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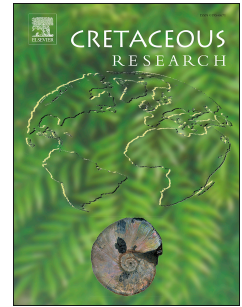
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Re-examination of the palynological content of the Lower Cretaceous deposits of

Angeac, Charente, south-west France: age, palaeoenvironment and taxonomic

determinations

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Abstract

Further to the work published by Néraudeau et al. six years ago, palynological matter

recovered from the lignitic bone bed of Angeac in Charente (south-west France) has been re-

examined in order to provide more evidence of its age, the previous Hauterivian–Barremian

interpretation being regarded as controversial. The samples come from four sedimentological

units, An2–An5, which together yielded an assemblage of 34 species, taxonomically

dominated by palaeoecologically significant lygodiaceous verrucate spores, including eight

species attributable to the genus *Concavissimisporites* and three species of *Trilobosporites*. A

few bisaccate pollen grains, including *Vitreisporites pallidus*, have been recovered, but the

gymnospermous pollen spectrum is clearly dominated by the cheirolepidiaceous genus

Classopollis, its abundance diminishing progressively upwards from units An4 to An2. The

great abundance and diversity of verrucate forms, along with the presence of other spores

27 typical of Lower Cretaceous deposits, such as *Aequitriradites verrucosus*, and the scarcity of

28 specimens referable to *Cicatricosisporites*, render this assemblage most similar to those of the

29 Hastings Group of southern England, and the Bückeberg Formation in north-western

30 Germany. The time of deposition is, therefore, more likely to have been Berriasian–

31 Valanginian rather than Hauterivian–Barremian, as previously stated. The associated small

32 assemblage of megaspores is consistent with this determination. Except for *Trilobosporites*

33 and *Concavissimisporites*, the use of several other genera commonly applied to Mesozoic

34 verrucate spores, such as *Converrucosisporites* and *Impardecispora*, is considered

35 unnecessary. To support this assertion, a Principal Components Analysis has been carried out

36 on 120 verrucate spores from sedimentological units An2–4, taking into account ten

37 morphological variables. The results show that specimens attributable to *Trilobosporites* are

38 well be separated from the main cluster, which corresponds to *Concavissimisporites*,

39 underlining the futility of using more than two genera for the species concerned.

40

41 *Keywords:* verrucate spores; Lygodiaceae; Schizaeaceae; megaspores; Wealden facies;

42 Berriasian; Valanginian; Charentes.

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50

51 **1. Introduction**

52

Comparatively little is known about the palaeontological content of French Lower
Cretaceous continental deposits, mainly because of the scarcity of outcrop. In this connection,
the lignitic bone-bed of Angeac in south-west France is remarkable in providing a rare
glimpse of the terrestrial palaeoenvironment in this part of the world. The flora and fauna
were described by Néraudeau et al. (2012). Since the discovery of the site in 2008, hundreds
of ornithomimosaur bones have been found (Allain et al., 2014), along with other vertebrate
remains, reminiscent of the fossil record from the Wealden succession of southern England
and Wealden-type facies in Spain.

Apart from the deposits of Angeac (Néraudeau et al., 2012), Cadeuil (Platel et al., 1976)
and Saint-Agnant (Vullo et al., 2012), no other outcrops of Wealden-type facies have been
described from south-western France. They have, however, been encountered in boreholes at
Saint-André de Lidon (Ternet and Berger, 1968), Soubran (Kromm et al., 1970), and Saint-
Romain-de-Benet (Deák and Combaz, 1967). The last of these yielded a rich palynological
assemblage that was considered by Deák and Combaz (1967) to be Valanginian–Hauterivian
in age. A few lowest Cretaceous outcrops, corresponding to "Purbeck facies", have also been
reported from the island of Oléron (Lantz, 1958) and from Cherves-Richemont (Bourgueil et
al., 1986; Colin et al., 2004; Benoit et al., 2017) (Fig. 1A).

Until recently, the time of deposition of the Angeac sediments was considered to be
Hauterivian–Barremian. Although it was noted in Néraudeau et al. (2012, p. 5) that verrucate
spores tend to be especially common in deposits of Berriasian–Valanginian age, this younger
determination was based on the basis of the recovery of a dinoflagellate cyst (dinocyst)
identified as *Odontochitina imparilis* (Duxbury) Jain et Khowaja-Ateequzzaman. However,
this age was questioned by Benoit et al. (2017), who dated the deposits as Berriasian owing to
the recovery of the charophyte *Clavator grovesii* var. *grovesii* (Harris) Martin-Closas. The

77 aim of our paper is, therefore, to re-assess the composition of the continental palynological

78 assemblage recovered from Angeac in the light of this recent development. We also discuss

79 the taxonomy of Early Cretaceous verrucate spores.

80

81 **2. Geological setting**

82

83   The Angeac site (45° 37' 59.08" N–0° 5' 7.27" W) is situated 700 m north of the village

84 of Angeac-Charente, between Angoulême and Cognac (Fig. 1A). The lignitic beds of

85 "Wealden-facies" underlie Pleistocene alluvium laid down by the Charente River. Seven

86 sedimentological units, An1–An7, were described by Néraudeau et al. (2012) from the top to

87 the base respectively. An1 is composed of 0.10–0.20 m of fine white sand, with abundant fish

88 micro-remains: it was mainly exposed during the first excavation campaigns of 2010 and

89 2011. An2 comprises 0.20–0.40 m of yellow and grey calcareous and marl deposits, with

90 numerous dinosaur bones, other vertebrate remains, ostracods, charophytes, and pieces of

91 wood (Fig. 1B). The stratification of this bed is difficult to determine because it has been

92 affected by the trampling of dinosaurs (dinoturbation). An3 is a calcareous conglomerate

93 0.20–40 m thick, with abundant vertebrate remains, ostracods, charophytes, insect coprolites,

94 pieces of wood and other plant debris (Colin et al., 2011; Néraudeau et al., 2012; Benoit et al.,

95 2017). An4 is about 0.5–1.20 m thick. It is composed of blue-grey lignitic clay, oxidized at

96 the top, and has yielded numerous plant and well-preserved vertebrate remains. The base of

97 An5 is not visible. It is more than 0.7 m thick and composed of green clay that is devoid of

98 macrofossils, and includes sub-angular limestone blocks that are likely to have been reworked

99 into this deposit (Néraudeau et al., 2012). An6 and An7 consist of grey limestone and red clay

100 respectively, but they were only seen in 2010, after the initial trench was extended laterally.

101 They did not yield any fossils.

102

3. Material and methods

104

3.1. Material and laboratory processing methods

106   Six samples were processed by E. Masure in order to provide the palynological results

107 presented in Néraudeau et al. (2012). Duplicates of these preparations (LEM1–LEM6) were

108 sent to one of us (DJB) in 2011 and these have now been (re)-examined for this paper. LEM1

109 comes from the An2 unit (Fig. 1B). LEM2 and LEM3 are from the An3 unit. LEM2

110 corresponds to the organic fraction in which the size of the particles ranges between 10 and 63

111 µm, whereas LEM3 includes particles ranging in size from 10 and 100 µm. LEM4 comes

112 from the boundary between units An3 and An4. LEM5 is from the boundary between An4

113 and An5, and LEM6 comes from within the An5 unit. There was no palynological preparation

114 from the An4 unit. However, a sample from this unit was processed in 2010 by DJB at

115 Aberystwyth University, Wales (preparation QPR 3669: QPR is an Aberystwyth University,

116 palynological preparation identifier), using a standard procedure involving immersion of the

117 sample in 10% HCl followed by digestion in 58–62% HF and brief oxidation of the organic

118 residue in fuming HNO_3, washing after each stage until the residue was neutral (for further

119 information, see Batten, 1999).

120   Four samples were also processed in Aberystwyth for their mesofossil content:

121 preparations MFP422 from the boundary between An3 and An4, and MFP415, MFP423 and

122 MFP512 from unit An4. All yielded very small assemblages of megaspores. Their extraction

123 involved initial soaking of 100 g of rock in warm water on a hot plate followed by immersion

124 of the sample in a solution of $Na_4P_2O_7$ in order to disaggregate it as much as possible before

125 sieving over a 70 µm mesh to reduce its bulk prior to standard palynological processing using

126 HCl and HF. The megaspores were picked out of the aqueous residues under a

127 stereomicroscope and housed dry in micropalaeontological slides. Some of the specimens

128 recovered were mounted on scanning electron microscope (SEM) stubs to which carbon tabs

129 had been fixed, coated with platinum–palladium, and examined under a Hitachi S47-100 SEM

130 in the Institute of Biological, Environmental and Rural Sciences (IBERS), Aberystwyth

131 University.

132

133 *3.2. Specimen counts*

134   For palynological preparations LEM1–LEM4, and QPR 3669, 250 specimens were

135 counted from the slides under a light microscope. LEM5 yielded just 94 specimens, and only

136 a few examples of *Classopollis* were recovered from LEM6.

137

138 *3.3. Analysis of verrucate spores*

139   Owing to their morphological resemblance to the products of the extant fern *Lygodium*,

140 Cretaceous verrucate spores are considered to belong to the Schizaeales (Bolchovitina, 1961;

141 Ivanova in Samoilovitch and Mtchedlishvili, 1961; Fensome, 1987: see Discussion, Section

142 5). From the 1950s to the late 1980s, tens of species of eight genera (*Concavissimisporites*,

143 *Converrucosisporites, Impardecispora, Maculatisporites*, *Rubinella*, *Trilobosporites*,

144 *Tuberositriletes* and *Varirugosisporites*) were erected to accommodate upper Mesozoic

145 verrucate spores, principally on the basis of the outline of their amb, and the size and

146 arrangement of the verrucae on a specimen. This led to considerable overlap between generic

147 and specific diagnoses (Potonié and Kremp, 1954; Delcourt and Sprumont, 1955; Döring,

148 1964; Venkatachala et al., 1969; Dörhöfer, 1977), as previously underlined and discussed by

149 Batten (1986).

150   The history of classification of these spores is well summarized by Fensome (1987, pp.

151 19, 20), who broadened the diagnosis of *Concavissimisporites*, and considered

152 *Tuberositriletes* and *Impardecispora* to be junior synonyms. *Tuberositriletes* was erected by

153 Döring (1964) to accommodate Mesozoic forms similar to *Converrucosisporites* Potonié et

154 Kremp, 1954, because he considered the Carboniferous holotype of the type species of the

155 latter to be an atypical developmental stage. Venkatachala et al. (1969) designated

156 *Impardecispora apiverrucata* (Couper, 1958) as the type of *Impardecispora*. This species had

157 previously been accommodated in *Trilobosporites*, a genus that is distinguishable from

158 *Concavissimisporites* by the fact that it possesses one or several valvae at each apex, and/or

159 displays a more or less complete network of muri in the apical region (Fensome, 1987).

160 Srivastava (1977) considered *Maculatisporites* Döring, 1964 to be a junior synonym of

161 *Concavissimisporites*, but Fensome (1987, p. 19) noted that the morphological features of the

162 type species, *M. undulatus* Döring, 1964 do not clearly demonstrate this. The genera

163 *Rubinella* and *Varirugosisporites* were erected by Maljavkina (1949, emended by Potonié,

164 1960) and Döring (1965) respectively to accommodate Jurassic verrucate forms, but have

165 rarely been used by other authors. The diagnoses of both are very broad and can easily be

166 accommodated within Fensome's (1987) emended diagnosis of *Concavissimisporites*.

167   A few years later, Waksmundzka (1992) adopted an even more reductive approach and

168 placed *Converrucosisporites*, *Concavissimisporites*, *Converrucitriletes*, *Gemmatriletes*,

169 *Tuberositriletes*, *Maculatisporites*, *Rubinella* and *Varirugosisporites* in synonymy with

170 *Verrucosisporites*. She considered the basis for separation of these genera was insufficient,

171 this being mainly the general outline of the spores. However, *Verrucosisporites* was

172 established by Ibrahim (1933), and emended later by Potonié and Kremp (1954) and Krutzsch

173 (1959), among others, to accommodate Palaeozoic spores covered with warts or small

174 verrucae, which more closely resemble those produced by the Osmundaceae than the

175 Lygodiaceae. Also, placing in synonymy too many taxa can defeat the purpose of achieving a

176 sensible, stratigraphically and biologically relevant taxonomy. Indeed, Waksmundzka (1992,

177 p. 47) noted that the spores belonging to her emended version of *Verrucosisporites* are

178 imprecisely related to the Pteridophyta. Hence, we do not accept her solution to the problem

179 of too many genera for verrucate miospores. We prefer to base our identifications on

180 Fensome's major revision (1987) which, despite his synthesis and practical approach, has

181 never been discussed, most of the genera noted above still being encountered in the literature

182 (e.g., Burden and Hills, 1989; Song et al., 2000; Dejax et al., 2007). This not only renders

183 comparisons between assemblages challenging, but also diminishes the stratigraphic

184 significance of the species, because too many names are available for the same morphotype

185 and closely similar forms.

186　　As a result, it was decided to carry out a Principal Components Analysis (PCA) of the

187 verrucate spores in the Angeac palynomorph assemblages, one of the purposes being to

188 determine whether *Concavissimisporites* can truly be regarded as encompassing a

189 morphological group that is well separated from *Trilobosporites* (see Section 4.2.). Indeed,

190 since numerous verrucate spores were recovered from the samples corresponding to

191 sedimentological units An2–4, we decided to identify them *a priori* following Fensome's

192 emended diagnoses as species of either *Concavissimisporites* or *Trilobosporites*. The PCA

193 was then carried out using 120 specimens from the three units (50, 20, and 50 for An2, An3

194 and An4, respectively). The purposes of this statistical analysis were to see whether it is

195 possible to (1) obtain several morphological groups that would cluster according to the

196 diagnoses of already established species, (2) determine those groups that can be divided into

197 two or more genera, and (3) ascertain whether there are any significant morphological

198 differences between the specimens recovered from the different lithological units.

199　　Ten variables were taken into account (Fig. 2):

200 S: size of specimen (= maximum diameter).

201 SA: smallest value of the reflex, acute or obtuse angle formed by the two tangents of the

202 starting and arrival points of the arc or curve formed by the outline of the interradial region of

203 a spore.

204 LA: largest value of the reflex, acute or obtuse angle formed by the two tangents of the

205 starting and arrival points of the arc or curve formed by the outline of the interradial region of

206 a spore.

207 MiD/MaD: ratio between the minimum and maximum distances from the centre to the edge of

208 the spore (excluding the verrucae).

209 mDV: mean diameter of verrucae on one spore; 32 verrucae were counted on each specimen,

210 when possible. Most of the means have been calculated based on approximately 20 values.

211 mHV: mean height of verrucae on one spore.

212 STDV: standard deviation of the diameter of verrucae on one spore.

213 STHV: standard deviation of the height of verrucae on one spore.

214 ET: exine thickness.

215 PC: per cent cover of the verrucae on the proximal face of a spore. 0.15: 0–30%; 0.45: 31–

216 60%; 0.75: 61–94%; 0.95: 95–100%.

217 All of the values have been divided by the size of the specimen, and scaled. They were

218 measured on clear images of the specimens under a light microscope. The angles were

219 measured using the free java application *OnScreenProtractor*. The various lengths and

220 diameters were measured using the software *Inkscape*. The PCA was carried out using the

221 software *Past*.

222

223 *3.4. Repository*

224 All of the palynological preparations and the megaspores illustrated are housed in the

225 Geological Institute of the University of Rennes 1, under collection numbers IGR-PAL-5735–

226 IGR-PAL-5753 for the palynological slides, and IGR-PAL-5780–IGR-PAL-5784 for the

227 megaspores illustrated.

228

229 **4. Results**

230

231 *4.1. Palynological assemblages*

232 Altogether 34 taxa (excluding those placed in comparison apart from

233 *Concavissimisporites* sp. cf. *C. crassatus*) have been identified at genus or species level in the

234 seven samples examined (Fig. 3). The most common of these are the cheirolepidiaceous

235 pollen grain *Classopollis* (Fig. 4C, D), verrucate spores such as *Concavissimisporites*

236 *montuosus* (Döring) Fensome (Fig. 5J, K, M), *Concavissimisporites apiverrucatus* (Couper)

237 Döring (Fig. 5A, B), *Concavissimisporites exquisitus* (Singh) Fensome (Fig. 5C, D) and

238 *Trilobosporites canadensis* Pocock (Fig. 6H), the papillate spore *Pilosisporites*

239 *trichopapillosus* (Thiergart) Delcourt et Sprumont (Fig. 4P), the hilate spore *Aequitriradites*

240 *verrucosus* (Cookson et Dettmann) Cookson et Dettmann (Fig. 4G), and various smooth

241 walled spores belonging to the genera *Cyathidites*, *Deltoidospora*, and *Gleicheniidites* (Fig.

242 4H, J). Freshwater algae such as *Ovoidites spriggi* (Cookson et Dettmann) Zippi (Fig. 4N) are

243 relatively common, but no more dinoflagellate cysts were encountered during the re-

244 examination.

245 An2 yielded an assemblage of 16 species (Fig. 3), numerically and taxonomically

246 dominated by verrucate spores (Fig. 7). It is the only assemblage in which there are no

247 *Classopollis* pollen, the gymnosperm component being represented by only two inaperturate

248 pollen grains referable to *Araucariacites australis* Cookson. Eighteen species were recovered

249 from the An3 unit. Verrucate spores are less diverse than in the An2 unit with eight species,

250 but the gymnosperms are better represented, with numerous specimens referable to

251 *Classopollis torosus* (Reissinger) Couper, and bisaccates such as *Abietineaepollenites* sp.

252 (Fig. 4A). This is the only assemblage in which a specimen of *Cicatricosisporites hallei*

253 Delcourt et Sprumont was found (Fig. 4M). The sample taken from the boundary between

254 An3 and An4 yielded 16 species, five of which are exclusive to this sample: *Callialasporites*

255 *dampieri* (Balme) Dev (Fig. 4B), *Densoisporites microrugulatus* Brenner (Fig. 4K), cf.

256 *Foraminisporis wonthaggiensis* (Cookson et Dettmann) Dettmann (Fig. 4L),

257 *Microreticulatisporites* sp. cf. *M. diatretus* Norris (Fig. 4I), and *Podocarpidites ellipticus*

258 Cookson (Fig. 4F). The assemblage from the lignitic clays of An4 is the most diverse, having

259 yielded 21 species, three of which were recorded only from this level: *Retitriletes* sp. (Fig.

260 4O), *Cerebropollenites mesozoicus* Couper, and *Vitreisporites pallidus* (Reissinger) Nilsson

261 (Fig. 4E). This sample yielded proportionally the greatest abundance of *Classopollis* (Fig. 7),

262 but also, and in common with An2, the most diverse verrucate spore assemblage (nine

263 species). The An4/An5 sample yielded a moderately diverse, albeit small assemblage of 15

264 species, including six verrucate taxa. Overall, the relative abundance of *Classopollis* tends to

265 decrease upwards in the succession from An4/An5 to An2, whereas the abundance of the

266 verrucate and smooth walled spores increases greatly in this direction.

267 Also, significant in this context is the fact that specimens identified as *Trilobosporites*

268 are more abundant in the palynomorph assemblage recovered from An2 than in the older

269 deposits, and that overall, verrucate spores in the An2 assemblage are generally larger and

270 more sparsely sculptured than those recovered from the other units (see PCA plots, Figs 8, 9).

271

272 *4.2. Megaspores*

273 The four samples processed for their mesofossil content yielded only a few megaspores

274 and fragments thereof, most of which are referable to the genus *Erlansonisporites* (Figs. 10,

275 11A, B), and faecal pellets, probably attributable to the activities of termites (Colin et al.,

276 2011). The sample from the boundary between An3 and An4 (preparation MFP422) also

277 proved to contain a few specimens of a form tentatively recorded here as *Minerisporites* sp.

278 (Fig. 11C–F). Apart from a couple specimens that are currently unidentifiable without

279 recourse to examination under an SEM, all other megaspore remains are too damaged or

280 fragmentary to be positively identified: among these are possible representatives of

281 *Paxillitriletes*. Associated with the megaspores in MFP422 are isolated, comparatively large

282 specimens of the freshwater algae *Schizosporis reticulatus* Cookson et Dettmann emend

283 Pierce and *Ovoidites spriggii* (Cookson et Dettmann) Zippi.

284   Most of the specimens of *Erlansonisporites* (Figs. 10E, F, 11A, B) are closely similar to

285 *Erlansonisporites* sp. *sensu* Batten, 1975, pl. 13, fig. 6, a selaginellalean megaspore from the

286 upper Berriasian–Valanginian Ashdown Formation in Sussex, south-east England (e.g.,

287 Batten, 2011): this is consistent with the suggested revised age determination of the Angeac

288 deposits herein. Numerous microspores, all exhibiting the same morphology, are lodged

289 within the muri of its reticulate sculpture, especially on the proximal surface close to the

290 triradiate flange. In the dispersed state, these are probably attributable to the small spore

291 genus *Patellasporites,* or perhaps *Uvaesporites*.

292   The specimens of *Minerisporites* sp. are atypical for this genus in that, although zonate,

293 they have a virtually smooth surface and a triradiate flange that is of uneven elevation, indeed

294 it can be partly spinose (Fig. 11C). The outer edge of the zona is also uneven to weakly

295 spinose, features that might equally suggest a representative of *Henrisporites*, albeit again

296 atypical. More specimens are required before this form can be satisfactorily identified.

297

298 *4.3. Systematic palaeontology of the verrucate spores*

299   The PCA2 plot (Fig. 9) supports Fensome's (1987) taxonomic approach to the

300 identification of verrucate spores, the specimens from Angeac only being attributable to two

genera, *Concavissimisporites* and *Trilobosporites*. They are morphologically well separated, principally on the account of their size, the relative size of their verrucae, and the variation in the dimensions of verrucae on a specimen. Three species of *Trilobosporites*, and eight species of *Concavissimisporites* have been identified, along with several intermediate forms. Except for *Concavissimisporites apiverrucatus*, specimens assigned to a particular species are clustered together, although the boundaries between the clusters are not always clearly defined. It was thought that the semi-quantitative variable corresponding to the per cent cover of verrucae (PC) might be biasing the results of the PCA in assuming too much importance compared to the other variables. Thus, another PCA was run without the per cent cover variable, but the results were very similar, indicating that this did not significantly affect the plot.

Genus *Concavissimisporites* Delcourt et Sprumont, 1955, emend. Fensome, 1987.

Type species: *Concavissimisporites verrucosus* Delcourt et Sprumont, 1955 emend. Delcourt et al., 1963.

Concavissimisporites apiverrucatus (Couper, 1958) Döring, 1965 (Fig. 5A, B)

Material. Angeac units An2, An3/4, An4, An4/5: 11 specimens, 57 (72) 105 µm in diameter.

Remarks. Concavissimisporites apiverrucatus is differentiated from the other species of this genus in that the sculpture of the apices is slightly to distinctly coarser than over the poles and in interradial regions. In the case of the Angeac specimens, the polar and interradial regions are almost smooth (Fig. 5B), granulate (Fig. 5A), or sculptured with verrucae. Specimens attributed to this species are the only ones that do not form a united cluster on PCA2 (Fig. 9),

326 principally because the main diagnostic characters mentioned above have not been considered

327 as a variable, these being very difficult to calculate.

328 *Occurrence.* This species occurs widely in rocks ranging in age from latest Jurassic to Albian

329 (e.g., Fensome, 1987; Burden and Hills, 1989). In France, it has been recorded, as

330 *Trilobosporites apiverrucatus* Couper, from "Wealden" (Delcourt and Sprumont, 1959),

331 lower Valanginian (Vakhrameev and Kotova, 1980), upper Barremian–lower Aptian

332 (Herngreen, 1971) and upper Albian (Bardet et al., 1991) deposits.

333

334 *Concavissimisporites* sp. cf. *C. crassatus* (Delcourt et Sprumont, 1955) Delcourt et al., 1963

335 (Fig. 5L, N)

336

337 *Material.* Angeac unit An2: three specimens 61 (63) 67 µm in diameter.

338 *Remarks.* Specimens Q35.4 and B28.4 (Fig. 5L, N) fit the description given by Delcourt et al.

339 (1963, p. 285), bearing in mind the changes made by Fensome to the generic diagnosis (1987,

340 p. 19). No formal size range is given by Delcourt et al., but their illustrated specimen is 78 µm

341 in diameter. Delcourt and Sprumont (1955, p. 26) stated that the "radius" of their form

342 *crassatus* is 40–55 µm. As a result, we only compare our specimens to this species because

343 they are smaller.

344   On the PCA2 (Fig. 9), the squares pertaining to *C.* sp. cf. *crassatus* are situated at the

345 edge of the cluster that corresponds to *C. montuosus*. It could be argued that these specimens

346 are also identifiable as *C.* sp. cf. *C. montuosus*, the limiting character being the small size of

347 the verrucae.

348 *Occurrence. Concavissimisporites crassatus* was originally described from Wealden-type

349 strata in Belgium (Delcourt and Sprumont, 1955; Delcourt et al., 1963). It has not been

350 encountered previously in France, but has been found in Albian strata of the Bay of Biscay

351 (Batten, 1979), Berriasian–mid-Valanginian strata in the Netherlands (Burger, 1966), upper

352 Berriasian, and upper Barremian–lower Aptian rocks in Germany (Dörhöfer, 1977; Lister and

353 Batten, 1995), and within Cenomanian deposits of Spain (Solé de Porta, 1978). It was also

354 recorded by Fensome (1987) from Upper Jurassic to lower Valanginian strata in western

355 Canada.

356

357 *Concavissimisporites exquisitus* (Singh, 1971) Fensome, 1987 (Fig. 5C, D)

358

359 *Material*. Angeac units An2, An3, An3/4, An4, An4/5: 19 specimens, 47 (59) 75 µm in

360 diameter.

361 *Remarks*. This species is defined by its triangular to convex outline, coupled with bulbous

362 verrucae 6–10 µm wide. In his original diagnosis, Singh (1971, p. 116) stated that the

363 verrucae are spaced 1–4 µm apart. The verrucae on the specimens from Angeac are more

364 closely spaced overall, being separated by no more than 1 µm. The size-range given by Singh

365 is 68 (71) 84 µm, but this is based on only four specimens, and the only specimen of this

366 species recovered by Fensome is 59 µm in diameter (1987, pl. 4, fig. 11). Some relatively

367 small, rounded specimens, such as R40.2 (Fig. 5E), are referred to *Concavissimisporites* sp.

368 cf. *C. exquisitus* because they show proportionally smaller verrucae. They are more similar to

369 *Verrucosisporites major* (Couper) Burden et Hills, a form that occurs widely in Jurassic and

370 Cretaceous strata.

371 The cluster corresponding to this species on the PCA2 plot is very close to that

372 representing *Concavissimisporites ferniensis* (Fig. 9), which is, however, distinguished from

373 *C. exquisitus* in having significantly lower verrucae separated by narrow canals that form a

374 more or less distinct negative reticulum.

375   *Occurrence*. This species was originally recovered from Albian strata in Alberta, Canada

376   (Singh, 1971), but Fensome (1987) found it in upper Jurassic deposits. It has not been

377   encountered previously in France, but Mohr (1989) mentioned its presence in upper

378   Tithonian–lower Berriasian strata in Portugal.

379

380   *Concavissimisporites ferniensis* (Pocock, 1970) Fensome, 1987 (Fig. 5F–H)

381

382   *Material*. Angeac units An2, An3, An3/4, An4: seven specimens 45 (56) 78 µm in diameter.

383   *Remarks*. For differences between *Concavissimisporites ferniensis* and *C. exquisitus*, see

384   remarks above under the latter species. In common with *C. exquisitus*, the specimens assigned

385   to *C. ferniensis* are very similar to *Verrucosisporites major*, which however differs in usually

386   being smaller and in lacking a negative reticulum (see Couper, 1958).

387   *Occurrence*. This species has only been recovered from Jurassic sedimentary rocks in western

388   Canada (Fensome, 1987), but very similar forms, identified as *Leptolepidites major* Couper,

389   have been found in various French Jurassic, Albian and Cenomanian strata (Fauconnier, 1979;

390   Fechner and Dargel, 1989; Bignot et al., 1994).

391

392   *Concavissimisporites montuosus* (Döring, 1964) Fensome, 1987 (Fig. 5J, K, M)

393

394   *Material*. Angeac units An2, An3, An3/4, An4, An4/5: 26 specimens 52 (72) 105 µm in

395   diameter.

396   *Remarks*. This species is characterized by being sculptured with typically well-spaced

397   verrucae 2–5 µm in diameter. It is the most common verrucate spore in the Angeac

398   succession. A few specimens have been referred to *Concavissimisporites* sp. cf. *C. montuosus*

399   (e.g., N26.1, not illustrated), because they have more closely spaced and smaller verrucae.

Occurrence. The stratigraphic range of *Concavissimisporites montuosus* extends from upper Oxfordian to Albian. It is a distinctive element in many Volgian–Valanginian palynofloras (Fensome, 1987). It has not been found in France previously, but has been recovered, as *Converrucosisporites montuosus* Döring, from lowest Cretaceous strata in north-western Germany (Dörhöfer and Norris, 1977). According to these authors, an abundance of this form is characteristic of their upper Berriasian palynofloral suite "Hils 1".

Concavissimisporites robustus Dörhöfer, 1977 (Fig. 5I)

Material. Angeac units An2, An3: two specimens 59 and 66 µm in diameter.

Remarks. *Concavissimisporites robustus* differs from the other species encountered in having a more or less uniformly thick exine coupled with poorly delineated verrucae that are either sparsely or densely distributed. The two specimens recovered from Angeac are weakly sculptured. The PCA2 plot shows that they cluster closest to the specimens identified as *C. uralensis*, mainly because of the scarcity of the verrucae on the proximal face.

Occurrence. This species was originally described from the upper Berriasian palynofloral suites "Hils 1" and "Hils 2" in north-western Germany (Dörhöfer, 1977). It has also been recorded from uppermost Jurassic strata in western Canada (Fensome, 1987) and middle Berriasian deposits in eastern Maryland, USA (Doyle, 1983).

Concavissimisporites uralensis (Bolchovitina, 1961) Fensome, 1987 (Fig. 6D)

Material. Angeac units An2, An4: three specimens 56 (68) 90 µm in diameter.

Remarks. This species can appear very similar to the specimens identified here as *Concavissimisporites apiverrucatus*: they differ in being more sparsely sculptured. They also

425 differ from specimens of *C. robustus* in having a thinner exine. It could be argued that they

426 are intermediate between *C. apiverrucatus* and *C. robustus*. However, the PCA clustered all

427 three specimens together, quite far away from the other clusters, which is why we decided to

428 regard them as belonging to a distinct species (see Section 6.2 for the biological relevance of

429 this decision).

430 *Occurrence*. *Concavissimisporites uralensis* was originally described from Barremian–Aptian

431 strata in western Kazakhstan (Bolchovitina, 1961). It has also been recorded from Ryazanian

432 (lowest Berriasian) strata in western Canada (Fensome, 1987).

433

434 *Concavissimisporites verrucosus* Delcourt et Sprumont, 1955 emend. Delcourt et al., 1963

435 (Fig. 6A, B)

436

437 *Material.* Angeac units An3, An4, An4/5: six specimens 73 (81) 100 µm in diameter.

438 *Remarks*. This species differs from the other verrucate spores from Angeac by its large size,

439 and in having relatively small, closely spaced verrucae. The specimen D20.4 (Fig. 6C) is

440 considered to be an intermediate form between *C. verrucosus* and *C. montuosus*, because it is

441 sculptured with relatively large, closely spaced verrucae.

442 *Occurrence*. The stratigraphic range of *C. verrucosus* extends from Middle Jurassic to Lower

443 Cretaceous. In western Europe, it occurs principally within lowest Cretaceous and

444 "Wealden"-type strata (Burger, 1966; Bolchovitina, 1971; Dörhöfer and Norris, 1977).

445

446 Genus *Trilobosporites* Pant, 1954 ex Potonié, 1956 emend. Fensome, 1987

447

448 Type species: *Trilobosporites hannonicus* (Delcourt et Sprumont, 1955) Potonié, 1956

449

450 *Trilobosporites aequiverrucosus* Dörhöfer, 1977 (Fig. 6I)

451

452 *Material*. Angeac unit An4: one specimen, 100 µm in diameter.

453 *Remarks*. This species differs from *Trilobosporites canadensis* in having proportionally

454 smaller unfused, closely spaced verrucae in polar and interradial regions. As stated by

455 Dörhöfer (1977, pp. 53, 54), this species is considered to include many specimens previously

456 attributed to *Trilobosporites bernissartensis* (Delcout et Sprumont) Potonié, for which the

457 type and size of the sculptural elements were not specified. The re-illustrations of the holotype

458 and paratypes in Delcourt et al. (1963, pl. 43, figs. 11–14) are considered inadequate, because

459 several morphotypes are displayed. As a result, Dörhöfer considered that a precise

460 interpretation of *T. bernissartensis* is not possible.

461 *Occurrence*. The species was originally described from upper Berriasian–lower Valanginian

462 beds in western Germany (Dörhöfer, 1977). As *Trilobosporites bernissartensis*, it has been

463 found in Wealden-type strata in Belgium (Delcourt and Sprumont, 1955; Delcourt et al.,

464 1963), and in Purbeck and Wealden beds in southern England and stratigraphically equivalent

465 deposits in western France (Couper, 1958; Lantz, 1958; Deák and Combaz, 1967). It has also

466 been reported from lowest Aptian strata in south-eastern France (de Reneville and Raynaud,

467 1981), and within upper Barremian–lower Aptian strata in northern France (Herngreen, 1971).

468 However, the specimen illustrated by Herngreen (1971, pl. 3, fig. 1) is in fact attributable to

469 *Trilobosporites hannonicus* (Delcourt et Sprumont) Potonié, so we do not accept this record

470 of occurrence.

471

472 *Trilobosporites aornatus* Döring, 1965 (Fig. 6E, F)

473

474 *Material*. Angeac units An2, An3, An4: three specimens 68 (78) 96 µm in diameter.

475 *Remarks*. The morphology of the specimens recorded as *Trilobosporites aornatus* have a

476 maculate sculpture and a large verruca or rounded valva in equatorial radial regions. K28.3

477 (Fig. 6G) is referred to *Trilobosporites* sp. cf. *T. aornatus*, because of the presence of a few

478 verrucae close to each of the angles, in common with the specimen illustrated by Norris as

479 *Trilobosporites obsitus* Norris (1969, pl. 106, fig. 7) (see Section 5.2. for the biological

480 relevance of this species).

481 *Occurrence*. Döring (1965) described this species from Upper Jurassic–lowermost Cretaceous

482 strata in eastern Germany. In southern England, it is typical of the upper Berriasian–lower

483 Valanginian palynofloral suite C of Norris (1969), and as discussed by Dörhöfer and Norris

484 (1977). In North America, it ranges into the lower Barremian (Burden and Hills, 1989).

485

486 *Trilobosporites canadensis* Pocock, 1962 (Fig. 6H)

487

488 *Material.* Angeac units An2, An3, An3/4, An4, An4/5: 11 specimens 69 (88) 105 µm in

489 diameter.

490 *Remarks*. *Trilobosporites canadensis* is characterized by its coarse interradial and polar

491 verrucae, which sometimes merge to form elongate elements, along with one or two large,

492 pronounced, strongly projecting verrucae or valvae in equatorial radial regions. This is the

493 most common form of *Trilobosporites* at Angeac, especially in the An2 unit.

494 *Occurrence*. This species was originally described from "Neocomian" deposits in western

495 Canada (Pocock, 1962). In Western Europe, it has been reported from upper Berriasian–lower

496 Valanginian beds in western Germany (Dörhöfer, 1977), probable Berriasian Purbeck beds in

497 southern England (as *T*. cf. *canadensis*; Hunt, 1985), Tithonian–Berriasian deposits in

498 Portugal (Mohr, 1989) and within upper Barremian–lower Aptian strata in northern France

499 (Herngreen, 1971). However, the morphology of the specimens illustrated in Herngreen's

500   paper (pl. 3, figs. 2–4) is closer to that of *Concavissimisporites montuosus* than to *T.*

501   *canadensis*.

502

503   **5. Discussion**

504

505   *5.1. Age determination and comparisons*

506   We discuss the previous identification in Néraudeau et al. (2012) of the dinoflagellate

507   cyst *Odontochitina imparilis* (Duxbury) Jain et Khowaja-Ateequzzaman in the Angeac

508   assemblage. In his description of *Muderongia imparilis*, Duxbury (1980, p. 128) indicated the

509   presence of three well-developed horns as a diagnostic feature, with the lateral horn being

510   greatly reduced. A lateral horn seems to be present on the Angeac specimen, but it is folded

511   behind the periblast. There are two antapical horns, one shorter than the other. The longer of

512   the two is very corroded. A vestigial apical horn is present. The original description also states

513   that the endoblast and periblast are joined together in the epicystal region, which does not

514   seem to be the case of the Angeac specimen, the endoblast being proportionally much smaller

515   than the periblast.

516   The species has usually been found within Hauterivian–Barremian deposits (Duxbury,

517   1980; Jain and Khowaja-Ateequzzaman, 1984; Leereveld, 1997), hence the previous

518   attribution of a Hauterivian–Barremian age to the Angeac deposits. However, the species has

519   also been recorded from upper Valanginian strata (Burger, 1996). Although the poor

520   preservation of the Angeac specimen renders the identification questionable, the short range

521   of the species may well be related to the general scarcity of this form and linked to specific

522   environmental conditions (Masure, pers. comm. 2017), so a find of *O. imparilis* in older

523   deposits is not impossible.

524   The Angeac specimen is also similar to *Muderongia simplex* Alberti, which has one

525   apical, two lateral, and two antapical horns. The holotype of this species is 151 µm long,

526   which is almost the same as the Angeac specimen at 152 µm. However, they differ in that the

527   latter possesses a proportionally small endoblast, and does not display a second lateral horn,

528   although it is possible that has been destroyed or is obscured by folding. The stratigraphic

529   range of *Muderongia simplex* extends from upper Tithonian to upper Valanginian (Riding et

530   al., 2000).

531   Dating Lower Cretaceous deposits using miospores can be challenging, the forms

532   encountered often being long ranging. For instance, *Aequitriradites verrucosus* and

533   *Pilosisporites trichopapillosus* are present through all of the Lower Cretaceous in western

534   Europe. In France, *A. verrucosus* has only been reported recently within Cenomanian deposits

535   (Fleury et al., 2017). Batten (1979) recorded it from Aptian–Albian strata in the Bay of

536   Biscay. It occurs rarely elsewhere in Europe but has nonetheless been documented from

537   Aptian and Wealden deposits in England (Ruffell and Batten, 1994 and Batten unpublished,

538   respectively) and in Wealden-type facies in Germany (Döring, 1964).

539   *Pilosisporites trichopapillosus* ranges from uppermost Jurassic (Couper and Hughes,

540   1963) to Upper Cretaceous (Robaszynski et al., 1985), but is more frequently recovered from

541   Lower Cretaceous deposits (Bolchovitina, 1971; Dörhöfer, 1977; Batten, 1979; Doubinger

542   and Mas, 1981; Batten and Li, 1987). In France, it has only been documented from Tithonian

543   strata (Couper and Hughes, 1963).

544   Nevertheless, dating can be more precise if the composition of entire assemblages is

545   taken into account. A few attempts at stratigraphic correlations using Lower Cretaceous

546   miospore assemblages were made during the late 1960s and early 1970s. A method

547   introduced by Hughes and Moody-Stuart (1969) consisted of using several types of

548   *Cicatricosisporites* to correlate between different beds in a Wealden borehole and an outcrop

549 in south-east England. Their abandonment of Linnaean nomenclature in favour of biorecords

550 (Hughes and Moody-Stuart, 1969; Hughes, 1970) meant that their method did not gain

551 widespread support among palynologists (Batten, 1986). Regardless, we could not apply a

552 similar approach to the Angeac assemblages using species of *Cicatricosisporites* because only

553 a few specimens of this taxon were recovered.

554 Another method involved the use of palynological assemblage-types for correlating

555 Wealden deposits in southern England (Batten, 1973). Seventeen assemblages were described,

556 taking into account preservation state, diversity of miospores, average size of trilete spores,

557 abundance of brown wood, and the abundance of certain taxa. The total Angeac assemblage

558 (i.e. the overall composition of the assemblages recovered from An2–5) is very similar to

559 Batten's Assemblage Type 15 (AT 15). This was characterized by the common presence of

560 *Concavissimisporites*, coupled with a "Trilete spore content dominated by average-sized or

561 large forms; miospore diversity average or large; general state of preservation of miospores

562 good or fair; brown wood and cuticle P, C or F [present, common, or frequent]; *Pilosisporites*

563 P or C [present or common], *Cicatricosisporites* C or V [common or very

564 common]…..*Trilobosporites* occurs in more than 70% of the assemblages referable to this

565 AT" (Batten, 1973, pp. 13, 14). The only difference from this description is the scarcity of

566 *Cicatricosisporites*. Following the same study, and using current stratigraphic terminology

567 (e.g., Batten, 2011), this assemblage-type has mostly been recovered from the Ashdown

568 Formation, including the Fairlight Clays facies, and the Grinstead Clay Formation, all of

569 which are part of the Hastings Group, which was deposited between the mid Berriasian and

570 the late Valanginian.

571 The Angeac assemblage overall is also very similar to those recovered from the

572 Bückeberg Formation, especially the upper Berriasian palynofloral suites "Hils 1" and "Hils

573 2", which are characterized by abundant *Concavissimisporites montuosus*, large

574 *Trilobosporites*, and the relative scarcity of *Cicatricosisporites* (Dörhöfer, 1977; Dörhöfer and

575 Norris, 1977). In France, Berriasian palynological assemblages have been recovered from

576 Jura (eastern France) and potentially Oléron island (Fig. 1). The Angeac assemblage is

577 somewhat similar to that recovered by Médus and Mojon (1991) from upper Berriasian strata

578 of southern Jura in that the latter is characterized by an abundance of *Densoisporites*

579 *microrugulatus* and *Trilobosporites*. It was compared to palynofloral suite "Hils 4" (Médus

580 and Mojon, 1991, p. 57), but only a few illustrations were provided to support the

581 identifications, and *D. microrugulatus* is not abundant in the Angeac assemblage. The

582 uppermost Berriasian assemblage from Jura recovered earlier by Taugourdeau-Lantz and

583 Donze (1971) is less similar, with few verrucate spores and several dinoflagellate cyst species

584 in association. The palynoflora recovered from the "Purbeck beds" of Oléron island (Lantz,

585 1958) includes similar forms of *Trilobosporites*, but the types of *Concavissimisporites* are less

586 diverse, and the specimens illustrated seem comparatively small.

587   The Angeac assemblage is, however, less clearly correlated with younger palynofloras,

588 such as that recovered from the Wealden-facies, dinosaur-bearing pit of Bernissart (Belgium,

589 Dejax et al., 2007), considered to be Hauterivian in age. The samples from this pit yielded

590 specimens of *Trilobosporites* that are similar to the species *T. hannonicus* (Delcourt et

591 Sprumont) Potonié, which has not been recorded from Angeac, more species of

592 *Cicatricosisporites*, and angiospermid pollen grains. Correlations with the assemblage

593 recovered from Saint-Romain-de-Benet, regarded as Valanginian–Hauterivian in age, are

594 quite difficult to make because of a lack of precision in the description of the assemblage as

595 indicated by such statements as …. "on n'observe pratiquement pas de pollens

596 d'Angiospermes" in Deák and Combaz (1967, p. 72), meaning that they "almost did not

597 observe any angiosperm pollen grains". Their stratigraphic range chart (p. 71) is rather

598 inaccurate because most of the species they note as restricted to the Valanginian–Hauterivian

599 have, in fact, wider ranges. In any case, they do not seem to have encountered many verrucate

600 spores, and their species of *Trilobosporites* are quite different from those recovered from

601 Angeac.

602   Although most of the palynomorphs identified herein indicate a stratigraphic

603 distribution that is not confined to the lowest Cretaceous, previous observations in Néraudeau

604 et al. (2012, p. 5) and our new data suggest that the Angeac assemblage is more likely to have

605 been deposited during the Berriasian–early Valanginian rather than in the Hauterivian–

606 Barremian, as previously stated.

607

608 *5.2. Biological relevance of the verrucate spores*

609   The family Schizaeaceae originally included five extant genera: *Schizaea* Sm.,

610 *Actinostachys* Wall., *Mohria* Sw., *Anemia* Sw., and *Lygodium* Sw., which are widely

611 distributed in predominantly tropical or southern warm-temperate parts of the world (Tryon

612 and Lugardon, 1991). However, Smith et al. (2006) considered that these genera in fact

613 belong to three families of the order Schizaeales: Schizaeaceae (for *Schizaea* and

614 *Actinostachys*), Anemiaceae (for *Anemia*, including *Mohria*), and Lygodiaceae (for

615 *Lygodium*).

616   Unequivocal members of this order first appeared in the Early or Middle Jurassic, but

617 they did not become widespread until the Early Cretaceous, as indicated by occurrences of

618 their spores in numerous deposits throughout Eurasia (Bolchovitina, 1971; Van

619 Konijnenburg-Van Cittert, 2002). The Schizaeaceae produce monolete, bean-shaped spores,

620 with diverse ornamentation. The Anemiaceae have trilete spores with coarse, compact ridges.

621 These have abundant Lower Cretaceous analogues, such as *Cicatricosisporites*, and

622 specimens found *in situ* within fertile plant organs associated with the ferns *Ruffordia*,

623 *Pelletieria*, and *Schizaeopsis* (e.g., Hughes and Moody Stuart, 1966). *Lygodium* spores are

624 trilete, and can be tuberculate, verrucate or reticulate (Tryon and Lugardon, 1991). Thus,

625 Early Cretaceous verrucate spores have often been compared to the genus *Lygodium* (e.g., in

626 Delcourt and Sprumont, 1955; Bolchovitina, 1961; Ivanova in Samoilovitch and

627 Mtchedlishvili, 1961; Fensome, 1987).

628   Mesozoic spores comparable to *Lygodium* have only been found *in situ* in Jurassic rocks

629 in northern England (Van Konijnenburg-Van Cittert, 1981), but they have a reticulate

630 sculpture. They have been encountered in sorophores from Turonian deposits in New Jersey,

631 USA (Gandolfo et al., 2000), and compared to the extant species *Lygodium palmatum*

632 (Bernh.) Sw. on account of their trilete, psilate spores, among other characters. Dispersed

633 spores are much more abundant. Bolchovitina (1961) produced a comprehensive monograph

634 on fossil and extant spores of the former family Schizaeaceae (now Schizaeales), in which she

635 listed 62 species of extant *Lygodium* (Smith et al., 2006 considered that the Lygodiaceae

636 comprise only about 25 species), remarked on and illustrated 27 of these, and listed,

637 commented, described or re-described, and illustrated 46 species of dispersed fossil spores

638 referable to *Lygodium*.

639   The spores of the extant species are usually described according to their shape,

640 thickness of exine, colour and sculpture. The last of these may vary within a species, such as

641 in *L. flexuosum* (L.) Sw. and *L. japonicum* (Thunb.) Sw., which produce smooth to slightly

642 tuberculate spores. However, when a species also displays a coarser sculpture, several authors

643 (e.g., Couper, 1958; Dettmann and Clifford, 1991) have considered associated smooth spores

644 to be immature forms. Spore polymorphism has been recognized in a few anemiaceous

645 species (Dettmann and Clifford, 1991), but it would seem that in general mature spores of

646 extant species of *Lygodium* can be well separated on the basis of their sculpture (Bolchovitina,

647 1961; Tryon and Lugardon, 1991; see also SEM micrographs of *Lygodium* spores in the

648 Cornell University website).

649   Hence, most of the morphological clusters of the verrucate spore species displayed by

650 PCA2 (Fig. 9) could well also have biological significance. Specimens assigned to

651 *Concavissimisporites uralensis*, which are defined by their weak sculpture, could in fact be

652 immature forms of other species of *Concavissimisporites*. The same applies to *Trilobosporites*

653 *aornatus*, which could comprise immature specimens of *T. aequiverrucosus* or *T. canadensis*.

654 Intermediate forms such as specimen K28.3 (Fig. 6G) would support this suggestion. The

655 most abundant verrucate spore in the Angeac palynomorph assemblages,

656 *Concavissimisporites montuosus*, is similar to the spores of the extant species *Lygodium*

657 *circinatum* (Burm. f.) Sw., in that both display quite well spaced, massive verrucae.

658 Specimens assignable to the genus *Trilobosporites* are somewhat similar to the spores of

659 *Lygodium merrillii* Copel., which display coarse distal muri that appear as a thickening of the

660 exine in apical regions on the proximal face. However, no spores of extant species of

661 *Lygodium* seem to develop valvae, which is all the more reason to maintain *Trilobosporites* as

662 a separate genus for fossil spores with this character. Some species of *Concavissimisporites*,

663 such as *Concavissimisporites exquisitus*, also do not seem to have any modern analogues.

664

665 *5.3. Palaeoenvironmental implications*

666

667   The great abundance of verrucate spores in the assemblages suggests the presence of

668 ferns showing a strong affinity with species of the extant genus *Lygodium*, a pantropical

669 climbing schizaealean, concentrated especially in Malaysia and Central America (Kramer in

670 Kramer and Green, 1990). These ferns are typical of warm, humid environments. Their fossil

671 analogues may well have grown along riverbanks or in understories of forests (Van

672 Konijnenburg-Van Cittert, 2002). The composition of the Angeac palynological assemblages

673 is consistent with the previous interpretation of the depositional environment at this site as a

674 swamp, but the absence of marine dinoflagellate cysts apart from the single specimen

675 identified as *Odontochitina imparilis*, suggests very limited connection to the sea (Néraudeau

676 et al., 2012). Nevertheless, this is attested by the relative abundance in unit An2 of brackish

677 ostracods such as *Fabanella boloniensis* (Schudack and Schudack, 2011) and the presence at

678 different levels (An3–4, An1) of a few benthic foraminifers (*Ammocycloloculina* sp.,

679 *Trocholina odukpaniensis*) and echinoid or bryozoan debris (Néraudeau et al., 2012 and

680 unpublished data).

681   No palaeoenvironmental variation has previously been noted for the period of

682 deposition of the sediments comprising units An5–An2. However, the relative composition of

683 Angeac palynological assemblages changes from An4/5 up to An2, the abundance of

684 verrucate spores clearly increasing at the expense of *Classopollis*, which diminishes greatly

685 (Fig. 7). The verrucate spores recovered from unit An2 appear to be generally larger than the

686 specimens recovered from the older units An3 and An4 (Fig. 8).

687   From a sedimentological perspective, the succession of green clay (An5), dark clay

688 (An4) and calcareous conglomerate (An3), and then of silty limestone (An2) and fine sand

689 (An1) implies two successive sequences of increasing energy in the depositional environment,

690 which suggests progressive flooding of the swamp by a river nearby, ending with the

691 establishment of a floodplain. This environmental change could explain the increase of the

692 abundance of verrucate spores up-section, ferns being generally more abundant than

693 gymnosperms in a floodplain (Coiffard et al., 2006, 2007).

694

695 **6. Conclusion**

696

697   Our taxonomic study of the Angeac palynological assemblages provides a rare insight

698 into French palynofloras of Berriasian–Valanginian age. They have previously only been

699 documented from deposits in the Jura mountains, the Vocontian Basin, and on Oléron island

700 (Lantz, 1958; Taugourdeau-Lantz and Donze, 1971; Médus and Mojon, 1991; Kujau et al.,

701 2013), but the Angeac assemblages seem more continental not only because of the abundance

702 of verrucate spores but also owing to the scarcity of marine indicators in the preparations.

703   All of the verrucate spores are attributable to either *Concavissimisporites* or

704 *Trilobosporites*, which in turn are believed to have been produced by ferns showing strong

705 affinities with extant *Lygodium*, a fern genus that typically inhabits warm, humid

706 environments. These ferns could well have grown on the margins of the swamp envisaged by

707 Néraudeau et al. (2012) and been widely dispersed on the developing floodplain.

708   Despite the important work of Bolchovitina (1961, 1971), in the light of recent research

709 on modern representatives of the Lygodiaceae a taxonomic revision of Lower Cretaceous

710 lygodiaceous spores in the Northern Hemisphere is now needed in which both their biological

711 affinities and stratigraphic distribution are taken into account.

712

721
722

723 **References**

724

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940

941

942 **Figure captions**

943

944 **Fig. 1. A**. Map showing the geographical and geological location of Angeac, along with other

945 outcrop localities and boreholes in which "Purbeck" and Wealden-type facies are preserved.

946 Soubran is mentioned in the introduction (Section 1), but is located about 50 km south-east of

947 Royan, and is not, therefore, indicated on the map. GPS coordinates of the site: latitude: 45°

948 37' 59.08" N; longitude: 0° 5' 7.27" W. **B**. Synthetic stratigraphic section of Angeac

949 sedimentological units. The solid circles indicate parts of the section from which the

950 palynological samples were taken (modified after Néraudeau et al., 2012, fig. 1).

951

952 **Fig. 2.** Schematic representation of a verrucate spore showing seven out of ten variables

953 measured to run a PCA. S: maximum diameter; SA, LA: smallest and largest value of the

954 reflex, acute or obtuse angle formed by the two tangents of the starting and arrival points of

955 the arc or curve formed by the outline of the interradial region of a spore; miD: minimum

956 distance from the centre to the edge of the spore (excluding the verrucae); maD: maximum

957 distance from the centre to the edge of the spore (excluding the verrucae); DV: diameter of

958 verrucae on one spore; HV: height of verrucae on one spore; ET: exine thickness.

959

960 **Fig. 3**. Species list of palynomorphs recovered from sedimentological units An2–An4 at

961 Angeac.

962

963 **Fig. 4.** Palynomorphs recovered from Angeac sedimentological units An2–An4.

964 Accompanying data are palynological preparation and slide numbers followed by England

965 Finder coordinates. Authors of taxa not otherwise cited in the text are not listed in the

966 references. Scale bar represents 10 µm. **A**. *Abietineaepollenites* sp.; LEM4-1, E23.4. **B**.

967 *Callialasporites dampieri* (Balme, 1957) Dev, 1961; LEM4-2, R53.0. **C**, **D**. *Classopollis*

968 *torosus* (Reissinger, 1950) Couper, 1958; QPR3669-2; V20.4, K47.3. **E**. *Vitreisporites*

969 *pallidus* (Reissinger) Nilsson, 1958; QPR3669-3, S35.3. **F**. *Podocarpidites ellipticus*

970 Cookson, 1947; LEM4-2, U31.0. **G**. *Aequitriradites verrucosus* (Cookson et Dettmann, 1958)

971 Cookson et Dettmann, 1961; QPR3669-3, W38.1. **H**. *Cyathidites australis* Couper, 1953;

972 LEM4-1, G52.2. **I**. *Microreticulatisporites* sp. cf. *M. diatretus* Norris, 1969; LEM4-1, X45.0.

973 **J**. *Gleicheniidites apilobatus* Brenner, 1963; QPR3669-4, Q20.2. **K**. *Densoisporites*

974 *microrugulatus* Brenner, 1963; LEM4-1, H30.4. **L**. cf. *Foraminisporis wonthaggiensis*

975 (Cookson et Dettmann, 1958) Dettmann, 1963; LEM4-1, E30.2. **M**. *Cicatricosisporites hallei*

976 Delcourt et Sprumont, 1955 *sensu* Burger, 1966; LEM3-2, G39.4. **N**. *Ovoidites spriggi*

977 (Cookson et Dettmann, 1959) Zippi, 1998; LEM3-2, L34.4. **O**. *Retitriletes* sp.; LEM3-2,

978 D33.2. **P**. *Pilosisporites trichopapillosus* (Thiergart, 1949) Delcourt et Sprumont, 1955;

979 QPR3669-3, V31.2.

980

981 **Fig. 5.** Species of *Concavissimisporites* recovered from Angeac sedimentological units An2–

982 An4. Accompanying data are palynological preparation and slide numbers followed by

983 England Finder coordinates. Authors of taxa not otherwise cited in the text are not listed in the

984 references. Scale bar represents 10 µm. **A**, **B**. *Concavissimisporites apiverrucatus* (Couper,

985 1958) Döring, 1965; LEM4-1, D33.1; QPR3669-2, E24.1. **C**, **D**. *Concavissimisporites*

986 *exquisitus* Singh, 1971; QPR3669-3, O27.4, G36.3. **E**. *Concavissimisporites* sp. cf. *C*.

987 *exquisitus* Singh, 1971; LEM2-1, R40.2. **F–H**. *Concavissimisporites ferniensis* (Pocock,

988 1970) Fensome, 1987; QPR3669-2, M53.4, N20.4; LEM2-3, C33.0. **I**. *Concavissimisporites*

989 *robustus* Dörhöfer, 1977; LEM2-3, R34.0. **J**, **K**, **M**. *Concavissimisporites montuosus* (Döring,

990 1964) Fensome, 1987; QPR3669-2, W31.0; LEM1-1, Q49.0; QPR3669-2, T28.1. **L**, **N**.

991 *Concavissimisporites* sp. cf. *C*. *crassatus* (Delcourt et Sprumont, 1955) Delcourt, Dettmann et

992 Hughes, 1963; LEM1-1, Q35.4, B28.4.

993

994 **Fig. 6.** Species of *Concavissimisporites* and *Trilobosporites* recovered from Angeac

995 sedimentological units An2–An4. Accompanying data are palynological preparation and slide

996 numbers followed by England Finder coordinates. Authors of taxa not otherwise cited in the

997 text are not listed in the references. Scale bar represents 10 µm. **A**, **B**. *Concavissimisporites*

998   *verrucosus* (Delcourt et Sprumont, 1955) Delcourt, Dettmann et Hughes, 1963; QPR3669-3,

999   E20.1, V23.0. **C**. *Concavissimisporites* sp. cf. *C. verrucosus* (Delcourt et Sprumont, 1955)

1000   Delcourt, Dettmann et Hughes, 1963; QPR3669-3, D20.4. **D**. *Concavissimisporites uralensis*

1001   (Bolkhovitina, 1961) Fensome, 1987; LEM1-1, Y42.3. **E–G**. *Trilobosporites aornatus*

1002   Döring, 1965; LEM2-1, S32.1; LEM3-2, B32.0; LEM1-1, K28.3. **H**. *Trilobosporites*

1003   *canadensis* Pocock, 1962; LEM1-1, A28.2. **I**. *Trilobosporites aequiverrucosus* Dörhöfer,

1004   1977; QPR3669-3, S30.0.

1005

1006   **Fig. 7.** Palynological composition of Lower Cretaceous sedimentological units An2–An4 at

1007   Angeac: 250 specimens were counted for each sample except for that from the boundary

1008   between An4 and An5, which yielded only 94 specimens.

1009

1010   **Fig. 8.** PCA1 plot of PC1 vs. PC2, with 76.2 % of the total variance extracted, showing the

1011   distribution of specimens according to their occurrence in the sedimentological units. For

1012   explanation of abbreviations, see caption to Fig. 2.

1013

1014   **Fig. 9.** PCA2 plot of PC1 vs. PC2, with 76.2 % of the total variance extracted, showing

1015   clusters corresponding to species of *Concavissimisporites* and *Trilobosporites*. For

1016   explanation of abbreviations, see caption to Fig. 2.

1017

1018   **Fig. 10.** Megaspores from Angeac. **A–D**. *Erlansonisporites* sp. from unit An4, mesofossil

1019   preparation MFP512, SEM stub DJB2014/18, specimen 23, IGR-PAL-5780. **A**. Whole

1020   specimen. **B**. Close-up of part of triradiate flange and adjacent reticulate wall. **C**. Detail of

1021   part of reticulate sculpture showing the structure of the outermost part of the protective wall:

1022   the surface consists of a network of sporopollenin threads, beneath which is an irregular,

perforated layer. **D**. The same at higher magnification. **E**, **F**. *Erlansonisporites* sp., cf.

Erlansonisporites sp. in Batten (1975, pl. 13, fig. 6). Mesofossil preparation MFP422, from

the boundary between An3 and An4, SEM stub DJB2014/20, specimen 1, IGR-PAL-5781. **E**.

whole specimen. **F**. Close-up of reticulate sculpture. Scale bars: A, E: 200 µm; B: 50 µm; C:

10 µm; D: 5 µm; F: 20 µm.

Fig. 11. Megaspores from Angeac, all from mesofossil preparation MFP422, from the

boundary between An3 and An4, SEM stub DJB2014/20, specimens 4 (IGR-PAL-5784), 2

(IGR-PAL-5782) and 3 (IGR-PAL-5783), respectively. **A**, **B**. *Erlansonisporites* sp., cf.

Erlansonisporites sp. in Batten (1975, pl. 13, fig. 6). **A**. Whole specimen in lateral view. **B**.

Close-up of a small part of the reticulate sculpture showing microspores lodged within the

muri of the reticulum. **C**, **D**. Specimen tentatively identified as *Minerisporites* sp., an atypical

representative of this genus (see discussion in text). **C**. Whole specimen in polar view. **D**.

Close-up of perforated surface. **E**, **F**. Another example. **E**. Specimen in lateral view. **F**. Close-

up of undulating distal surface just below equatorial flange (zona). Scale bars: A, C, E: 200

µm; B, D, F: 20 µm.
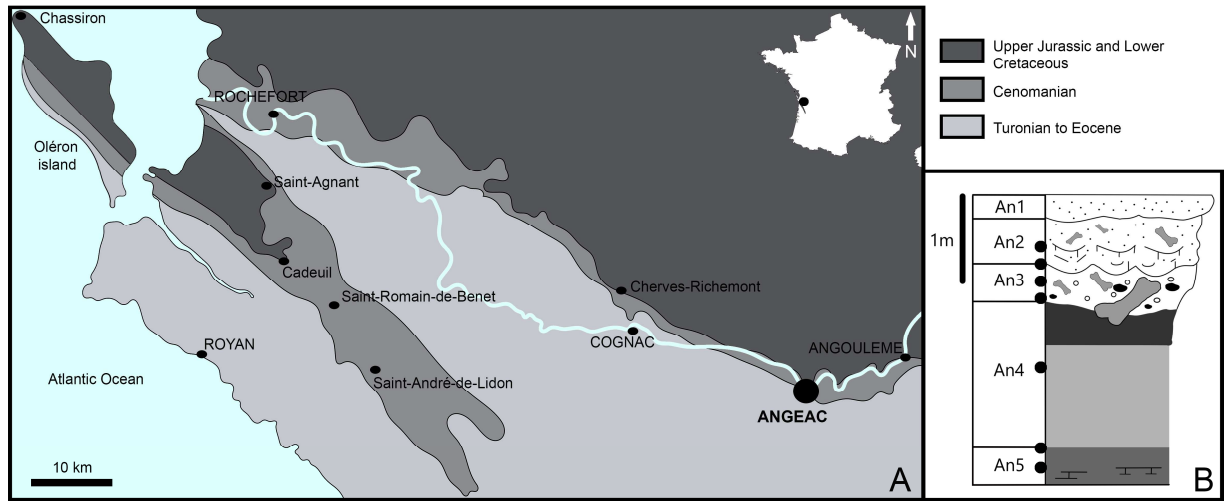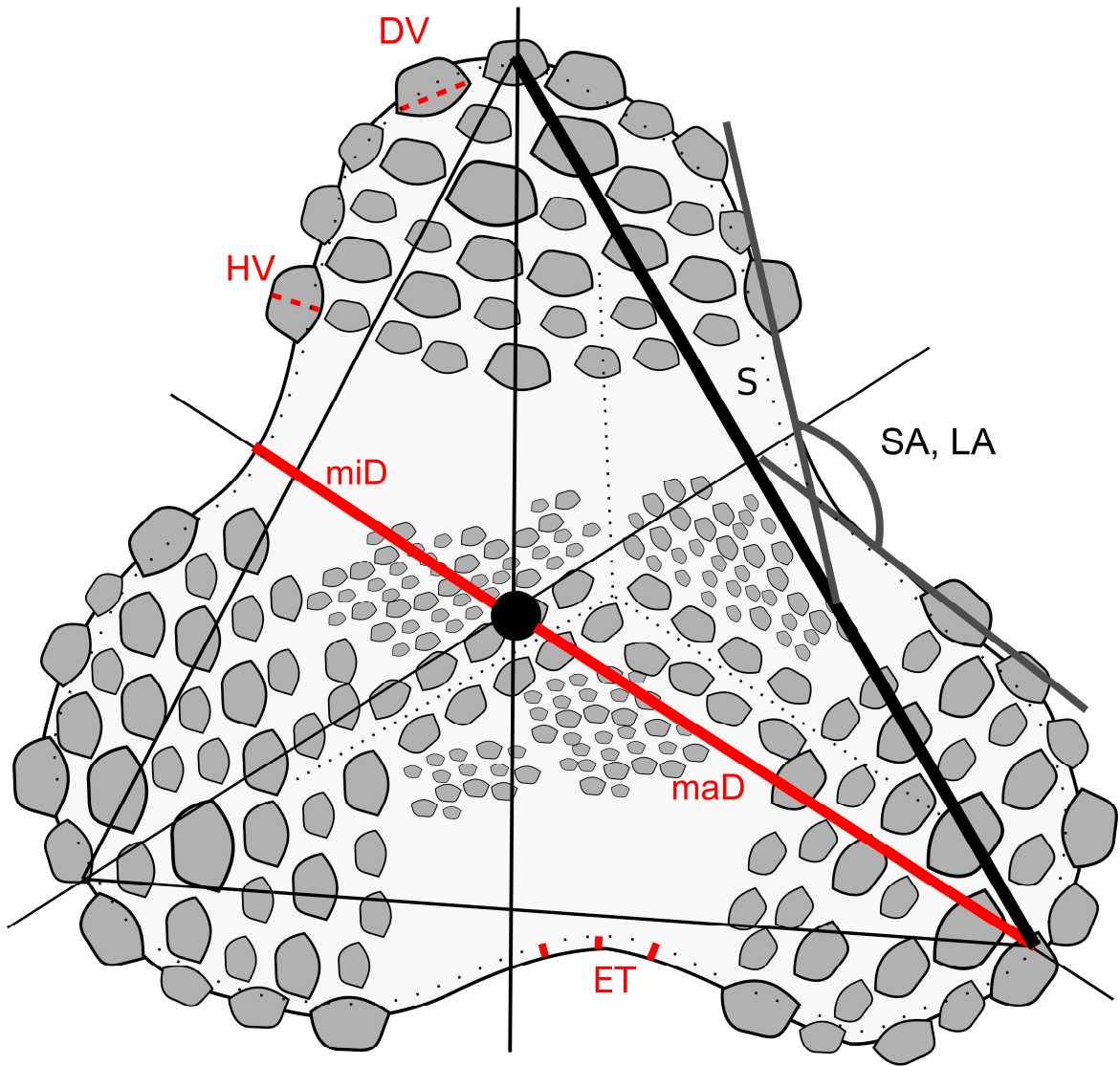
|	An2	An3	An3/4	An4	An4/5	An5
Abietineaepollenites sp.		°				
Aequitriradites verrucosus		°	°	°	°	
Araucariacites australis	°					
Callialasporites dampieri			°			
Cerebropollenites mesozoicus				°		
Cicatricosisporites hallei sensu Burger, 1966		°				
Cicatricosisporites sp. cf. *C. sternum sensu* Burger, 1966		°		°		
Classopollis torosus		°	°	°	°	°
Concavissimisporites apiverrucatus	°		°	°	°	
Concavissimisporites exquisitus	°	°	°	°	°	
Concavissimisporites ferniensis	°	°	°	°		
Concavissimisporites montuosus	°	°	°	°	°	
Concavissimisporites robustus	°	°				
Concavissimisporites sp. cf. *C. crassatus*	°					
Concavissimisporites sp. cf. *C. exquisitus*	°	°		°		
Concavissimisporites sp. cf. *C. montuosus*	°	°				
Concavissimisporites sp. cf. *C. robustus*	°					
Concavissimisporites uralensis	°			°		
Concavissimisporites verrucosus		°		°	°	
Cyathidites australis			°	°		
Cyathidites sp.	°	°	°	°	°	
Deltoidospora sp.	°	°	°	°	°	
Densoisporites microrugulatus			°	°	°	
cf. *Foraminisporis wonthaggiensis*			°			
Gleicheniidites apilobatus	°			°	°	
Microreticulatisporites sp. cf. *M. diatretus*			°			
Ovoidites spriggi		°				
Ovoidites sp.	°	°			°	
Pilosisporites trichopapillosus	°	°	°	°	°	
Podocarpidites ellipticus			°			
Retitriletes austroclavatidites		°			°	
Retitriletes sp.				°		
Trilobosporites aequiverrucosus				°		
Trilobosporites aornatus	°	°		°	°	
Trilobosporites canadensis	°	°	°	°	°	
Trilobosporites sp. cf. *T. aornatus*	°					
Vitreisporites pallidus				°		
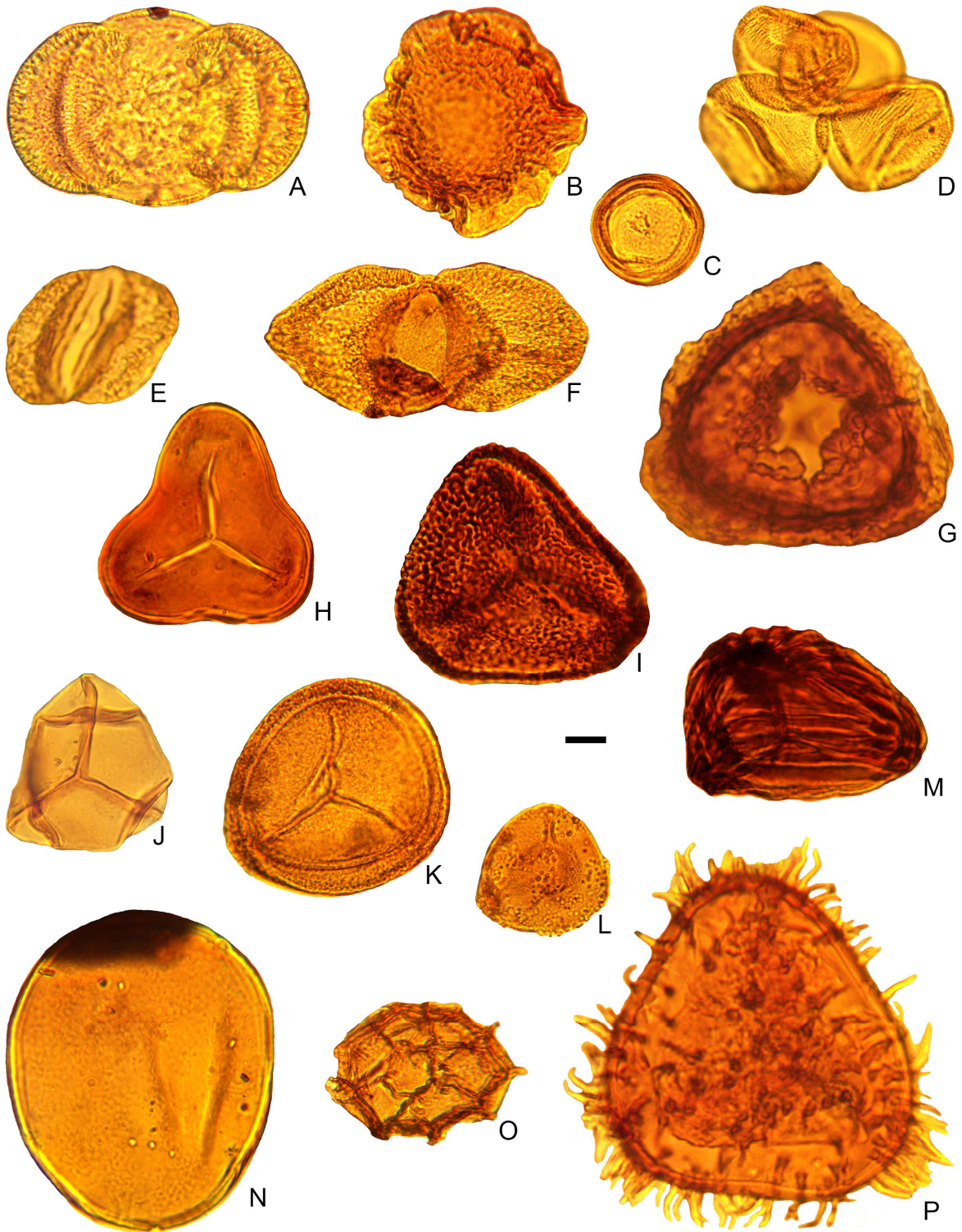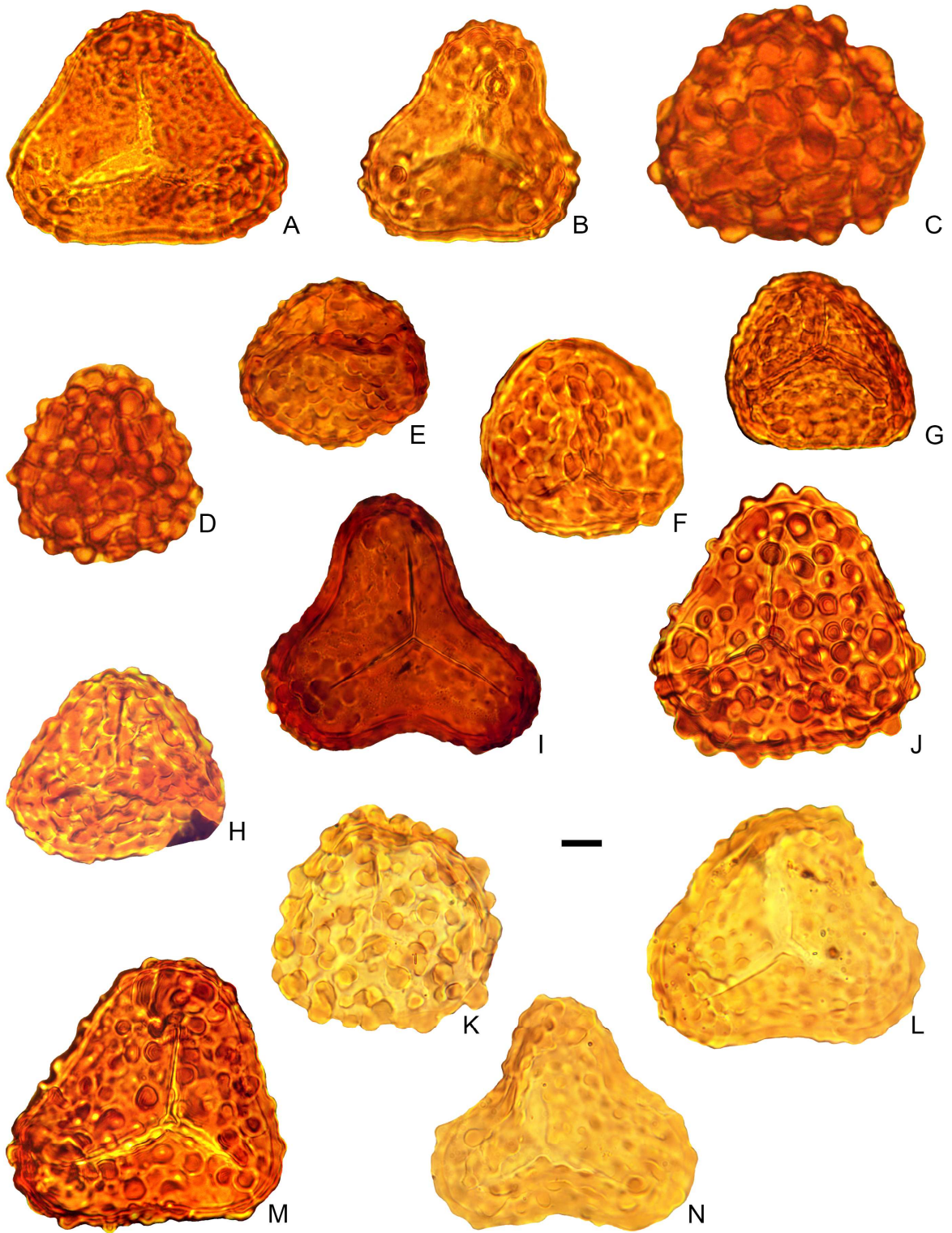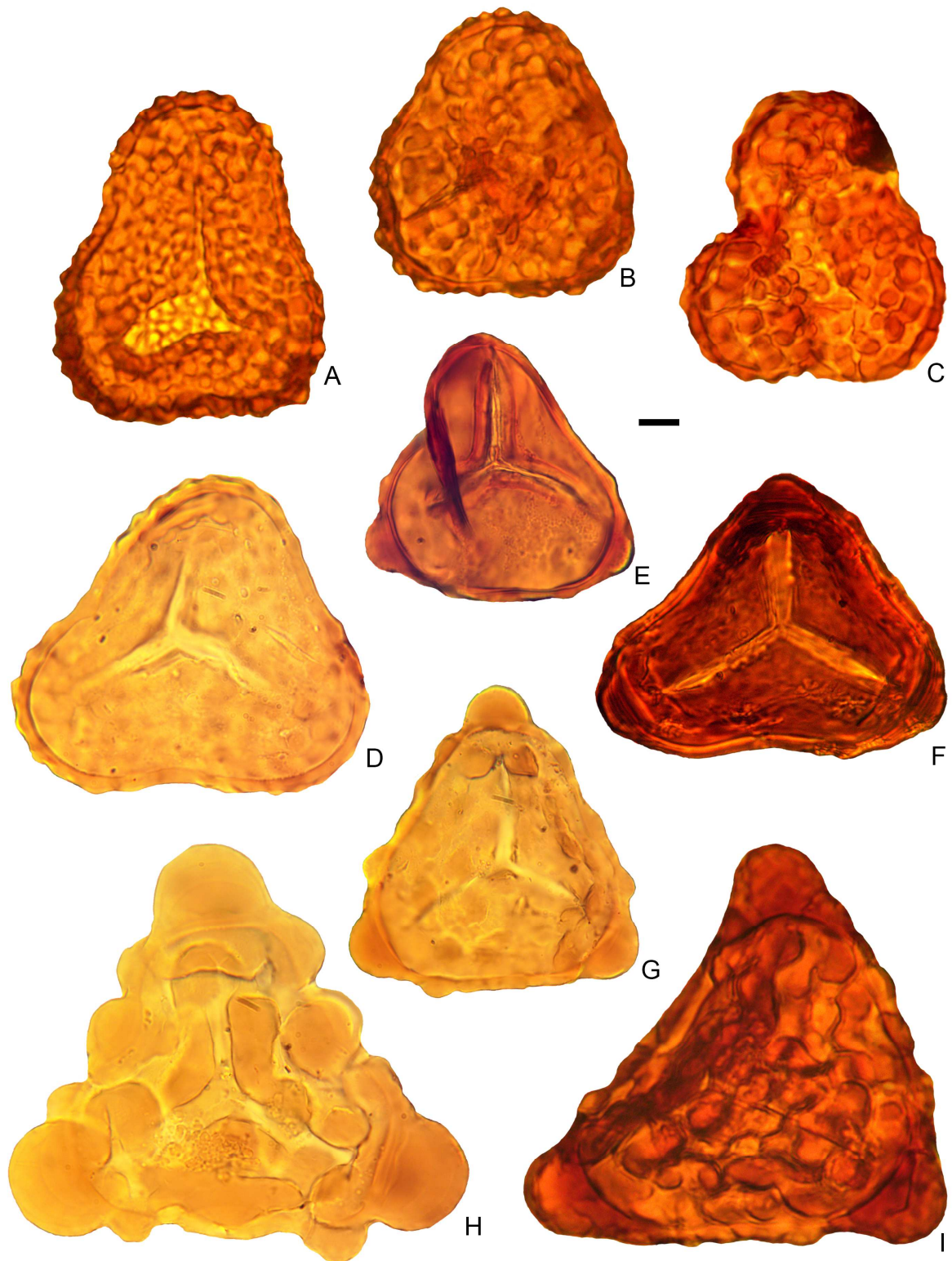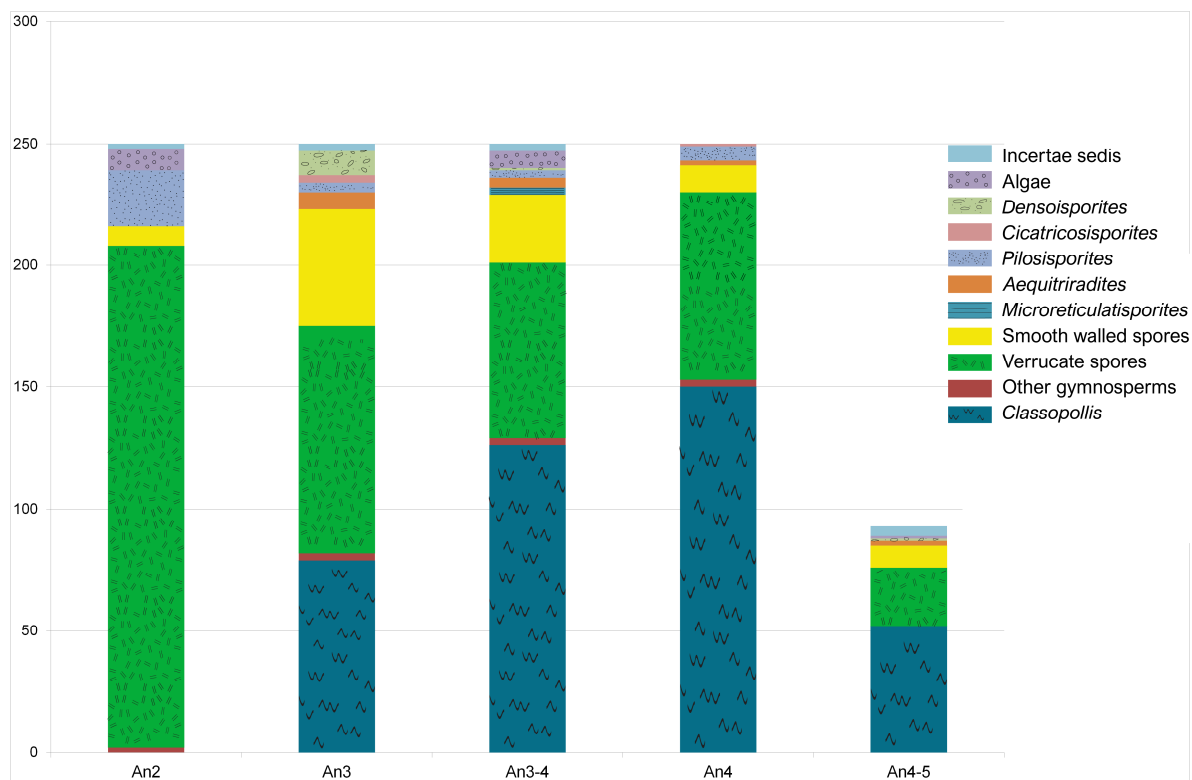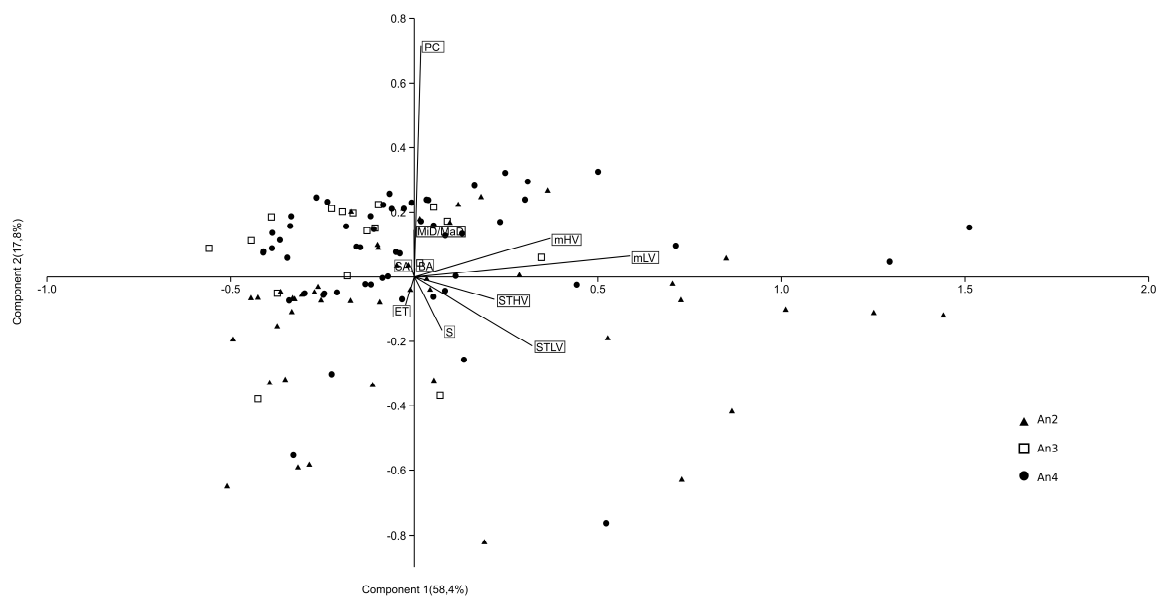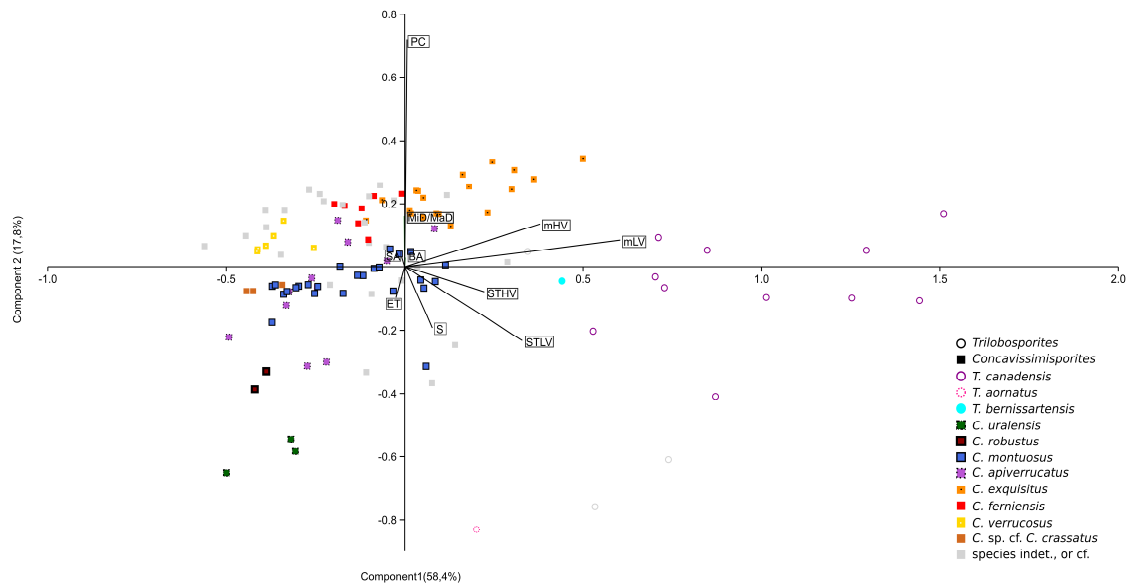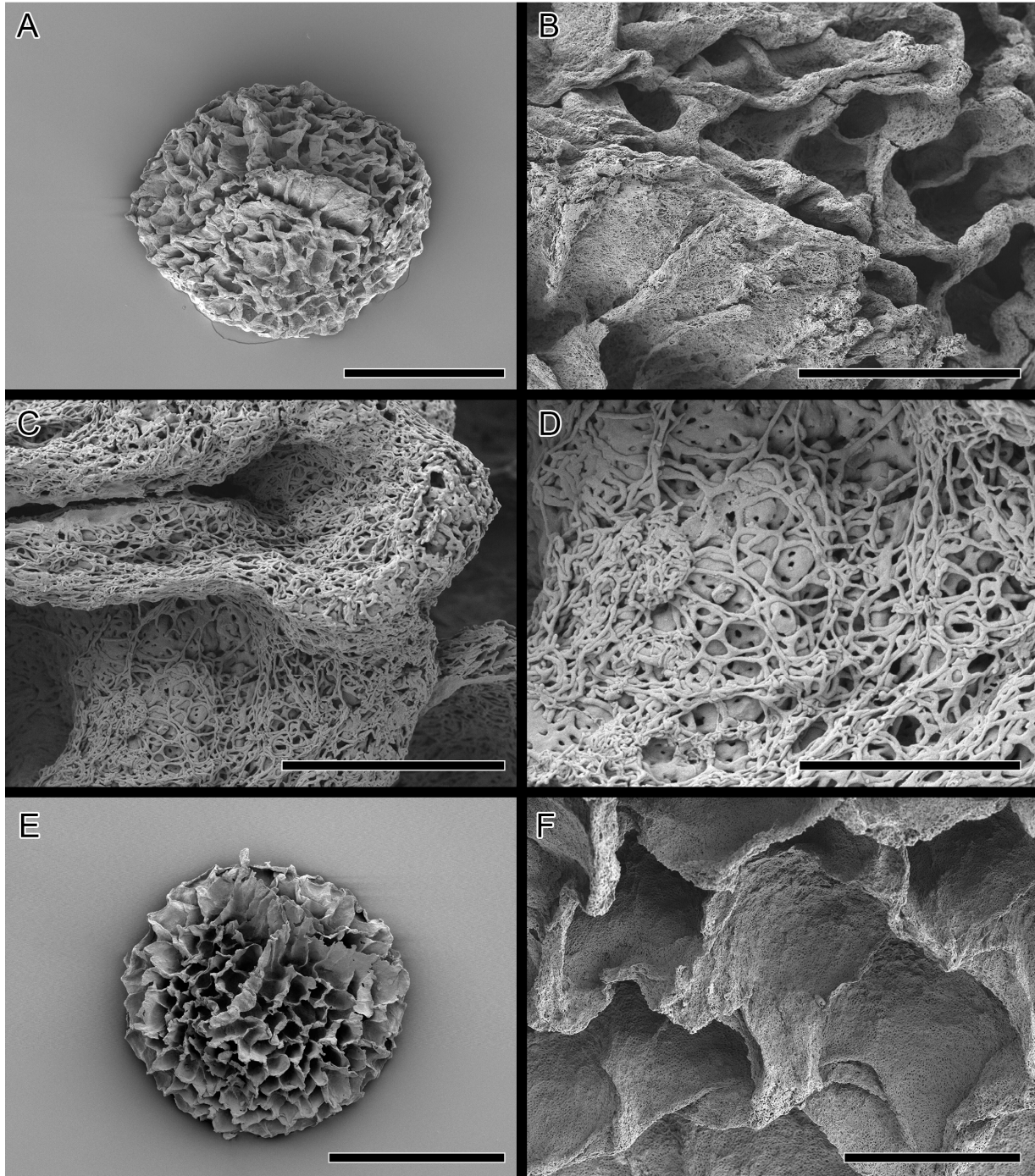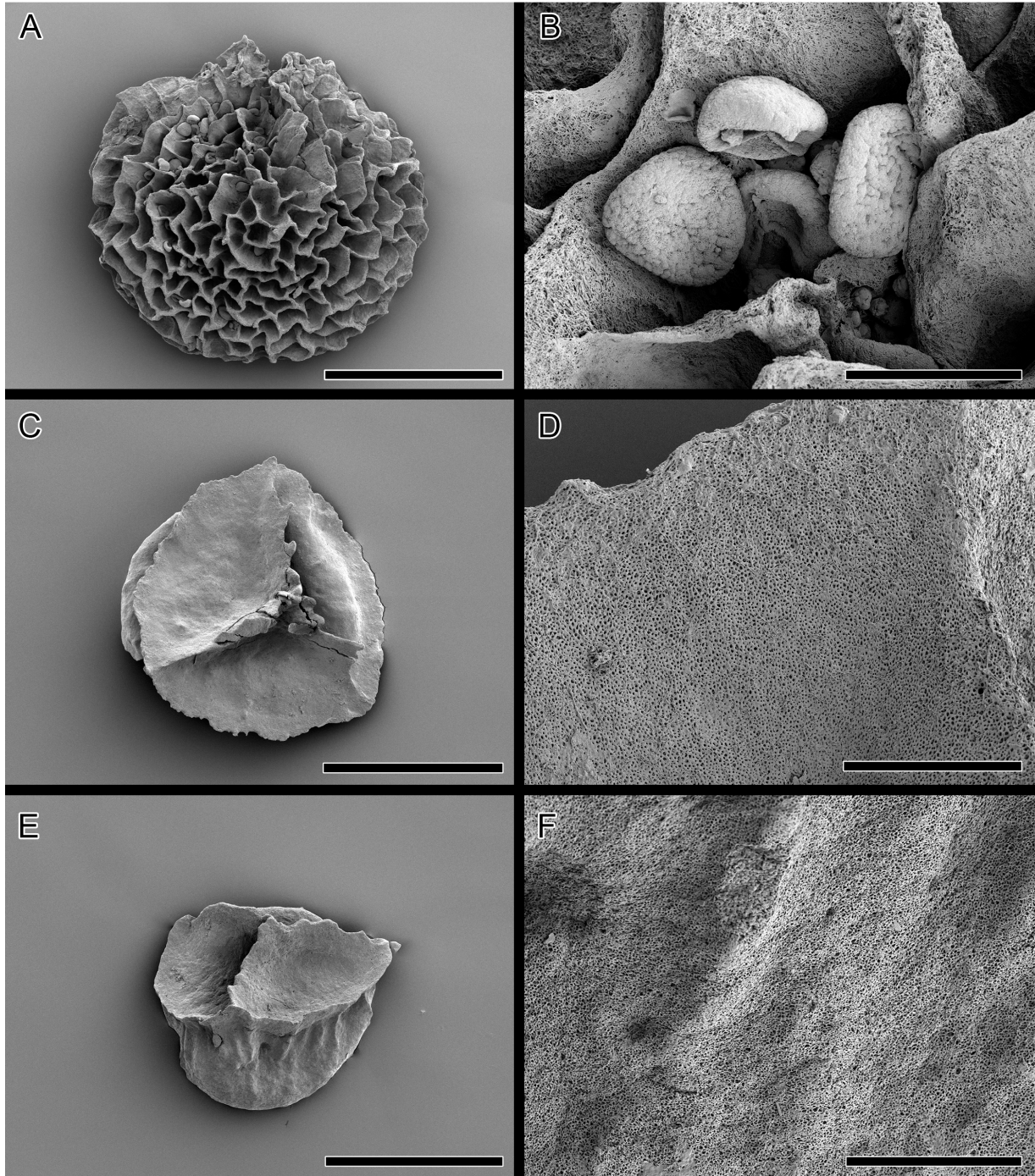
Highlights

Revision of the palynology of Lower Cretaceous strata at Angeac, western France

Deposition is considered to have occurred during the Berriasian–Valanginian

Eight species of verrucate spores were recovered from the non-marine deposits

All are referred to either *Concavissimisporites* or *Trilobosporites*

The taxonomy and biological relevance of the verrucate spores are discussed