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1 **Palynological assemblage from the lower Cenomanian plant-bearing Lagerstätte of**
2 **Jaunay-Clan-Ormeau-Saint-Denis (Vienne, western France): stratigraphic and**
3 **palaeoenvironmental implications**

4
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25

26 **Abstract**

27 We describe here the palynological content from the lower Cenomanian plant-rich site of
28 Jaunay-Clan (Vienne, western France), a site that previously yielded exceptional leaf
29 impressions. Altogether, 184 species of palynomorphs have been identified, and two
30 palynological intervals were recognized in the sedimentary sequence. The lower interval is
31 characterized by the taxonomical and numerical dominance of spores of Gleicheniaceae,
32 Cyatheales, and Anemiaceae, while the upper interval is characterized by an abrupt increase
33 in the abundance of *Classopollis* and the appearance of dinocysts. This shift in the
34 palynological composition, coupled with palaeobotanical observations, is interpreted as
35 reflecting a transition from a calm freshwater environment, with occasional droughts to an
36 environment more open to occasional marine inputs, such as in an inner lagoon.

37 The association of *Tehamadinium coummia*, *Trichodinium spinosum*, *Tricolpites nemejcii*,
38 *Retitricolporites decorosus*, and *Microreticulatiporites sacalii*, coupled with the absence of
39 Normapolles pollen grains, suggests that the Jaunay-Clan assemblage is early Cenomanian in
40 age, corroborating the previous determination based on lithological and palaeontological
41 proxies. However, the Jaunay-Clan palynoflora is considered to be slightly younger than the
42 numerous earliest Cenomanian assemblages described from Charente-Maritime, owing to
43 their resemblance with the palynological assemblages from the mid-lower Cenomanian
44 palynofloras. The paleoflora and palynoflora from Jaunay-Clan are similar to other
45 assemblages found in the upper Albian of Spain (Teruel Province), and in the Cenomanian of
46 France and Czech Republic (Peruc-Korycany Formation, La Buzinie, Archingeay). The
47 combined Jaunay-Clan palynoflora and palaeoflora is considered to be the most diversified
48 Cenomanian palaeobotanical-palynological assemblage described so far in Western Europe.

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51

52 **1. Introduction**

53

54 The study of mid-Cretaceous palaeobotanical and palynological assemblages has been
55 historically essential for our understanding of the rise to dominance of angiosperms (Wing
56 and Boucher, 1998). In Europe, our knowledge of this key interval for angiosperm evolution
57 comes from several Albian-Cenomanian fossil sites with angiosperm-rich palaeofloras and
58 palynofloras, mostly from Czech Republic (Pacltová, 1971; Greguš and Kvaček, 2015;
59 Kvaček and Dilcher, 2000; Kvaček and Friis, 2010; Kvaček et al., 2012, 2016), Spain (Gomez
60 et al., 2009; Sender et al., 2010, 2012), and France (see captions of Fig. 1 for references).

61 In western France, numerous palaeobotanical and palynological investigations have been
62 carried out on Cenomanian deposits since the mid-19th Century, owing to the high abundance
63 of quarries and coastal cliffs. The large majority of the plant macroremains have been
64 recovered from Charente-Maritime and Maine-et-Loire as fossil wood and diverse foliage
65 preserved as impressions or in flints, and the highest diversity of continental palynomorphs
66 has been recorded in Charente-Maritime, Charente and Vendée (Fig. 1, see caption for
67 references). However, very little has been published on localities yielding both plant macro-
68 and microremains, along with their potential affinities (Table 1). The rare deposits containing
69 diversified macrofossil assemblages have so far yielded either a surprisingly poor palynoflora
70 or none at all, such as the plant-bearing clays from the Hucheloup and the Puy-Puy quarries in

71 Maine-et-Loire (Pons, 1979 ; Fleury et al., 2017) and Charente-Maritime respectively
72 (Néraudeau et al., 2005; Peyrot et al., 2005; Table 1). Conversely, deposits that have yielded
73 abundant palynomorphs rarely contain a diversified macroflora, as is the case for the majority
74 of the Cenomanian deposits from Vendée (Azéma and Ters, 1971; Azéma et al., 1972), and
75 for Archingeay-Les Nouillers in Charente-Maritime (Moreau et al., 2017; Table 1).
76 The locality of Jaunay-Clan-Ormeau-Saint-Denis (Vienne) is in this regard a notable
77 exception. During the construction of the LGV SEA railway line in 2012 and 2014,
78 palaeontological investigations were carried out by the team of X. Valentin in the temporarily
79 outcropping lower Cenomanian clay deposits near the village of Jaunay-Clan (Fig. 2, Valentin
80 et al., 2014). They described an assemblage composed of leaf impressions, various bivalves,
81 crustacean, ichnofossils, insect body, wing impressions, and theropod feathers (Valentin et al.,
82 2014; Nel et al., 2015). The astoundingly well-preserved palaeoflora is composed of four
83 genera of ferns, three genera of gymnosperms, and two genera of angiosperms, namely
84 *Ploufolia* and *Eucalyptolaurus* (Valentin et al., 2014), making Jaunay-Clan Ormeau-Saint-
85 Denis (JCO) one of the most diversified Cenomanian plant-bearing localities of France (Table
86 1). The Jaunay-clan locality is thus regarded as a true *Lagerstätte*, according to the excellent
87 preservation and the diversity of its fossil assemblage. In contrast to the other assemblages of
88 western France, the Jaunay-clan yielded a rich palynoflora in combination to its rich
89 macroflora. The stratigraphic, taxonomic, and palaeoecological details of this assemblage are
90 presented herein, in the hope of achieving a clearer understanding of this unique French
91 Cenomanian palaeoenvironment, and more generally of the Cenomanian vegetation of
92 western France.

93

94

95 **2. Geological setting**

96

97 The Jaunay-Clan area is situated about 15 km north of Poitiers, in the southwestern part of the
98 Paris Basin, and is crossed from southeast to northwest by the Clain River (Fig. 2).

99 Outcropping deposits are constituted by Callovo-Oxfordian limestones unconformably

100 overlain by lower Cenomanian deposits (Bourgueil et al., 1976). The contact between the

101 Callovo-Oxfordian limestones and the lower Cenomanian deposits is marked by a ferrallitic

102 alteration surface developed on a palaeo-karst which has been eroded in places (Valentin et

103 al., 2014). The fossiliferous deposits at Jaunay-Clan consist of 1-5 m thick deposits filling up

104 small (~30 m wide) depressions on the post-Oxfordian surface. At the site of sampling, the
105 JCO locality, (Fig. 3), they specifically consist of, from bottom to top:
106 -about 10 cm of massive reddish clay, with numerous calcareous nodules, ferruginous
107 pisolites and cm-thick sand layers;
108 -30 to 40 cm of clast supported, brecciated limestones and ferruginous pisolites, likely
109 reworked from the alteration surface (Valentin et al., 2014);
110 -about 1.20 m of calcareous mudstones interlaminated with millimetre-scale layers of fine-
111 grained sand and organic-rich mudstone, containing plant remains, worm ichnofossils,
112 invertebrates trackway and wings, a theropod feather, crustaceans and bivalves (Valentin et
113 al., 2014).
114 This sequence progressively grades into non-fossiliferous laminated grey siltstones and coarse
115 ferruginous sand and is capped by Lower Cenomanian glauconitic sandstones that can be
116 found regionally (Joubert, 1980).

117

118 **3. Material and Methods**

119

120 *3.1. Extraction method*

121 Ten samples (JCO A–JCO D, JCO 5, JCO 6b, JCO 8, JCO 12, JCO 13, JCO 15) were
122 collected by X. Valentin and A. Cincotta from the JCO locality and analyzed for their
123 palynological content (Fig. 3). Samples were processed at the University of Liege following a
124 method consisting of immersion of 25 g of sample in 15% HCl followed by digestion in 30%
125 HF, and sieving through mesh sizes of 12 and 200 μm , washing between each stage until
126 neutral pH.

127 Another sample was sent to DJB by DN in 2014, and was processed at Aberystwyth
128 University for its microfossil (QPR3670) and mesofossil (MFP513) content, following the
129 extraction procedure of Batten (1999) for the microfossils. The extraction of megaspores
130 involved initial soaking of 100 g of rock in warm water on a hot plate followed by immersion
131 of the sample in a solution of $\text{Na}_4\text{P}_2\text{O}_7$ in order to disaggregate it as much as possible before
132 sieving through a 70 mm mesh to reduce its bulk prior to standard palynological processing
133 using HCl and HF. A few megaspores were recovered, and picked out of the aqueous residues
134 under a stereomicroscope and housed dry in micropalaeontological slides. Some of the
135 specimens recovered were mounted on scanning electron microscope (SEM) stubs to which
136 carbon tabs had been fixed, and sent by DJB to FP for examination under a Phenom table
137 SEM.

138 Seven samples (JCO D, JCO 8, JCO B, JCO 12, JCO A, JCO 13, JCO 15) were shown to be
139 particularly productive. Others are either barren (JCO C) or very poor in fossil content
140 (QPR3670, JCO 5, JCO 6b). The fossil site being no longer exposed, it was not possible to
141 analyze more samples from those levels.

142

143 3.2. *Specimen counts*

144 250 specimens were counted and identified in order to compare the relative abundance of the
145 different botanical families or taxa of higher ranks (see Section 4) for samples JCO B, JCO
146 12, JCO A, JCO 13, JCO 15; note that all the palynomorphs present on the slides (between
147 506 and 4300) were counted and observed in order to note the presence of new species, and
148 produce rarefaction curves (see Section 4). The two other productive palynological
149 preparations, JCO D and JCO 8, yielded 241 and 163 palynomorphs respectively. Sample
150 JCO 5 yielded 15 specimens, and samples JCO 6b and QPR3670 only yielded the freshwater
151 algae *Schizosporis reticulatus*.

152 Rarefaction curves are the product of the relation between the cumulative specific diversity
153 and the number of palynomorphs encountered in a sample. They were established in order to
154 see whether the diversity of the different palynological assemblages described herein is well
155 represented, and if they could be thoroughly compared to each other. The use of rarefaction
156 analyses in Quaternary strata instead of more common diversity indices, such as Shannon's
157 and Simpson's, was extensively discussed by Birks and Line (1992). Rarefaction curves are
158 used to estimate the observed richness of palynomorphs in a sample, and are different from
159 other standard rarefaction analyses used to estimate the potential richness of an incomplete
160 assemblage (Birks and Line, 1992). Their purpose is not to infer an estimate of diversity, but
161 only to observe the actual diversity of the sample; they do not require any mathematical or
162 statistical treatment to be calculated. All the palynological preparations are housed in
163 University of Poitiers (CVCU) under collection numbers UP/JCO log 2013 and log 2014.

164

165 4. Results

166

167 A taxonomic list of species encountered in the productive samples of Jaunay-Clan Ormeau-
168 Saint-Denis is provided in Appendix 1. Authors of species that are listed in Appendix 1 are
169 not indicated in the text.

170

171 The palynomorphs recovered from the Jaunay-Clan Ormeau-Saint-Denis (JCO) palynoflora
172 are generally well preserved, and only a few specimens were too distorted for reliable
173 identification. Altogether, 184 species of megaspores, spores, pollen grains, dinocysts and
174 algae were recovered from the seven productive samples of JCO, with a specific diversity
175 ranging from 34 to 84 species (Appendix 1). The rarefaction curves show that a plateau is
176 usually reached between 700 and 1000 specimens when enough specimens are present, as for
177 JCO A, JCO B, and JCO 15 (Fig. 4). However, the richest and most diversified assemblage
178 JCO 13 reaches a plateau at 3500 specimens, a little more than 60% of the entire specific
179 diversity being recovered at 1000 specimens (Fig. 4). The other assemblages (JCO D, JCO 8,
180 JCO 12) were not rich enough to reach a plateau, but the slopes of their lines are similar to
181 those of JCO A and JCO B, except for JCO D, which is steeper. Thus, the comparative
182 specific diversity of those three assemblages has to be considered cautiously (Fig. 5A2).
183 Spores are the most diversified group with 103 species of bryophyte (Pl. I.I–I.N), lycophyte
184 (Pl. I.O–T; Pl. II.A–II.Q), and filicophyte (Pls. I.IR–V.H) related forms (Fig. 5A3; see
185 Appendix 2 for botanical affinities of palynological genera). Gymnosperm pollen spectrum is
186 composed of 33 species (Pls. V.I–V.Q, VI.T), and is taxonomically dominated by bisaccate
187 pollen grains related to Pinaceae and Podocarpaceae (Appendix 1; Fig. 5C2). Angiosperms
188 (Pls. VI.R, VI.S, VII.A–VII.R) are represented by 31 species of Chloranthaceae,
189 ?Chloranthaceae/?Ceratophyllaceae, probable monocots or more basal angiosperms, eudicots,
190 and angiosperms of uncertain botanical affinities (Appendix 1; Fig. 5D2). They are
191 taxonomically dominated by the eudicots (Appendix 1; Fig. 5D2). Two palynological
192 intervals can be inferred from the relative abundance of the different taxa (Fig. 5A1–D1).

193

194 *JCO D–JCO 8: spore dominated assemblages*

195 The oldest assemblages are characterized by the numerical dominance of spores, representing
196 more between 60% and 70% of the whole assemblages (Fig. 5A1). They are dominated by
197 forms belonging to the Gleicheniaceae (20–25%), ascribed to the genera *Gleicheniidites* (Pl.
198 II.T; Pl. III.A–III.C) and *Clavifera* (Pl. II.S), and by spores of the Cyatheales (20%), ascribed
199 to the genera *Cibotiumspora* (Pl. IV.K), *Cyathidites* (Pl. IV.L), and *Deltoidospora*
200 (Appendices 1, 2). The spores associated with the Anemiaceae represent 5% of the whole
201 assemblages, but are the most diversified group, with ten and five species of
202 *Appendicisporites* (Pl.III.K–III.S), *Cicatricosisporites* (Pl. IV.A–IV.F),
203 *Costatoperforosporites* (Pl. IV.G), and *Distaltriangulisporites* (Pl. IV.H), including three
204 species only recorded in those two assemblages: *Appendicisporites fucosus*, A. cf. A.

205 *potomacensis*, and *Distaltriangulisporites perplexus* (Appendix 1). Lycophytes also represent
206 ca. 5% of the assemblages, mostly represented by species belonging to *Camazonosporites*
207 (Pls. I.O–II.G). The other spore groups are less abundant, less diversified, and are represented
208 by species belonging to *Microreticulatisporites* (Filicophyte indet.; Pl. IV.S, IV.T),
209 *Laevigatosporites* (Polypodiales; Pl. IV.M) and *Triporoletes* (Bryophyta; Pl. I.L–I.N).
210 The gymnosperm spectrum is dominated by bisaccate pollen grains ascribed to the
211 Pinaceae/Podocarpaceae (Pls. V.J–VI.A), and identified as *Pristinuspollenites*, *Parvisaccites*,
212 and *Rugubivesiculites*. Gymnosperm pollen grains are taxonomically well balanced between
213 species of *Araucariacites* (Pl. VI.B), *Balmeiopsis* (Araucariaceae; Pl. VI.C), *Classopollis*
214 (Cheirolepidiaceae; Pl. VI.G), *Inaperturopollenites* (Cupressaceae-including Taxodiaceae; Pl.
215 VI.H), *Equisetosporites* (Pl. VI.L), *Eucommiidites* (Gnetophyta; Pl. VI.M, VI.N), *Afropollis*
216 (Pl. VI.K), and *Vitreisporites* (Caytoniales).
217 Eight species of angiosperm pollen grains were recovered from the first interval, especially
218 from JCO D, two species having only been recovered from JCO 8 (Fig. 5D2; Appendix 1).
219 They are composed of one species of *Clavatipollenites* (Chloranthaceae; Pl. VII.A), one
220 species of *Pennipollis* and *Transitoripollis* (?Chloranthaceae/?Ceratophyllaceae; Pls. VI.O,
221 VI.P, VII.B, VII.C), two species of *Monosulcites* (probable monocots or more basal
222 angiosperms; Pl. VI.Q), one species of *Nyssapollenites* and *Retitrescolpites* (eudicots, Pl.
223 VII.D, VII.F, VII.G), and one species of *Dichastopollenites* (uncertain botanical affinities; Pl.
224 VII.P–VII.R). One species, identified as *Nyssapollenites albertensis* (Pl. VII.D) was
225 recovered from JCO D, but is absent from the younger assemblages. Angiosperm pollen
226 grains always represent less than 10% of the whole assemblage (Fig. 5A1). Dinoflagellates
227 are absent, and only a few fresh water algae have been recovered (Appendix 1).
228 These two assemblages are overall less diverse than the younger ones (Fig. 5A2), but this
229 difference cannot be taken into account because their potential maximum diversity has not
230 been reached (Fig. 4).

231

232 *JCO B–JCO 15: pollen dominated assemblages*

233 An abrupt change of the general composition of the palynoflora is observed from JCO B
234 onward. While still taxonomically dominated by spores, the abundance of gymnosperm pollen
235 grains rises significantly, representing between 50% and 70% of the whole assemblages (Fig.
236 5A1, 5A2). A great increase of the abundance of *Classopollis* (Cheirolepidiaceae) is observed,
237 representing from less than 10% in the oldest assemblages to 40-50% of the whole
238 assemblages from JCO B onward (Fig. 5C1). The pollen grains of Araucariaceae and

239 Cupressaceae (including Taxodiaceae) become more diversified, with the appearance of
240 *Callialasporites dampieri* (Pl. VI.D) and *Uesuguipollenites callosus* (Pl. VI.F) in JCO 13 and
241 JCO 15, and *Perinopollenites halonatus* (Pl. VI.I) and *Taxodiaceapollenites hiatus* (Pl. VI.J)
242 from JCO B to JCO 15 (Appendix 1; Fig. 5C2). Several species of *Podocarpidites* (Pl. V.Q),
243 *Cerebropollenites* (Pl. VI.E), and *Cedripites* (Pl. V.M) also appear in this interval, along with
244 representatives of the genus *Alisporites*, of uncertain gymnosperm botanical affinities (Pl.
245 V.K, V.L).

246 Along with the increasing abundance of gymnosperm pollen grains, the spore content
247 significantly declines in comparison with the first interval, representing between 25% and
248 40% of the assemblages. However, the distribution of the different botanical groups stays
249 fairly similar to that of the first interval (Fig. 5B1); only a slight decrease in the abundance of
250 Cyatheales (ca. 5%) and Anemiaceae (ca. 2,5%) is noted (Fig. 5B1). Spores are still the most
251 diversified group, represented by 20 to 45 species for each assemblage of JCO B–JCO 15
252 (Fig. 5A2, 5B2). Several genera appear in this interval, namely *Cingutritetes*, *Stereisporites*
253 (Bryophyta; Pl. I.I–I.K), *Densoisporites*, *Foveosporites*, *Leptolepidites*, *Lycopodiacidites*,
254 *Wilsonisporites* (Lycophyta; Pls. II.I, IV.O, IV.P, II.K, II.L, II.Q), all representatives of
255 Osmundaceae (Pl. II.R), *Matonisporites* (Matoniaceae; Pl. III.G), *Ischyosporites*
256 (Lygodiaceae; Pl. III.H), *Crybelosporites* (Marsileaceae; Pl. IV.J), *Lophotritetes*,
257 *Foveotritetes*, *Patellasporites*, *Scopusporis*, and *Undulatisporites* (Filicophytes indet.; Pls.
258 II.J, V.C–V.F, III.J, V.G; Appendix 1).

259 Only few angiosperm pollen grains (Pl. VI.O–VI.T; Pl. VII.A–VII.R) were encountered,
260 almost always representing less than 10% of the whole assemblages, except in the youngest
261 assemblage JCO 15, in which 12% of the assemblage consists of angiosperm grains (Fig.
262 5A1). The assemblages JCO A and JCO 13 are the most diversified, with 12 and 16 species
263 recovered respectively, mostly represented by eudicots for JCO 13 (Fig. 5D2).

264 Representatives of the genus *Stellatopollis* (monocots or more basal angiosperms; Pl. VI.R,
265 VI.S) were only encountered in this interval. In addition, grains of *Dichastopollenites* (Pl.
266 VII.P–VII.R), of uncertain botanical affinity, become more diversified and better represented
267 than in the first interval (Ap; Fig. 5D2). The effective abundance of the angiosperms (Fig.
268 5D1) shows that ?Chloranthaceae/ ?Ceratophyllaceae content declines while the tricolpate
269 forms belonging to the eudicots are progressively better represented. The abundance of the
270 monosulcate grains linked to probable monocots or more basal angiosperms (Pl. VI.O–VI.S)
271 is variable (Fig. 5D1). A diversification of eudicot content is also visible along the succession,
272 with six out of 14 species encountered only in the JCO 13 and JCO 15 assemblages (Table 1).

273 Several species belonging to *Phimopollenites* (Pl. VII.E), *Striatopollis* (Pl. VII.J, VII.I),
274 *Retitrescolpites* (Pl. VII.F), *Retitricolporites* (Pl. VII.H), *Tricolpites* (Pl. VII.L–VII.O), and
275 *Rousea* (Pl. 7G) were only encountered in these two assemblages (Appendix 1).
276 Parallel to the abrupt increase in the abundance of *Classopollis*, this interval is also
277 characterized by the appearance of dinocysts (Pl. I.A–I.H), absent in the first interval. Their
278 relative abundance is very low, representing between 1% and 2% of the whole assemblages.
279 They are mostly represented by *Surculosphaeridium longifurcatum* (Pl. I.E), but nine species
280 were recorded altogether, with a peak of diversity in the JCO 13 assemblage which yielded
281 five species (Appendix 1). Occasional freshwater algae have also been observed, mostly
282 belonging to *Schizosporis* (Pl. VII.S, VII.T). They are more diversified in the JCO B–JCO A
283 assemblages than in the youngest assemblages.

284

285 A small assemblage of megaspores was recovered from preparation MFP513, including
286 *Minerisporites* sp. (Pl. VIII.A), *Minerisporites* cf. sp. 1 *sensu* Batten in Batten et al. (2010)
287 (Pl. VIII.B), *Paxillitriteles* sp. (Pl. VIII.C), and *Molaspora* cf. *lobata* (Pl. VIII.D). A specimen
288 attributed to *Arcellites reticulatus* (Pl. IV.I) has been found amongst the miospore
289 preparations.

290

291

292

293

294

295 **5. Discussion**

296

297 *5.1. Biostratigraphic implications*

298

299 The sedimentary sequence of Jaunay-Clan is part of a formation that has been dated to the
300 lower Cenomanian (Louail et al., 1978; Alvarez, 1980; Joubert, 1980; Valentin et al., 2014),
301 notably based on the presence of *Acompsoceras essendiense* in an hardground layer overlying
302 the glauconious sandstones, indicative of uppermost lower Cenomanian or lowermost middle
303 Cenomanian in Normandy and Sarthe (Louail et al., 1978). However, the Jaunay-Clan
304 locality, located below these glauconious sandstones, has never been properly dated and could
305 be older; moreover, no this upper Cenomanian biostratigraphic age has never been tested in
306 the light of dinoflagellate and palynomorph assemblages.

307 Most of the dinoflagellates recovered from the the JCO locality are relatively long-ranging
308 species, thus not biostratigraphically informative. For example, *Spiniferites ramosus* is often
309 the dominant form in Early Cretaceous assemblages, ranging from the early Valanginian to at
310 least the Campanian. *Surculosphaeridium longifurcatum*, which is the dominant form in the
311 JCO assemblage, ranges from the Early Cretaceous to the Santonian (Costa and Davey, 1992),
312 and *Achomosphaera ramulifera*, while mostly encountered from Cenomanian onward, has
313 been recorded several times in Aptian-Albian deposits of the Paris Basin (Davey and Verdier,
314 1971; Fauconnier, 1975). However, the presence of *Tehamadinium coummia* and
315 *Trichodinium spinosum* agrees with an age of deposition no younger than early Cenomanian.
316 They both are usually encountered in Lower Cretaceous deposits, mostly Albian, but the
317 presence of one or the other has been noted in lower Cenomanian deposits of Charente-
318 Maritime (Peyrot et al., 2019) and Alberta (Bloch et al., 1999).

319 The continental palynomorphs include *Tricolpites nemejci*, which is a fairly common form in
320 the JCO palynoflora, and is considered to appear during the early Cenomanian (Doyle and
321 Robbins, 1977; Hochuli et al., 2006). Less abundant tricolpate forms include *Nyssapollenites*
322 *albertensis*, which is not known until the uppermost Albian (Singh, 1971), and
323 *Retitricolporites decorosus*, which has only been recorded in Cenomanian strata of North
324 America (Singh, 1983; Lupia, 1999). *Microreticulatiporites sacalii* has been suggested as a
325 stratigraphic marker of the upper Albian-Cenomanian in northern America and Europe (Ravn,
326 1986), but Ludvingson et al. (2010) indicate that this species seems to be restricted to
327 Cenomanian strata of Nebraska. In France, this species has been almost exclusively
328 encountered in Cenomanian deposits (Deák and Combaz, 1967; Azéma and Ters, 1971;
329 Médus and Triat, 1969; Peyrot et al., 2005, 2019), but has also been encountered in deposits
330 considered as latest Albian in Charente-Maritime (Dejax and Masure, 2005). Elsewhere, this
331 species is also very common in Cenomanian deposits but has been recorded in upper Albian
332 deposits in Hungary and Wyoming (Juhász, 1975; Ravn, 1995). The common presence of *M.*
333 *sacalii* and *M. urkuticus* at Jaunay-Clan would rather suggest an early Cenomanian rather than
334 an upper Albian age. The absence of Normapolles is worth being noted, as this group does not
335 appear before the mid-Cenomanian in France (Azéma et al., 1972).

336 Thus, the presence of *Tehamadinium coummia*, *Trichodinium spinosum*, *Tricolpites nemejci*,
337 *Retitricolporites decorosus*, and common *Microreticulatiporites sacalii*, coupled with the
338 absence of Normapolles pollen grains suggests that the Jaunay-Clan assemblage is no older
339 nor younger than lower Cenomanian, corroborating the previous age determination of the
340 deposits. In addition, this assemblage is more similar to the assemblages recovered from the

341 B1-B2 lithological subunits of Charente-Maritime and Charente than the slightly oldest ones
342 recovered from the A1-A2 lithological subunits (see Section 5.4. for further explanation). It
343 could be possible that the Jaunay-Clan strata were deposited simultaneously with the clay
344 levels of the subunits B1 or B2 (mid-lower Cenomanian) described in Charente-Maritime (for
345 further details concerning the Cenomanian lithological units, see Moreau, 1993a-b, and
346 Néraudeau et al., 1997).

347

348

349 *5.2. Palaeoenvironmental reconstruction*

350

351 The first palynological interval (JCO D to JCO 8) described here-above is characterized by
352 the numerical and taxonomical dominance of fern spores. The majority of extant ferns
353 flourishes in wet conditions, and are generally used as indicators of humid settings. The high
354 spore content likely represents the local vegetation: being generally heavier than pollen
355 grains, spores tend to be dispersed less widely, commonly being deposited close to their
356 producers (Ferguson, 1995). This is supported by the several well-preserved fern
357 macroremains recovered in the lower part of the succession (Valentin et al., 2014; Fig. 3).
358 Other plant remains, such as the Nymphaeales-related *Ploufolia*, were only recovered from
359 clay layers situated below the conglomerate layer rich in limestone breccias and reworked
360 pisolites, corresponding to the first palynological interval (Valentin et al., 2014). The
361 outstanding preservation of these freshwater taxa suggests a calm depositional environment,
362 which can be associated with a lacustrine-type environment (Sender et al., 2010). The
363 presence of the megaspore *Arcellites*, ascribed to the Marsileaceae, supports the hypothesis of
364 a calm freshwater environment, modern Marsileaceae being water ferns, growing in
365 seasonally wet or aquatic habitats (Zavialova and Batten, 2018; Appendix 2).

366 Dominant fern spores belong to Cyatheales, Gleicheniaceae and Anemiaceae families.

367 Modern Cyatheales are concentrated at the tropics, but can occupy varied habitats (Kramer in
368 Kramer and Green, 1990; Appendix 2). Their high abundance at Jaunay-Clan agrees with a
369 globally warm mid-Cretaceous climate (Kujau et al., 2013). The dominance of *Gleicheniidites*
370 is fairly common in Lower and mid-Cretaceous continental deposits of Western Europe, and
371 has already been noted several times in France (Herngreen, 1971; Peyrot et al., 2005, 2019).

372 Modern Gleicheniaceae are considered as opportunistic, pioneering tropical to subtropical
373 plants, adapted to long droughts, growing in unstable habitats including dry forests and

374 wetlands that occasionally dry out (Coiffard et al., 2007; Mehlreter et al., 2012; Kujau et al.,

375 2013; Appendix 2). Representatives of the Anemiceae usually develop under warm and humid
376 environments, and their Mesozoic relatives may have grown along riverbanks, or as
377 understorey in forests (Dettmann and Clifford, 1991; Van Konijnenburg-Van Cittert, 2002).
378 However, some species of Anemiceae are adapted to more arid conditions, such as found in
379 heathlands, and may tolerate partial desiccation (Proctor and Tuba, 2002; Schrank, 2010;
380 Appendix 2).

381 Owing to their high dispersal potential, the relatively high content of bisaccate pollen grains is
382 not necessarily informative regarding the local depositional environment, but they can provide
383 valuable information about general palaeoenvironmental settings. Bisaccate pollen grains
384 from the first interval are mostly represented by Podocarpaceae, Pinaceae being absent.
385 Modern Podocarpaceae usually grow on mountain areas of tropical to subtropical regions,
386 with a preference for humid settings (Schrank, 2010; Kujau et al., 2013; Appendix 2). The
387 presence of *Vitreisporites*, recovered from the JCO B assemblage, corroborates the prevalence
388 of humid conditions, as inferred by Abbink et al. (2004), who suggested that this member of
389 the Caytoniales group may have grown on the transition between floodplain
390 and backswamp peats under warm conditions (Appendix 2).

391 The palaeocology of the mid-Cretaceous angiosperms from Western Europe has been
392 extensively discussed by Peyrot et al. (2019). Based on the wide range of possible habitats of
393 Cretaceous representatives of Lauraceae (e.g. *Ecalyptaulorus depreii*, abundantly found at
394 Jaunay-Clan) and Chloranthaceae (e.g. *Clavatipollenites*), they conclude that Cenomanian
395 angiospermous assemblages could have developed within several types of plant communities,
396 including aquatic, frequently disturbed and more stable hygrophilous and xerophilous
397 associations.

398 Thus, the macropalaeontological and palynological information covering the lower
399 palynological interval of the Jaunay-Clan succession suggest that the depositional settings
400 were likely to have occurred in a calm freshwater environment, potentially submitted to
401 occasional droughts, such as a floodplain or a pond, where abundant ferns and a few aquatic
402 and terrestrial angiosperms could have grown along the banks under warm and relatively
403 humid general conditions.

404

405 The upper palynological interval (JCO B to JCO 15) is largely dominated by gymnosperm
406 pollen grains. The composition of the assemblages indicates an abrupt palaeoenvironmental
407 change, highlighted by the marked increase of grains belonging to *Classopollis*, along with
408 the appearance of dinocysts. *Classopollis* were produced by the extinct members of the

409 Cheirolepidiaceae family. Members of the Cheirolepidiaceae can develop in a wide range of
410 habitats, but are mostly associated with arid low-lying water margins environments under
411 subtropical or tropical climate (Alvin, 1982; Schrank, 2010; Appendix 2). Numerous
412 cheirolepidaceous macroremains display xeromorphic adaptations which have been
413 interpreted to reflect dry and/or saline environments (Pons et al., 1980; Mendes et al., 2010).
414 This sudden increase is associated with the appearance and progressive increase of dinocysts
415 from JCO B onward, which would suggest an opening to very occasional marine inputs, the
416 dinocysts only representing less than 2% of the assemblages. The macrofossils recovered
417 from the Jaunay-Clan succession show a similar trend, with only well-preserved angiosperm
418 leaves and fern fronds at the base of the succession, and the progressive appearance of more
419 brackish organisms such as the bivalve *Brachidontes* sp., and various worm traces from JCO
420 8 onward (Valentin et al., 2014; Fig. 3).

421 The recovery of a few specimens of *Densoisporites* in the youngest assemblages, along with
422 the slight increase of the abundance and diversity of *Alisporites* grains could infer the
423 existence of a distant tidally-influenced habitat (Abbink et al., 2004; Appendices 1, 2).
424 However, too few grains were encountered to consider this observation as a strong
425 palaeoenvironmental argument. The appearance of several species of inaperturate pollen
426 grains, including *Taxodiaceapollenites hiatus*, *Perinopollenites halonatus* and
427 araucariaceous related forms (Appendix 1) suggests the existence of conifer forests linked to
428 wet lowlands, such as in low salinity back-swamp environments, based on the ecological
429 requirement of some modern Cupressaceae (Schrank, 2010; Peyrot et al., 2019; Appendix 2).
430 Moreover, the recurring presence of bryophytic species of *Stereisporites* and *Cingutritetes*
431 from JCO B to JCO 15 suggests the possible existence of low-oxygenation related
432 environments, such as in swamps or peat bogs (Kujau et al., 2013; Appendices 1, 2). Thus, the
433 palaeontological and palynological composition corresponding to the second palynological
434 interval suggests progressive establishment of inner lagoonal-type or backswamp
435 environment, becoming increasingly open to very occasional marine inputs, and characterized
436 by a more xeric vegetation dominated by plants producing pollen grains attributed to the
437 Cheirolepidiaceae and Cupressaceae families (including Taxodiaceae), associated with a
438 similar fern and angiosperm community as described for the first palynological interval. This
439 type of environment, periodically flooded by marine or brackish waters, is known to be
440 colonized by mangrove vegetation in tropical and subtropical latitudes (Peyrot et al., 2019).
441 Batten (1974) and Gomez et al. (2008) already suggested that Cenomanian vegetation from

442 Western Europe and notably Charentes (western France) could be related to mangroves or
443 salt-marsh environments, which could also be the case of the Jaunay-Clan vegetation.

444

445

446

447 5.3. Botanical relationships between macro- and microfossils

448

449 Authors of species that are listed in Appendix 1 are not indicated in the text.

450

451 Abundant fern fronds have been recovered from the Jaunay-Clan clay deposits, and have been
452 identified as *Ruffordia goeppertii* (Dunker) Seward, *Cladophlebis* sp., *Sphenopteris* sp., and
453 *Osmundophyllum* sp. (Valentin et al., 2014; Table 1).

454 The dispersed spores produced by *Ruffordia goeppertii* have been previously documented
455 with details (Hughes and Moody-Stuart, 1966; Deng, 1998). They belong to the anemiaceous
456 genus *Cicatricosisporites*, and several species have been described as associated dispersed
457 spores, namely *Cicatricosisporites goeppertii* (Seward) Groot et Penny, *Cicatricosisporites*
458 *aralica* (Bolchovitina) Brenner, and *Cicatricosisporites australiensis* (Cookson) Potonié.

459 Because the specific epithet applied to *C. goepperti* and *C. aralica* also refers to a form genus
460 of foliage, those species cannot be considered as valid; *C. australiensis* is thus considered as
461 the effective name of the taxon (Ames and Spackman, 1981; Deng, 1998). No form identified
462 as *C. australiensis* has been recovered from the Jaunay-Clan samples, but fairly similar
463 palynomorphs to the holotypes of *C. goeppertii* and *C. aralica* have been encountered, and
464 identified as *Cicatricosisporites hughesii* (Pl. IV.C). Specific differences of anemiaceous
465 Cretaceous dispersed spores are often based on slight morphological variations, and do not
466 take into account a large spectrum of possible intraspecific variability, resulting in numerous
467 overlapping diagnoses. It is then possible that the spores identified as *C. hughesii* could
468 belong to the same biological species as those identified as *C. australiensis*.

469 Reproductive structures of a Cretaceous fern recovered from Canada, and identified as
470 *Cladophlebis dunkeri* (Schimper) Seward have been observed by Radforth and Woods (1950).
471 They described associated cicatricose trilete spores, which Balme (1995) treated as
472 *Cicatricosisporites ludbrookii*. Although more typical of older assemblages, this species has
473 been recorded herein in the JCO 13 assemblage (Table 1; Pl. IV.D), and could well have been
474 produced by similar forms as the foliage identified as *Cladophlebis* sp. However, Valentin et
475 al. (2014) specify that this specimen of *Cladophlebis* sp. belongs to the family Osmundaceae.

476 The potential corresponding dispersed spores could then belong to the only osmundaceous
477 species recorded, *Todisporites major* (Pl. II.R), which could be the case for *Osmundophyllum*
478 sp.

479 It is quite difficult to discuss the nature of the spores produced by the specimen identified as
480 *Sphenopteris* sp., because of the wide use of this morphogenus for various foliage types from
481 both Palaeozoic and Mesozoic assemblages. Spores as varied as *Deltoidospora*,
482 *Cicatricosisporites*, *Apiculatasporites*, and *Leiotriletes* have been identified as dispersed
483 spores of foliage of *Sphenopteris* (Balme, 1995).

484 Greguš and Kvaček (2015) described pseudodichotomous leaf fronds which they linked to
485 Gleicheniaceae species and called *Gleicheniaceaphyllum kurrianum*. No spores were
486 recorded *in situ*, but one can infer that *Gleicheniidites* producers may have resembled this
487 form, and based on the great abundance of *Gleicheniidites*, similar specimens could well be
488 found in the Jaunay-Clan area in due course.

489 The gymnosperm foliage genera have been identified as *Brachyphyllum*, *Dammarophyllum*,
490 and *Pagiophyllum*. Numerous reproductive parts associated with *Brachyphyllum* have been
491 found with *in situ* pollen grains. They were attributed to the araucariaceous genera
492 *Araucariacites* (Balme, 1995), which is fairly abundant at Jaunay-Clan, and *Callialasporites*,
493 which has only been found as a single specimen. Those two genera could actually belong to
494 the same biological species, as noted by Van Konijnenburg-van Cittert (1971), who found
495 both fossil-genera within pollen sacs attributed to a Jurassic species of *Brachyphyllum*.

496 The morphogenus *Pagiophyllum* is often considered to belong to the family
497 Cheirolepidiaceae. Several species of the fertile organ *Classostrobus* have been found with
498 both leafy shoots of *Pagiophyllum* and associated pollen grains, always belonging to
499 *Classopollis* (Thévenard, 1993; Balme, 1995), which is the dominant form at Jaunay-Clan. It
500 is interesting to note that the common Cenomanian cheirolepidiaceous foliage species
501 *Frenelopsis alata* (Feistmantel) Knobloch, which has been found in Cenomanian deposits
502 from Maine-et-Loire associated with *in situ* *Classopollis* pollen grains (Pons, 1979), has not
503 been recorded from the Jaunay-Clan deposits. This is probably because this form is associated
504 with fairly rigorous xeric conditions due to the immediate proximity of the coast line (Pons et
505 al., 1980), while the Jaunay-Clan assemblage was probably formed in a more proximal
506 environment. The great abundance of *Classopollis* could then be explained by the presence of
507 *Pagiophyllum*. The morphogenus *Dammarophyllum* sp. has been linked to either the
508 Araucariaceae or Podocarpaceae (Kvaček, 2003), but no fertile organs or pollen grain have
509 been found in connection with the leafy stems so far.

510 Valentin et al. (2014) recorded two species of angiosperm foliage. *Eucalyptolaurus depreii*
511 Coiffard et al. is considered to belong to the Lauraceae family, but no pollen grains have been
512 associated with this species (Coiffard et al., 2009). Pollen produced by modern Lauraceae can
513 be of four morphological types: A. spheroidal, apolar, spinulose; B. oblate-peroblate, isopolar,
514 slightly to strongly verrucate; C. spheroidal, apolar, strongly verrucate/spinuloid; D.
515 spheroidal, para-isopolar, striate (Van der Merwe et al., 1990). No pollen grains meeting those
516 criteria have been recognized in the Jaunay-Clan palynoflora. The resulting lack of pollen
517 evidence for Lauraceae in Late Cretaceous and Cenozoic floras that are rich in lauraceous
518 leaves has been long recognized by paleobotanists, and might be related to the preferential
519 degradation of the associated pollen grains (Peyrot et al., 2019).
520 Finally, *Ploufolia* sp. is believed to be an aquatic angiosperm belonging to the Nymphaeales,
521 which genus has been first described in upper Albian deposits of Spain (Sender et al., 2010).
522 No pollen grain has been associated with this species, and fossil pollen grains of Nymphaeales
523 are very scarce. Modern Nymphaeaceae are associated with zonosulculate pollen grains
524 characterized by their echinate, baculate, or gemmate ornamentation (Jones and Clarke,
525 1981), but no pollen grains meeting those criteria have been recognized in the Jaunay-Clan
526 palynoflora. It has to be noted that the association of *Ploufolia* with Nymphaeales is uncertain,
527 since it is much smaller than leaves of modern Nymphaeaceae and lacks fine venation that
528 might support this (Doyle, comm. pers.). *Ploufolia* could well belong to another basal
529 angiosperm group which has yet to be determined, and associated pollen grains could in fact
530 be present in the Jaunay-Clan association.

531

532

533 *5.4. Comparisons with Cenomanian assemblages from France and neighboring areas*

534

535 The taxonomic composition of the JCO palynoflora has been compared to 12 other
536 Cenomanian palynological assemblages recovered from lowest Cenomanian (lithological
537 subunits A1-A2), mid-lower Cenomanian (lithological subunits B1-B2), and middle
538 Cenomanian strata of western France (Table 2; Appendix 3; see Fig. 1 for location of the
539 studied sites and references). The JCO assemblage is most similar to the assemblages
540 recovered from the mid-lower Cenomanian lithological subunits B1-B2 from Charente-
541 Maritime and Charente, displaying the highest similarity index (Table 2). While less
542 diversified than the oldest and youngest assemblages, the four palynofloras considered herein
543 share between 45% and 62% of common species with the JCO assemblage. However, the

544 associated macroremains recovered from Fouras and Aix Island are far less diversified than
545 the Jaunay-Clan paleoflora, gathering only a few specimens identified as *Frenelopsis alata*,
546 *Glenrosa* sp., *Brachyphyllum* sp., and several wood fragments (Gomez et al., 2004;
547 Néraudeau et al., 2009; Table 1). No angiosperm remains were identified.

548 The JCO assemblage is also very similar to the Archingeay Les-Nouillers and Cadeuil
549 assemblages, which were recovered from the lower Cenomanian A2 subunit of Charente-
550 Maritime (Peyrot et al., 2019). They share between 40 and 50 common species, which are
551 well balanced between the miospores, gymnosperm pollen grains, and angiosperm pollen
552 grains (Appendix 3; Table 2). Their high similarity index could however be related to the
553 great diversity of palynomorphs identified at these two sites, which have been abundantly
554 sampled in comparison to the other Cenomanian outcrops from Charente-Maritime and
555 Charente (Peyrot et al., 2019). The Archingeay-Les Nouillers palynoflora is associated with a
556 fairly rich macroflora, including various siliceous gymnosperm remains and leaves of
557 *Eucalyptolaurus depreii* (Néraudeau et al., 2002; Dejax and Masure, 2005; Gomez et al.,
558 2008; Coiffard et al., 2009; Moreau et al., 2014, 2017; Table 1). Most of the macroflora is
559 preserved in flints, but a few specimens of fossil wood and angiosperm leaves have been
560 found as impressions/compressions. They are less diverse and well-preserved than the Jaunay-
561 Clan paleoflora, mostly including portions of *Frenelopsis* cuticles and wood remains (Moreau
562 et al., 2017). Another exceptional lower Cenomanian angiosperm leaf-bearing site has been
563 discovered in the strata ascribed to the lithological subunit A2, at Puy-Puy (Charente-
564 Maritime; Fig. 1; Le Diouren, 2005, unpublished; Table 1). However, while the underlying
565 layers have yielded numerous spores and pollen grains, the plant-bearing clay levels were
566 proven to be barren of any palynomorphs (Peyrot et al., 2005; pers. obs.).

567

568 The JCO palynological assemblage shares the least similarities with the middle Cenomanian
569 palynofloras from Vendée, Mayenne, and Maine-et-Loire, presenting a similarity index of
570 only 0.14 (Fig. 1; Table 2). However, they share the highest number of exclusive common
571 species, mostly represented by species of *Camarozonosporites* recovered from both Jaunay-
572 Clan and La Garnache (Appendix 3). Also, specimens attributed to *Molaspora lobata* and
573 similar forms were only recovered from Ecoflant quarries and Jaunay-Clan (Pl. VIII.D),
574 while absent from lower Cenomanian mesofossil assemblages of Charente-Maritime (Fig. 1;
575 Batten et al., 2010). On other aspects, these assemblages are quite different from the JCO
576 assemblage, mainly because of the increasing diversity of angiosperm pollen grains,
577 especially Normapolles (Juignet and Médus, 1971; Azéma and Ters, 1971; Azéma et al.,

578 1972; Néraudeau et al., 2017; Appendix 3). The composition of the Hucheloup palynoflora
579 differs greatly from the JCO assemblage (Table 2), but a similar paleoflora has been
580 recovered from the associated strata. It is composed of several taxa of plant preserved in
581 impressions/compressions, ascribed to filicophytes, gymnosperms and angiosperms (Fleury et
582 al., 2017; Table 1). While differing by the dominance of *Frenelospsis alata*, which is absent
583 from JCO, and the poorer state of preservation of the macroremains, the Hucheloup paleoflora
584 is the most similar plant assemblage to JCO recovered from France so far.

585

586 Elsewhere in Europe, numerous mid-Cretaceous outcrops have yielded abundant and
587 diversified angiosperm-rich plant assemblages (see Coiffard et al., 2006 for overview), but
588 only a few studies have acknowledged their associated palynoflora. The Peruc-Korycany
589 Formation (Bohemian massifs, Czech Republic) yielded numerous plant remains (Kvaček and
590 Dilcher, 2000), some of which have already been compared to the JCO paleoflora (Valentin et
591 al., 2014). Numerous associated angiosperm pollen grains have also been described, including
592 several forms recovered from the JCO assemblage, such as *Tricolpites nemejicii* and *T.*
593 *vulgaris* (Pactlová, 1971, 1977, 1978). However, the overall palynological assemblage differs
594 by the high abundance of Normapolles pollen grains, the Peruc-Korycany Formation being
595 considered as middle Cenomanian (Pactlová, 1978).

596 No Cenomanian macro- and microflora has been described from Spain and Portugal, but both
597 the palaeobotanical and palynological assemblages from Jaunay-Clan present numerous
598 similarities with the uppermost Albian Spanish flora recovered from Teruel Province. They
599 both yielded very well-preserved angiosperm macro and micro-remains, including *Plouffolia*
600 (Sender et al., 2012). The Teruel Province palynoflora is however less diversified, and lacks
601 typical Cenomanian stratigraphic markers, such as *Tricolpites nemejicii* and *Retitricolporites*
602 *decorosus* (Sender et al., 2012). The same comment applies for the latest Albian palynoflora
603 from the Maestrazgo Basin (Spain), which is in every other way very similar to the JCO
604 palynoflora (Villanueva-Amadoz et al., 2011). The presence of leaves macroremains was
605 noted by Villanueva-Amadoz et al. (2011), but their taxonomical content has yet to be
606 described. Numerous other studies on well-preserved Spanish Cretaceous plant macroremains
607 have been published, but most of them deal with Early Cretaceous assemblages (Alvarez-
608 Ramis et al., 1981; Gomez et al., 1999, 2000, 2001, 2002a). Their associated palynological
609 content has sometimes been independently described (Peyrot et al., 2007; Barrón et al., 2015).
610 Finally, several middle to upper Cenomanian palaeofloras have been described from Veneto
611 and Campania regions (Italy; Gomez et al., 2002b; Bartiromo et al., 2019), but these are

612 mostly composed of *Frenelopsis* remains, and no associate palynoflora was presented. The
613 association of the Jaunay-Clan continental palynoflora and palaeoflora is thus considered to
614 be the most diversified Cenomanian combined palaeobotanical and palynological assemblage
615 described from Western Europe so far.

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617

618

619 **Conclusion**

620

621 The Jaunay-Clan botanical assemblage is exceptional as it gathers both a rich and diverse
622 macro- and palynoflora, allowing us to sketch a more complete picture of the French
623 Cenomanian vegetation than previously known. The seven productive palynological
624 assemblages show slight environmental changes, grading from a calm freshwater environment
625 to an environment more open to occasional marine inputs, in a backswamp or an inner lagoon.
626 These changes mark the beginning of the Cenomanian-Turonian transgression, progressively
627 flooding emerged areas in a southwestern-northeastern direction (Moreau, 1993a-b, 1996).
628 This hypothesis corroborates a slightly younger age for the Jaunay-Clan assemblage than the
629 age of the assemblages recovered from the lower Cenomanian of Charente-Maritime and
630 Charente, except for the localities of Fouras and La Buzinie (Peyrot et al., 2019). Other mid-
631 Cretaceous assemblages from Europe yielded either rich macroflora or relatively rich
632 palynoflora, but at the exception of Bohemian assemblages, both types of fossils are rarely as
633 well-preserved and/or diversified, making the association of the Jaunay-Clan continental
634 palynoflora and palaeoflora the most diversified Cenomanian assemblage with both
635 palaeobotanical & palynological data described so far in Western Europe.

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638

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646

647

648 **References**

649 *References only mentioned in Appendix 2 are also listed hereafter.*

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1036 a Cenomanian deposit in western France: occurrence, sporoderm ultrastructure and
1037 evolutionary relationships. *Grana* 57, 325–344.

1038

1039

1040

1041 **Figure captions**

1042

1043

1044 **Figure 1.** Comparative table of the specific diversity of plant macro- and microfossils
1045 recovered from Cenomanian deposits of departments from western France in previous work,
1046 along with geographical location of the studied sites and their respective references. The

1047 location of Jaunay-Clan is indicated in red. The data are based on several publications, listed
1048 and numbered hereafter. ¹Azéma, 1979; ²Azéma et al., 1972; ³Azéma et al., 1981; ⁴Azéma et
1049 al., 1990; ⁵Batten et al., 2010; ⁶Berthelin and Pons, 1999; ⁷Boura et al., 2019; ⁸Boureau and
1050 Veillet-Bartoszewska, 1955; ⁹Coiffard et al., 2009; ¹⁰Crié, 1890; ¹¹Deák and Combaz, 1967;
1051 ¹²Fleury et al., 2017; ¹³Gomez et al., 2004; ¹⁴Juignet and Médus, 1971; ¹⁵Le Diouron, 2005
1052 (unpublished); ¹⁶Méon et al., 2004; ¹⁷Moreau, 1993a-b; ¹⁸Moreau et al., 2014; ¹⁹Moreau et al.,
1053 2017; ²⁰Néraudeau et al., 2002; ²¹Néraudeau et al., 2005; ²²Néraudeau et al., 2009;
1054 ²³Néraudeau et al., 2013; ²⁴Néraudeau et al., 2017; ²⁵Perrichot, 2003; ²⁶Peyrot et al., 2005;
1055 ²⁷Peyrot et al., 2019; ²⁸Pons, 1979; ²⁹Pons et al., 1980; ³⁰Robin et al., 2018; ³¹Valentin et al.,
1056 2014; ³²Azéma and Ters, 1971; ³³Durand and Ters, 1958; ³⁴Lecointre and Carpentier, 1939;
1057 ³⁵Alvárez-Ramis et al., 1981; ³⁶Néraudeau et al., 2003.

1058

1059 **Figure 2.** Geological map of the Jaunay-Clan area based on the BRGM geological map
1060 1/50000 n°567 –Vouneuil-sur-Vienne (Bourgueil et al., 1976), with location of the outcrop
1061 (red star).

1062

1063 **Figure 3.** Stratigraphic section of Jaunay-Clan-Ormeau-Saint-Denis outcrop, with location of
1064 recovered samples and main features.

1065

1066 **Figure 4.** Rarefaction curves of the palynological assemblages recovered from the Jaunay-
1067 Clan-Ormeau-Saint-Denis productive samples. Numerical data are provided in Appendix 3.

1068

1069 **Figure 5.** Plots of the abundance and diversity of the Jaunay-Clan-Ormeau-Saint-Denis
1070 palynological assemblages, based on the botanical affinities of the various spore and pollen
1071 morphotypes (Appendix 2). **A.** Abundance and diversity of the main groups of palynomorphs.
1072 **B.** Abundance and diversity of bryophytic and fern spores. **C.** Abundance and diversity of
1073 gymnosperm pollen grains. **D.** Number of specimens and diversity of angiosperm pollen
1074 grains, which were not abundant enough to be displayed in a comparative relative abundance
1075 plot. Abundance plots are based on N=250 (except for JCO 8, N=163). Diversity plots are
1076 based on N=163–4100. Species list and numerical data are provided in Appendices 1, 3.

1077

1078 **Plate I.** Dinoflagellate cysts, bryophyte and lycophyte spores recovered from the Jaunay-
1079 Clan-Ormeau-Saint-Denis samples. Accompanying data are palynological preparation
1080 followed by England Finder coordinates. Authors of taxa are noted in the species list (Table

1081 1). Scale bars represent 10 μm . **A.** *Achomosphaera ramulifera*, JCO 13, N26.4. **B.**
1082 *Cribooperidinium* sp., JCO 13, N43.1-2. **C, D.** *Spiniferites ramosus*, JCO 13, L52.0. **E.**
1083 *Surculosphaeridium longifurcatum*, JCO B, S42.0. **F.** *Tehamadinium coummia*, JCO 12,
1084 E29.3. **G.** *Trichodinium castanea*, JCO 15, W36.3. **H.** *Trichodinium spinosum*, JCO 13,
1085 W38.1. **I.** *Cingutriteles clavus*, JCO B, R41.0. **J.** *Stereisporites antiquasporites*, JCO A,
1086 W28.4. **K.** *Stereisporites* sp., JCO 15, X47.0. **L.** *Triporoletes cenomanianus*, JCO 8, H42.4.
1087 **M.** *Triporoletes reticulatus*, JCO 13, T33.3. **N.** *Triporoletes simplex*, JCO 8, J34.0. **O, P.**
1088 *Camarozonosporites ambigens*, JCO A, S38.2. **Q.** *Camarozonosporites annulatus*, JCO D,
1089 E41.4. **R.** *Camarozonosporites hammenii*, JCO A, M31.3. **S.** *Camarozonosporites insignis*,
1090 JCO B, N44.4-2. **T.** *Camarozonosporites rudis*, JCO A, S35.3.

1091

1092 **Plate II.** Lycophyte and filicophyte spores recovered from the Jaunay-Clan-Ormeau-Saint-
1093 Denis samples. Accompanying data are palynological preparation followed by England Finder
1094 coordinates. Authors of taxa are noted in the species list (Table 1). Scale bars represent 10
1095 μm . **A, B.** *Camarozonosporites* sp. A, JCO A, H42.3; JCO B, X39.0. **C, D.**
1096 *Camarozonosporites* sp. B, JCO 13, D31.4; JCO B, H37.2. **E, F.** *Camarozonosporites*
1097 *triradius*, JCO A, Q44.0; JCO 13, J46.1. **G.** *Camarozonosporites wrenni*, JCO 15, X38.0. **H.**
1098 cf. *Coronatispora valdensis*, JCO 8, V39.3. **I.** *Densoisporites microrugulatus*, JCO 13, P29.4.
1099 **J.** cf. *Lophotriteles babsae* or basal Angiosperm pollen grain?, JCO 12, N35.2. **K.**
1100 *Lycopodiacidites wardii*, JCO 13, V43.0. **L.** aff. *Lycopodiacidites tortus* sensu Peyrot et al.,
1101 2019, JCO 13, V34.2. **M.** *Retitriteles expansus*, JCO 13, R36.1. **N.** *Retitriteles* sp. cf.
1102 *Reticulatasporites dupliexinoux*, JCO 13, W33.2. **O.** *Sestrosporites pseudoalveolatus*, JCO 12,
1103 H45.0. **P.** *Staplinisporites caminus*, JCO 13, N28.4. **Q.** cf. *Wilsonisporites coronarius*, JCO
1104 D, C27.0. **R.** *Todisporites major*, JCO 12, P38.0. **S.** cf. *Clavifera triplex*, JCO D, Q27.3. **T.**
1105 *Gleicheniidites* sp. A, JCO D, U27.2.

1106

1107 **Plate III.** Filicophyte spores recovered from the Jaunay-Clan-Ormeau-Saint-Denis samples.
1108 Accompanying data are palynological preparation followed by England Finder coordinates.
1109 Authors of taxa are noted in the species list (Table 1). Scale bars represent 10 μm . **A–C.**
1110 *Gleicheniidites senonicus*; JCO 15, S40.0; JCO 13, R34.1; JCO 13, Y41.1. **D.**
1111 *Dictyophyllidites equiexinus*, JCO B, O35.1. **E.** *Dictyophyllidites harrisii*, JCO 5, S48.0. **F.**
1112 *Dictyophyllidites trianguliformis*, JCO D, W33.1. **G.** *Matonisporites cooksoniae*, JCO A,
1113 P32.0-2. **H.** *Ischyosporites punctatus*, JCO 13, V33.3. **I.** *Trilobosporites trioreticulosus*, JCO
1114 A, Q34.4. **J.** *Scopusporis lautus*, JCO A, O39.1. **K.** *Appendicisporites bilateralis*, JCO B,

1115 O32.1. **L.** *Appendicisporites bifurcatus*, JCO 8, H46.0. **M.** *Appendicisporites erdtmanii*, JCO
1116 13, V35.3. **N.** *Appendicisporites fucosus*, JCO 5, H50.3. **O.** *Appendicisporites potomacensis*,
1117 JCO B, P38.2. **P.** *Appendicisporites robustus*, JCO 15, W48.0. **Q.** *Appendicisporites sellingsii*,
1118 JCO 15, P32.0. **R.** *Appendicisporites tricornitatus*, JCO 13, H33.1. **S.** *Appendicisporites*
1119 *undosus*, JCO 13, W38.0. **T.** *Ceratosporites* sp. cf. *C. equalis*, JCO 12, C31.0.

1120

1121 **Plate IV.** Lycophyte, filicophyte spores and megaspore recovered from the Jaunay-Clan-
1122 Ormeau-Saint-Denis samples. Accompanying data are palynological preparation followed by
1123 England Finder coordinates. Authors of taxa are noted in the species list (Table 1). Scale bars
1124 represent 10 µm. **A.** *Cicatricosisporites annulatus*, JCO A, Q47.0. **B.** *Cicatricosisporites*
1125 *exilioides*, JCO 13, N38.0. **C.** *Cicatricosisporites hughesi*, JCO 13, M34.2. **D.**
1126 *Cicatricosisporites ludbrooki*, JCO 13, H46.0. **E.** *Cicatricosisporites pseudotripartitus*, JCO
1127 13, E33.1. **F.** *Cicatricosisporites venustus*, JCO 12, W49.3. **G.** *Costatoperforosporites* sp.,
1128 JCO B, V36.1. **H.** *Distaltriangulisporites perplexus*, JCO D, G37.1. **I.** *Arcellites reticulatus*,
1129 JCO 5, W45.0. **J.** *Crybelosporites pannuceus*, JCO 13, O36.4. **K.** *Cibotiumspora juncta*, JCO
1130 13, N29.4. **L.** *Cyathidites minor*, JCO B, T47.2. **M.** *Laevigatosporites ovatus*, JCO D, W43.3.
1131 **N.** *Polypodiaceoisporites* sp., JCO A, O30.0. **O, P.** *Foveosporites subtriangularis*, JCO 12,
1132 D41.4. **Q.** *Foveotriletes* sp. cf. *F. parviretus*, JCO 13, M29.0. **R.** *Auritulinasporites* sp., JCO
1133 8, M31.3. **S.** *Microreticulatisporites sacalii*, JCO 13, X28.4. **T.** *Microreticulatisporites*
1134 *urkuticus*, JCO 8, V42.3.

1135

1136 **Plate V.** Filicophyte spores and gymnosperm pollen grains recovered from the Jaunay-Clan-
1137 Ormeau-Saint-Denis samples. Accompanying data are palynological preparation followed by
1138 England Finder coordinates. Authors of taxa are noted in the species list (Table 1). Scale bars
1139 represent 10 µm. **A.** *Microreticulatisporites* sp., JCO A, J41.4. **B.** *Natronaspora?* sp. 1 *sensu*
1140 Ravn, 1995, JCO B, T36.0. **C.** *Patellasporites tavadensis*, JCO 13, P35.1. **D–F.**
1141 *Patellasporites distaverrucosus*, JCO 15, H44.1; JCO 13, S33.1. **G.** *Undulatisporites* sp. cf.
1142 *Psilatrilletes circumundulatus*, JCO 13, Y42.4. **H.** *Rugulatisporites* sp. *sensu* Singh 1983, JCO
1143 13, V39.4-3. **I.** *Cycadopites* sp., JCO B, T33.0. **J.** *Alisporites bilateralis*, JCO 8, D39.2. **K.**
1144 *Alisporites thomassii*, JCO 8, W32.1. **L.** *Cedripites canadensis*, JCO B, L35.3. **M.** *Cedripites*
1145 *cretaceus*, JCO 13, V39.4. **N.** *Parvisaccites enigmatus*, JCO A, O40.0. **O.** *Parvisaccites*
1146 *radiatus*, JCO D, H41.3. **P.** *Pityosporites constrictus*, JCO A, Q41.0. **Q.** *Podocarpidites*
1147 *naumovai*, JCO 13, V40.0. **R, S.** *Pristinuspollenites inchoatus*, JCO D, T42.2. ; JCO B,
1148 H45.2. **T.** *Pristinuspollenites minimus*, JCO D, D44.0.

1149

1150 **Plate VI.** Gymnosperm and angiosperm pollen grains recovered from the Jaunay-Clan-
1151 Ormeau-Saint-Denis samples. Accompanying data are palynological preparation followed by
1152 England Finder coordinates. Authors of taxa are noted in the species list (Table 1). Scale bars
1153 represent 10 μm . **A.** *Rugubivesiculites* sp. cf. *R. convolutus*, JCO 8, T29.3. **B.** *Araucariacites*
1154 *australis*, JCO 13, G36.4. **C.** *Balmeiopsis limbata*, JCO 12, Q43.1. **D.** *Callialasporites*
1155 *dampieri*, JCO 15, U27.2. **E.** *Cerebropollenites mesozoicus*, JCO A, N37.3. **F.**
1156 *Uesuguipollenites callosus*, JCO 13, O34.0. **G.** *Classopollis torosus*, JCO B, V44.0. **H.**
1157 *Inaperturopollenites dubius*, JCO 15, W51.0. **I.** *Perinopollenites halonatus*, JCO 13, X35.3.
1158 **J.** *Taxodiaceapollenites hiatus*, JCO B, X52.0. **K.** *Afropollis jardinus*, JCO 13, V33.0. **L.**
1159 *Equisetosporites ovatus*, JCO 15, G35.3. **M.** *Eucommiidites minor*, JCO A, Q49.4. **N.**
1160 *Eucommiidites troedssonii*, JCO A, M46.1. **O, P.** *Transitoripollis anulisulcatus*, JCO B,
1161 T32.3; JCO B, S29.3. **Q.** *Monosulcites chaloneri*, JCO A, Y41.2. **R.** *Stellatopollis*
1162 *barghoornii*, JCO A, L36.4. **S.** *Stellatopollis largissimus*, JCO 13, P49.2. **T.** *Eucommiidites*
1163 sp., JCO B, G49.4. JCO 13, U36.3.

1164

1165 **Plate VII.** Angiosperm pollen grains and algae recovered from the Jaunay-Clan-Ormeau-
1166 Saint-Denis samples. Accompanying data are palynological preparation followed by England
1167 Finder coordinates. Authors of taxa are noted in the species list (Table 1). Scale bars represent
1168 10 μm . **A.** *Clavatipollenites hughesii*, JCO B, T32.0. **B.** *Pennipollis* sp. cf. *P. reticulatus*, JCO
1169 15, W25.0. **C.** *Pennipollis peroreticulatus*, JCO 13, H34.0. **D.** *Nyssapollenites albertensis*,
1170 JCO D, T25.0. **E.** *Phimopollenites pannosus*, JCO 13, N43.1. **F.** *Retitrescolpites* sp. cf. *R.*
1171 *kempiae*, JCO A, E32.3. **G.** *Rousea brenneri*, JCO 15, Q51.3. **H.** *Retitricolporites decorosus*,
1172 JCO 13, W46.2. **I.** *Striatopollis trochuensis*, JCO 13, M45.1. **J.** *Striatopollis paraneus*, JCO
1173 13, P51.1. **K.** Aberrant tricolpate form, JCO 13, U36.3. **L.** *Tricolpites nemejcii*, JCO 15,
1174 X33.1. **M.** *Tricolpites* sp. cf. *T. parvus*, JCO B, G32.4. **N.** *Tricolpites* sp. cf. *T. amplifissus*
1175 *sensu* Ward 1986, JCO 15, V32.2. **O.** *Tricolpites* sp. cf. *T. vulgaris*, JCO 13, K32.4. **P.**
1176 *Dichastopollenites ghazalatensis*, JCO D, W39.1. **Q.** *Dichastopollenites* sp. cf. *D.*
1177 *dunveganensis*, JCO 13, Q52.2. **R.** *Dichastopollenites reticulatus*, JCO B, T46.4. **S.**
1178 *Schizosporis reticulatus*, JCO A, U47.2. **T.** *Schizosporis rugulatus*, JCO A, F35.2.

1179

1180 **Plate VIII.** Megaspores recovered from the clay sample MFP513. Scale bars represent 100
1181 μm . **A.** *Minerisporites* sp. **B.** *Minerisporites* sp. cf. *M.* sp. 1 *sensu* Batten in Batten et al.,

1182 2010. *C. Paxillitriletes* sp. *D. Molaspora* sp. cf. *M. lobata* (Dijkstra, 1949) Hall, in Hall and
1183 Peake, 1968.

1184

1185 **Table 1.** Systematic list of foliage remains recovered from Cenomanian outcrops in western
1186 France, along with number of pollen and spores species identified in the associated strata. For
1187 location of outcrops and references, see Figure 1.

1188

1189 **Table 2.** Similarity comparison of the JCO palynological assemblage with 12 Cenomanian
1190 assemblages from western France. For location of the sites, references and species list, see
1191 Figure 1 and Appendix 3.

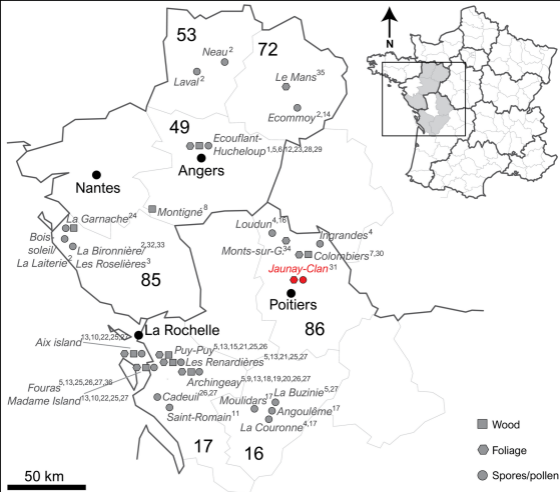
1192

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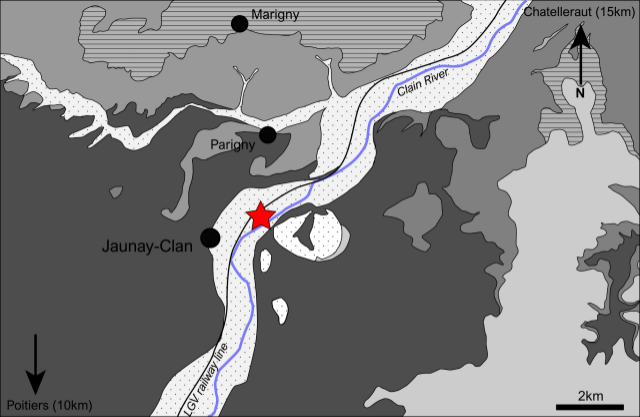
1194

1195

1196



Type of fossils	French department name with corresponding area code						
	Charente-Maritime 17	Charente 16	Vienne 86	Vendée 85	Maine-et-Loire 49	Mayenne 53	Sarthe 72
sp. Wood	8	0	2	0	6	0	0
sp. Foliage	35	0	11	0	29	0	9
sp. Spores/pollen	264	196	119 (+186)	149	28	51	97
Total sp.	307	196	132 (+186)	149	63	51	106



Lower Cenomanian

10 cm

JCO 15

JCO 13

JCO A

JCO 12

JCO B

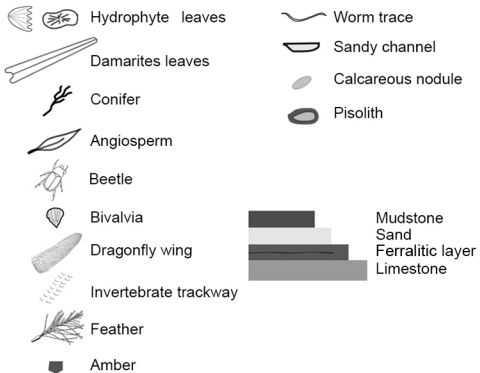
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JCO C

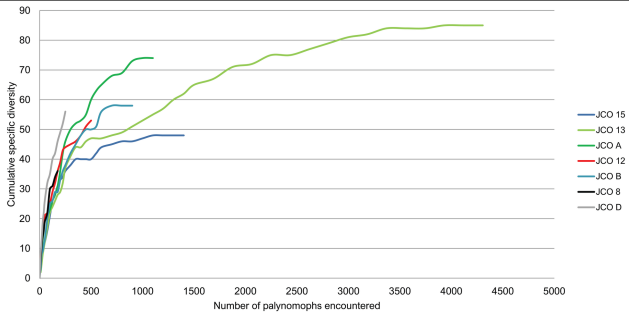
JCO 6b

JCO 5

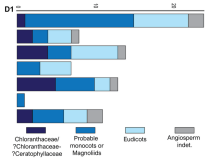
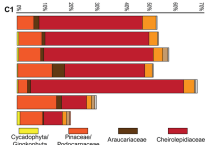
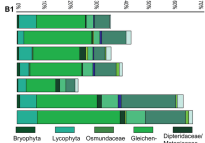
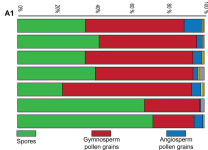
JCO D



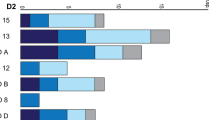
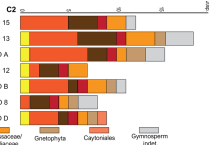
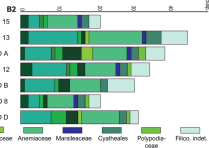
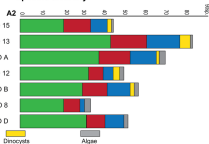
1 Oxfordian Limestone



Abundance



Specific diversity



	Jaunay-Clan	Les Renardières	Archingeay A2	Puy-Puy	Fouras	Aix Island	Madame Island	Colombiers	Monts-sur-Guesne	Hucheloup (Ecouflant)	Le Mans
Ferns											
<i>cf. Osmonda cretacea</i>				●						●	
<i>Adiantites lacerus</i>										●	●
<i>Cladophlebis sp.</i>	●									●	
<i>Filicites vedensis</i>											●
<i>Laccopteris sp.</i>											●
<i>Osmondophyllum sp.</i>	●										
Pteridophyte type 2				●							
Pteridophyte type 3				●							
<i>Ruffordia goeppertii</i>	●										
<i>Sphenopteris sp.</i>	●										
<i>Tempskya sp.</i>								●			
Gymnosperms											
<i>?Geinitzia reichenbachii</i>				●							
<i>Brachyphyllum sp.</i>	●		●			●				●	
<i>Cycadale indet.</i>		●									
<i>Cycadites sarthacensis</i>											●
<i>Dammarophyllum sp.</i>	●			●							
<i>Dioonites sp.</i>										●	
<i>Eretmophyllum obtusum</i>										●	
<i>Frenelopsis alata</i>		●	●		●	●	●		●	●	
<i>Geinitzia reichenbachii</i>										●	
<i>Genitzia sp.</i>			●								
<i>Glenrosa spp.</i>		●	●	●	●	●				●	
<i>Nehvizdya andegavense</i>		●	●								
<i>Pagiophyllum sp.</i>	●										
<i>Widdringtonia sarthacensis</i>											●
<i>Zamites sp.</i>				●							

<p>Angiosperms Angiosperme Types A- Type U ; Types 1-types 4 (20 forms described; see Gomez et al., 2004; Le Diuron, 2005)</p> <p><i>Dicotylophyllum</i> sp. 1. <i>Dicotylophyllum</i> sp. 2. <i>Dicotylophyllum</i> sp. 3. <i>Eucalyptolaurus depreii</i> <i>Eucalyptolaurus</i> sp. cf. <i>E.</i> <i>depreii</i> <i>Magnolia sarthacensis</i> <i>Palaeospathe</i> <i>sarthacensis</i> <i>Phyllites cenomanensis</i> <i>Ploufolia</i> sp.</p>	
Number of pollen and spores species in associated strata	171 59 137 0 55 39 27 0 0 29 0

	Number of continental species (spores/pollen/megaspores)	Number of common species with JCO	Number of exclusive species shared with JCO	Similarity coefficient (Jaccard)	Percentage of similarity based on lowest diversity	Presence of foliage remains
☐ Les Renardières (A1)	59	29	0	0,14	49,2	Yes
☐ Archingeay (A2)	137	49	0	0,19	35,8	Yes
☐ Cadeuil (A2)	105	40	0	0,17	38,1	No
■ Aix Island (B1)	32	20	0	0,11	62,5	Yes
■ Aix Island (B2)	39	21	0	0,11	53,8	Yes
■ Fouras (B2)	55	25	1	0,12	45,5	Yes
■ La Buzinie (B2)	64	34	0	0,17	53,1	No
● Neuau	50	11	1	0,05	22,0	No
● Laval	17	6	0	0,03	35,3	No
● La Garnache	45	20	5	0,10	44,4	No
● La Bironnière	74	17	0	0,07	23,0	No
● Hucheloup	29	10	2	0,05	34,5	Yes
Lower Cenomanian sites unit A (☐)	157	51	8	0,18	32,5	–
Lower Cenomanian sites unit B (■)	108	48	2	0,21	44,4	–
Middle Cenomanian sites (●)	154	41	15	0,14	26,6	–