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

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Abstract

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

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

1. Introduction

The study of mid-Cretaceous palaeobotanical and palynological assemblages has been historically essential for our understanding of the rise to dominance of angiosperms (Wing and Boucher, 1998). In Europe, our knowledge of this key interval for angiosperm evolution comes from several Albian-Cenomanian fossil sites with angiosperm-rich palaeofloras and palynofloras, mostly from Czech Republic (Pacltová, 1971; Greguš and Kvaček, 2015; Kvaček and Dilcher, 2000; Kvaček and Friis, 2010; Kvaček et al., 2012, 2016), Spain (Gomez et al., 2009; Sender et al., 2010, 2012), and France (see captions of Fig. 1 for references). In western France, numerous palaeobotanical and palynological investigations have been carried out on Cenomanian deposits since the mid-19th Century, owing to the high abundance of quarries and coastal cliffs. The large majority of the plant macroremains have been recovered from Charente-Maritime and Maine-et-Loire as fossil wood and diverse foliage preserved as impressions or in flints, and the highest diversity of continental palynomorphs has been recorded in Charente-Maritime, Charente and Vendée (Fig. 1, see caption for references). However, very little has been published on localities yielding both plant macro- and microremains, along with their potential affinities (Table 1). The rare deposits containing diversified macrofossil assemblages have so far yielded either a surprisingly poor palynoflora or none at all, such as the plant-bearing clays from the Hucheloup and the Puy-Puy quarries in

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

2. Geological setting

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

Outcropping deposits are constituted by Callovo-Oxfordian limestones unconformably overlain by lower Cenomanian deposits (Bourgueil et al., 1976). The contact between the Callovo-Oxfordian limestones and the lower Cenomanian deposits is marked by a ferrallitic alteration surface developed on a palaeo-karst which has been eroded in places (Valentin et al., 2014). The fossiliferous deposits at Jaunay-Clan consist of 1-5 m thick deposits filling up

small (~30 m wide) depressions on the post-Oxfordian surface. At the site of sampling, the JCO locality, (Fig. 3), they specifically consist of, from bottom to top:

- about 10 cm of massive reddish clay, with numerous calcareous nodules, ferruginous pisolites and cm-thick sand layers;
- 30 to 40 cm of clast supported, brecciated limestones and ferruginous pisolites, likely reworked from the alteration surface (Valentin et al., 2014);
- about 1.20 m of calcareous mudstones interlaminated with millimetre-scale layers of fine-grained sand and organic-rich mudstone, containing plant remains, worm ichnofossils, invertebrates trackway and wings, a theropod feather, crustaceans and bivalves (Valentin et al., 2014).

This sequence progressively grades into non-fossiliferous laminated grey siltstones and coarse ferruginous sand and is capped by Lower Cenomanian glauconitic sandstones that can be found regionally (Joubert, 1980).

3. Material and Methods

3.1.Extraction method

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

Another sample was sent to DJB by DN in 2014, and was processed at Aberystwyth University for its microfossil (QPR3670) and mesofossil (MFP513) content, following the extraction procedure of Batten (1999) for the microfossils. The extraction of megaspores involved initial soaking of 100 g of rock in warm water on a hot plate followed by immersion 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 sieving through a 70 mm mesh to reduce its bulk prior to standard palynological processing using HCl and HF. A few megaspores were recovered, and picked out of the aqueous residues under a stereomicroscope and housed dry in micropalaeontological slides. Some of the specimens recovered were mounted on scanning electron microscope (SEM) stubs to which carbon tabs had been fixed, and sent by DJB to FP for examination under a Phenom table SEM.

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

3.2. *Specimen counts*

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

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

4. Results

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

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

JCO D–JCO 8: spore dominated assemblages

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

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

JCO B–JCO 15: pollen dominated assemblages

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

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

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

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

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

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

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

5. Discussion

5.1. Biostratigraphic implications

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

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

5.2. Palaeoenvironmental reconstruction

The first palynological interval (JCO D to JCO 8) described here-above is characterized by the numerical and taxonomical dominance of fern spores. The majority of extant ferns flourishes in wet conditions, and are generally used as indicators of humid settings. The high spore content likely represents the local vegetation: being generally heavier than pollen grains, spores tend to be dispersed less widely, commonly being deposited close to their producers (Ferguson, 1995). This is supported by the several well-preserved fern macroremains recovered in the lower part of the succession (Valentin et al., 2014; Fig. 3). Other plant remains, such as the Nymphaeales-related *Ploufolia*, were only recovered from clay layers situated below the conglomerate layer rich in limestone breccias and reworked pisolites, corresponding to the first palynological interval (Valentin et al., 2014). The outstanding preservation of these freshwater taxa suggests a calm depositional environment, which can be associated with a lacustrine-type environment (Sender et al., 2010). The presence of the megaspore *Arcellites*, ascribed to the Marsileaceae, supports the hypothesis of a calm freshwater environment, modern Marsileaceae being water ferns, growing in seasonally wet or aquatic habitats (Zavialova and Batten, 2018; Appendix 2). Dominant fern spores belong to Cyatheales, Gleicheniaceae and Anemiaceae families. Modern Cyatheales are concentrated at the tropics, but can occupy varied habitats (Kramer in Kramer and Green, 1990; Appendix 2). Their high abundance at Jaunay-Clan agrees with a globally warm mid-Cretaceous climate (Kujau et al., 2013). The dominance of *Gleicheniidites* is fairly common in Lower and mid-Cretaceous continental deposits of Western Europe, and has already been noted several times in France (Herngreen, 1971; Peyrot et al., 2005, 2019). Modern Gleicheniaceae are considered as opportunistic, pioneering tropical to subtropical plants, adapted to long droughts, growing in unstable habitats including dry forests and wetlands that occasionally dry out (Coiffard et al., 2007; Mehlreter et al., 2012; Kujau et al.,

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

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

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

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

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

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

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

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

5.3. Botanical relationships between macro- and microfossils

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

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

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

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

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

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

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

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

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

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

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

5.4. Comparisons with Cenomanian assemblages from France and neighboring areas

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

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

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

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

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

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

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

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

Conclusion

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

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Figure captions

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

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

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

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

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

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

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

1081 1). Scale bars represent 10 μ m. **A.** *Achomosphaera ramulifera*, JCO 13, N26.4. **B.**
 1082 *Cribroperidinium* 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.** *Cingutritetes 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 μ m. **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. *Lophotritetes 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.** *Retitritetes expansus*, JCO 13, R36.1. **N.** *Retitritetes* sp. cf.
 1102 *Reticulatasporites dupliexinus*, 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 μ m. **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 selligii*,
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 *Psilatritetes 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 thomasi*, 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 μ m. **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 μ m. **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.

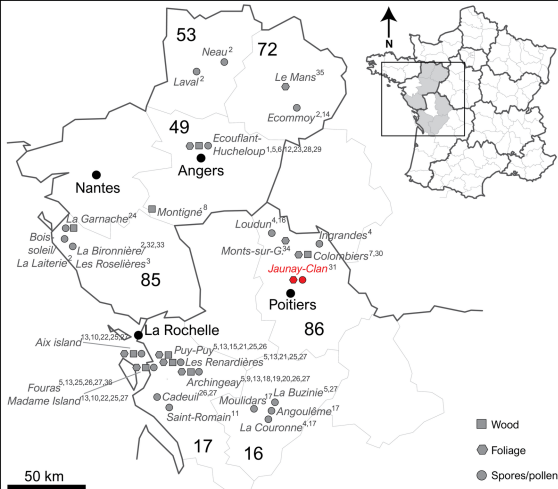
1179

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

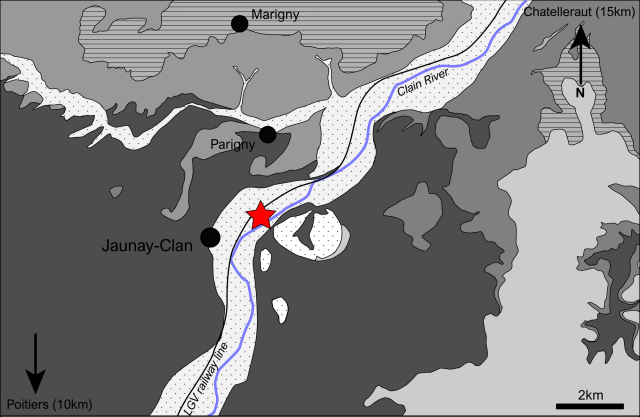
2010. **C.** *Paxillitriletes* sp. **D.** *Molaspora* sp. cf. *M. lobata* (Dijkstra, 1949) Hall, in Hall and Peake, 1968.

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

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



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

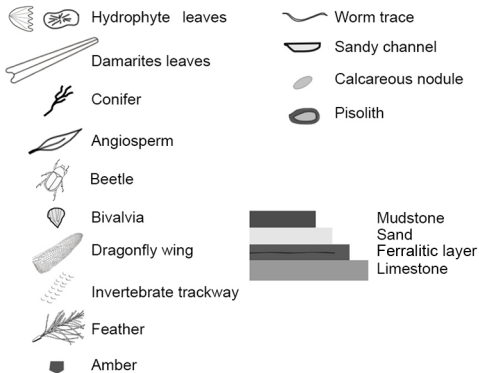
JCO 8

JCO C

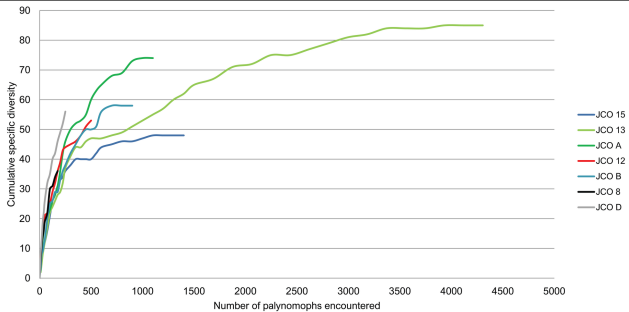
JCO 6b

JCO 5

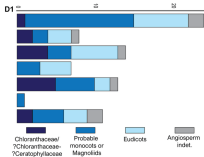
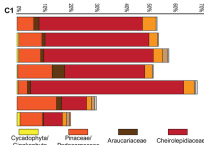
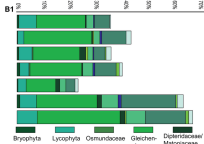
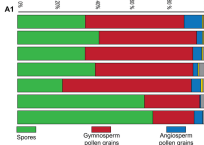
JCO D



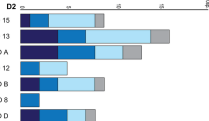
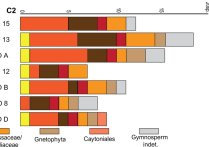
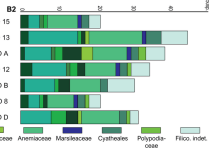
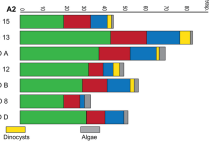
1 Oxfordian Limestone














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											
cf. <i>Osmonda cretacea</i>				●						●	
<i>Adiantites lacerus</i>											●
<i>Cladophlebis</i> sp.	●									●	
<i>Filicites vedensis</i>											●
<i>Laccopteris</i> sp.											●
<i>Osmondophyllum</i> sp.	●										
Pteridophyte type 2				●							
Pteridophyte type 3				●							
<i>Ruffordia goeppertii</i>	●										
<i>Sphenopteris</i> sp.	●										
<i>Tempskya</i> sp.								●			
Gymnosperms											
? <i>Geinitzia reichenbachii</i>				●							
<i>Brachyphyllum</i> sp.	●		●			●				●	
<i>Cycadale indet.</i>		●									
<i>Cycadites sarthacensis</i>											●
<i>Dammarophyllum</i> sp.	●			●							
<i>Dioonites</i> sp.										●	
<i>Eretmophyllum obtusum</i>										●	
<i>Frenelopsis alata</i>		●	●		●	●	●		●	●	
<i>Geinitzia reichenbachii</i>										●	
<i>Genitzia</i> sp.			●								
<i>Glenrosa</i> spp.		●	●	●	●	●				●	
<i>Nehvizdya andegavense</i>		●	●								
<i>Pagiophyllum</i> sp.	●										
<i>Widdringtonia sarthacensis</i>											●
<i>Zamites</i> sp.				●							

Angiosperms Angiosperme Types A- Type U ; Types 1-types 4 (20 forms described; see Gomez et al., 2004; Le Diouron, 2005) <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.	          											
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
● Neu	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	–