local vegetation. Other  
322 taphonomic effects relating to sedimentation or diagenesis may be indicated through the  
323 assemblages themselves and particularly through disproportionate percentages of durable taxa,  
324 with supporting evidence from sedimentological techniques, particularly micromorphology. Many  
325 issues relating to taphonomy can be avoided, or at least minimised, by taphonomic evaluation of the  
326 site and selection of sampling sites within areas dominated by relatively simple pollen fallout near  
327 the mouth of the cave. Given these constraints, pollen from caves can indeed be said to be reliable.

328 Further systematic investigations are still needed of pollen taphonomy in complex cave systems, of  
329 some of the less well-understood sedimentary mechanisms such as mudflows, and of pollen  
330 degradation in cave environments. It would also be highly desirable if high-quality inside-outside  
331 paired studies took place, where cave pollen records were compared to sequences from nearby  
332 localities such as lakes or bogs.

333

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342

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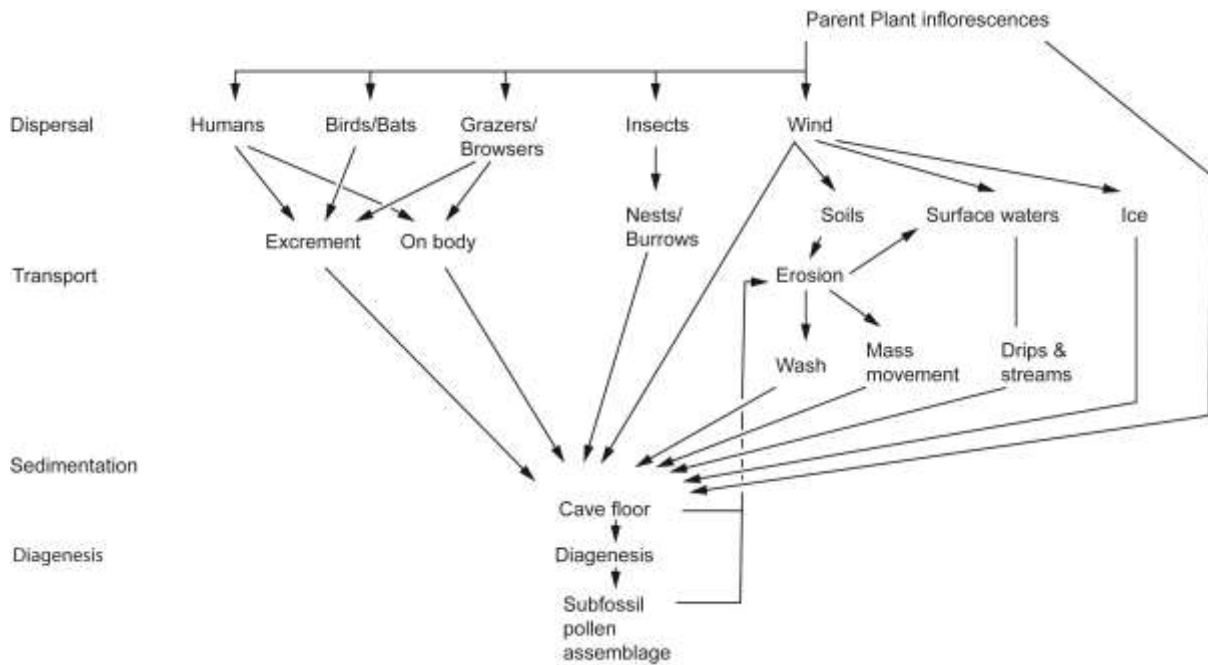
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625 CAPTIONS TO FIGURES

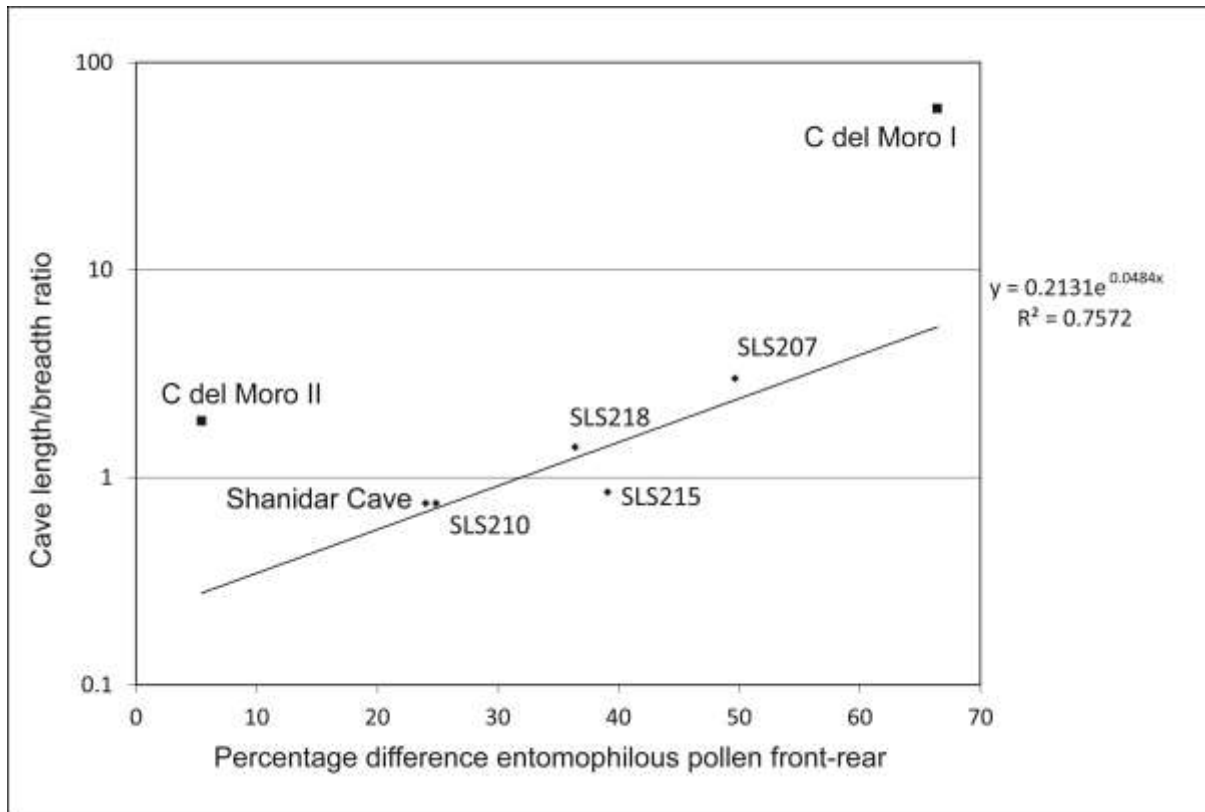
626 Figure 1. Sketch of taphonomic pathway from vegetation outside caves to the subfossil pollen  
 627 assemblages in cave deposits



628

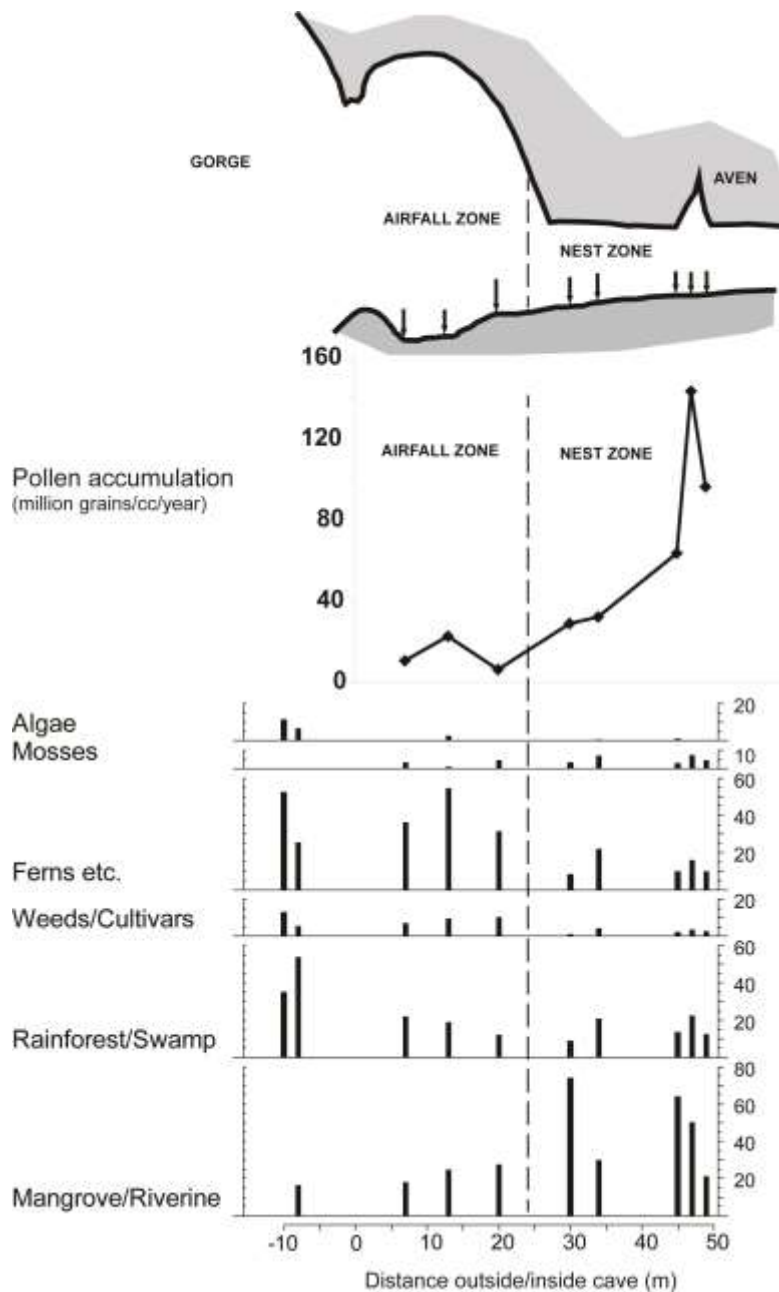
629 Figure 2. Plot of differences in the % anemophilous pollen between the front and the rear of the  
 630 cave against cave geometry (as summarised by the cave length/breadth ratio) from sac-like caves in  
 631 Kurdish Iraq. This shows that the proportion of anemophilous pollen declines most markedly from  
 632 the front to the rear of caves which are long relative to their breadth ( $r^2=0.7572$ ). Data from the

633 Cueva del Moro I and II from Navarro et al. (2001) is plotted to show that a similar pattern may hold  
634 in Spanish caves, but this is not included in the calculation of the trendline.



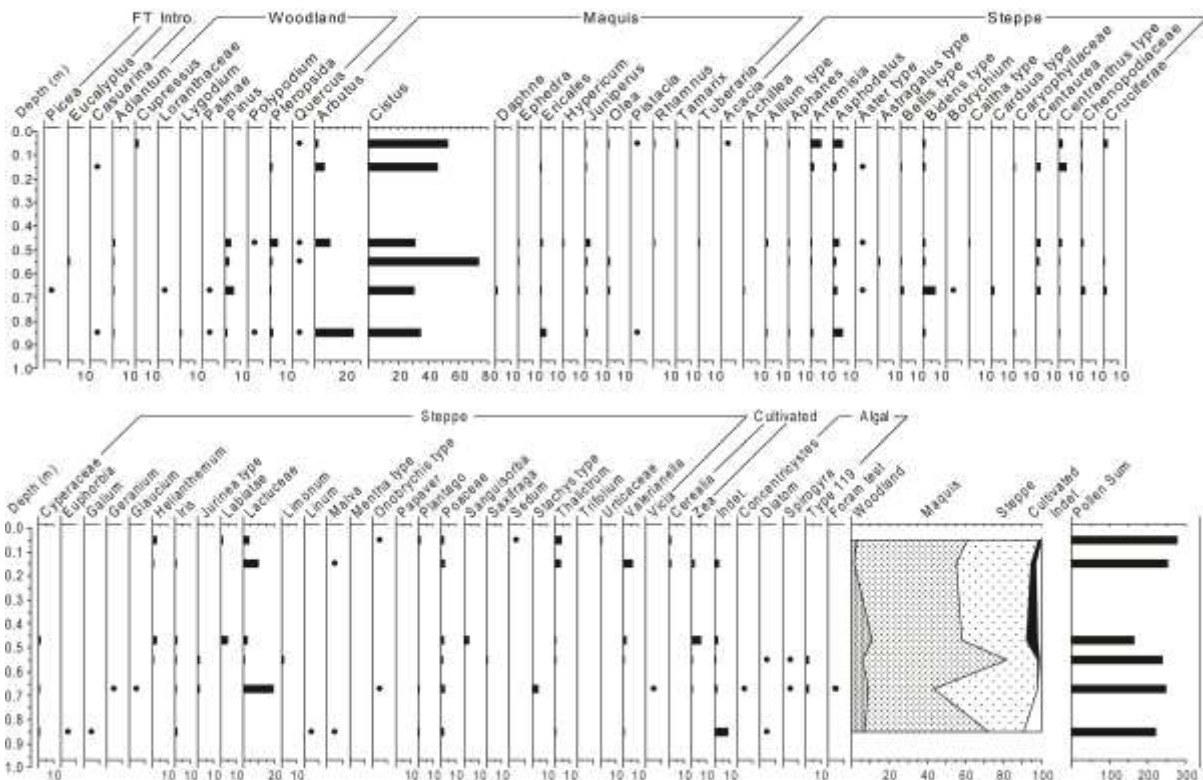
635

636 Figure 3. Pollen taphonomic summary for the Great Cave of Niah (data from Hunt & Rushworth  
637 2005; Hunt et al. 2016). Mangrove and riverine taxa is disproportionately represented in the pollen  
638 accumulating under the nesting zone, where it arrives mostly in guano, reflecting the feeding  
639 behaviour of the bats and swiftlets over coastal and riverine vegetation communities. 'Hell Trench' –  
640 the area from which stratigraphic pollen work (Hunt et al. 2016) was done in the cave – lies in the  
641 front of the airfall zone, in the topographic low between the entrance talus/flowstone rampart and  
642 the guano mound which dominates the rear of the cave.



643

644 Figure 4. At the Haua Fteah, Libya, subrecent *fumier* deposits are dominated by *Cistus* and *Arbutus*,  
 645 reflecting sheep, goats and cattle grazing in wadis where vegetation is dominated by these maquis  
 646 species, several km away from the cave. Pollen traps and sticky slides suggest that the local airfall  
 647 pollen is dominated by *Juniperus* and *Poaceae* (Simpson & Hunt 2009; Simpson 2016).



648

649 CAPTIONS TO TABLES

650 Table 1: Airfall pollen accumulation rates in caves compared with pollen influx figures outside the  
 651 same caves

Vegetation type	Cave pollen influx: pollen grains per cm <sup>2</sup> per year	External pollen influx: pollen grains per cm <sup>2</sup> per year	Author
Temperate woodland, shrubs and herbaceous vegetation	84-488	7800	Coles & Gilbertson (1994)
Mesic temperate forest	61-1685	8605-48200	Burney & Piggott Burney (1993)
Herb-rich steppe with some trees	4-6	n/a	Fiacconi & Hunt (in press)
Wet lowland tropical forest	62-225	n/a	Hunt & Rushworth (2005)

652

