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Inclusions of conifers, echinoids, foraminifers and sponges in flints from the Cenomanian of Charente-Maritime (France): Contribution of synchrotron microtomography

Des inclusions de conifères, échinides, foraminifères et spongiaires dans des silex cénomaniens de Charente-Maritime (France) : apport de la microtomographie synchrotron

Jean-David Moreau [a,b,*], Didier Néraudeau [a], Bernard Gomez [c], Paul Tafforeau [b], Éric Dépré [d]

[a] *Université Rennes 1, CNRS UMR 6118 Géosciences Rennes, campus de Beaulieu, bâtiment 15, 263, avenue du Général-Leclerc, 35042 Rennes, France*
[b] *European Synchrotron Radiation Facility, 6, rue Jules-Horowitz, BP 220, 38043 Grenoble, France*
[c] *Université Lyon-1 (Claude-Bernard), CNRS UMR 5276 LGL-TPE, Campus La Doua, bâtiment Géode, 43, boulevard du 11-Novembre-1918, 69622 Villeurbanne, France*
[d] *GIP-GEVES (Groupement d'Étude et de Contrôle des Variétés et Semences), Le Magneraud, 17700 Surgères, France*

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ABSTRACT

Deposits containing silica-rich nodules were recently collected from the Font-de-Benon quarry, between Archingeay and Les Nouillers, Charente-Maritime, western France. Nodules contain diverse fossil inclusions such as conifers, urchins, foraminifers and sponge spicules. Cenomanian deposits were transformed during the Eocene-Oligocene by a delayed silicification. This occurred under a warm climate and a long pedogenic alteration. X-ray synchrotron tomography was used to locate and produce three-dimensional reconstruction of flint fossil inclusions. The plant fossils constitute an unusual case of late permineralization. The conifer and invertebrate fossil assemblage suggests a coastal palaeoenvironment close to a forest.

Mots clés :
Plantes
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RÉSUMÉ

Des dépôts contenant des nodules siliceux ont récemment été mis au jour dans la carrière de Font-de-Benon, entre Archingeay et Les Nouillers, Charente-Maritime, Ouest de la France. Ces silex contiennent diverses inclusions fossiles, telles que des conifères, des oursins, des

* Corresponding author at: European Synchrotron Radiation Facility, 6, rue Jules-Horowitz, BP 220, 38043 Grenoble, France.
E-mail address: jean.david.moreau@gmail.com (J.-D. Moreau).

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Microtomographie synchrotron
Crétacé moyen
Ouest de la France

foraminifères et des spicules d'éponges. Les dépôts d'âge Cénomanien ont été affectés par une silicification tardive durant l'Éocène-Oligocène. Celle-ci s'est déroulée sous un climat chaud et via une altération pédogénétique prolongée. La microtomographie synchrotron par rayonnement X est utilisée pour détecter et visualiser en trois dimensions les inclusions fossiles. Les plantes contenues dans ces silex représentent un cas original de préservation exceptionnelle par perminéralisation tardive. L'assemblage fossile mixte, associant restes de conifères et invertébrés marins, témoigne d'un milieu de dépôt littoral bordé d'une forêt.

1. Introduction

Silicified plants have been reported from many geological formations across a broad stratigraphic interval (Channing et al., 2007; Hernández-Castillo and Cevallos-Ferriz, 1999; Krings et al., 2007; Little et al., 2009; Miller, 1973; Remy et al., 1997; Smith and Stockey, 2007; Smith et al., 2006; Stockey and Pigg, 1991; Stockey et al., 1999; Taylor et al., 1999). Most of them show exquisite preservations, resulting from an early silicification that occurred during sedimentation or during the early stages of diagenesis. Because of this early silicification, these rocks are called cherts. In contrast, they are called flints when they result from late post-sedimentary silicifications, associated with decalcification processes (Gallois, 2009). Flints bearing fossil plants are particularly uncommon (Bertrand, 1930; Bruet, 1932, 1933; Saporta, 1876–1884).

Flint nodules bearing both terrestrial plants and marine invertebrates were recently collected from Cenomanian deposits of Charente-Maritime, western France. In other regional Albian-Cenomanian deposits, only impressions and compressions of plant fossils have been studied (Coiffard et al., 2009; Gomez et al., 2004, 2008; Kvaček et al., 2012; Néraudeau et al., 2002, 2005, 2009). The new material provides unusual preservation of fossil conifers useful for a three-dimensional study. We used propagation phase-contrast X-ray synchrotron tomography (PPC-SRμCT), which is a non-destructive method of examination. In palaeobotany, only small and low-density plant specimens removed from sediments were studied using X-ray microtomography, because of technical limitations (Feist et al., 2005; Friis and Pedersen, 2011; Friis et al., 2007, 2009, 2010, 2011, 2013; Heřmanová et al., 2011; Moreau et al., 2014a; Schönenberger et al., 2012; Scott et al., 2009; von Balthazar et al., 2007). In the present work, synchrotron X-ray microtomography has allowed us to study both plants and invertebrate remains included inside dense and large rocks, which is a new technical challenge.

2. Geological setting

The flint nodules were collected from the Font-de-Benon quarry, between the villages of Archingeay and Les Nouillers, Charente-Maritime, western France (Fig. 1). At the base of the quarry, Uppermost Albian deposits consist of lignitic clay and sand with cross-bedded stratifications, from estuarine and brackish deposit environments (Néraudeau et al., 2002). The lignites yielded fossil leaves and wood (Gomez et al., 2004), and amber containing

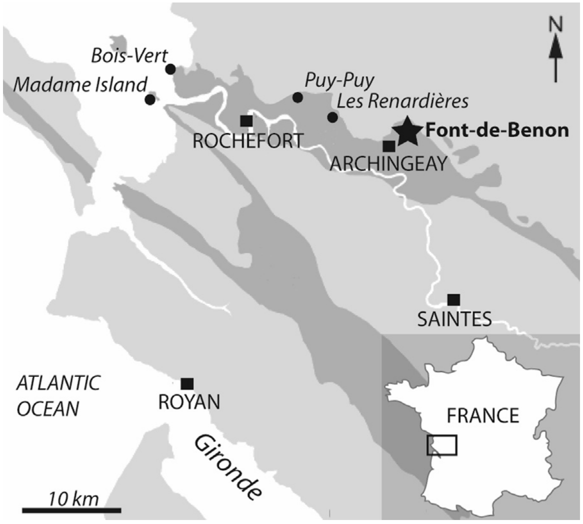

Fig. 1. Geological map of the Charente-Maritime department showing the Font-de-Benon quarry and other palaeontological localities. Dark grey corresponds to the Cenomanian.

Fig. 1. Carte géologique du département de la Charente-Maritime indiquant la carrière de Font-de-Benon et d'autres localités paléontologiques. Le gris sombre correspond aux dépôts cénomaniens.

diverse fossil inclusions such as arthropods (Nel et al., 2004; Néraudeau et al., 2002, 2008), microorganisms (Girard et al., 2009), rare feathers (Perrichot et al., 2008), and mammalian hair (Vullo et al., 2010).

Overall, the Lowermost Cenomanian beds show alternations of sand and clay. The clayey beds yielded abundant and diverse plant meso- and macroremains bearing cuticles (Coiffard et al., 2009; Gomez et al., 2008). The upper part of the quarry corresponds to the oldest regional Cenomanian marine deposits. They contain a rich coastal fauna including molluscs, echinoderms, foraminifers (*Orbitolina*) and vertebrates (Vullo et al., 2003).

Locally, at the top of the topography, the sandy marine deposits are overlapped by a one-to-two-metres-thick clay-with-flints. The flint bed is parallel to the topography and locally yields oval to irregular, 10–50-cm-wide, silica-rich nodules.

3. Material and methods

Forty fragments of flint nodules containing fossil plants were collected. Their size varies from 5 to 15 cm long. They are housed in the collections of the Université Lyon-1

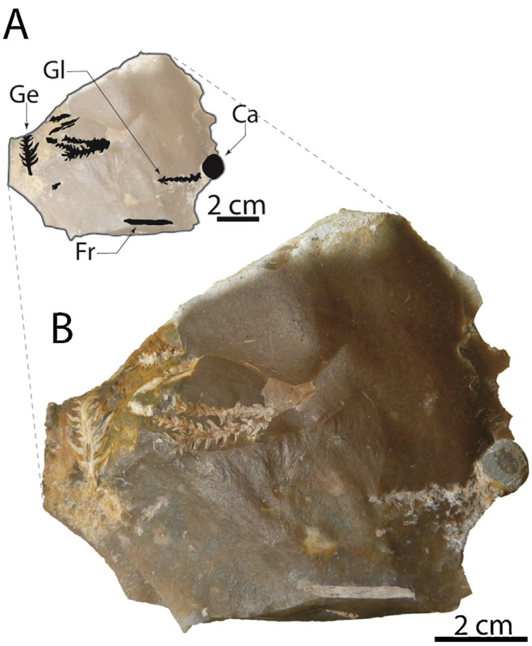

Fig. 2. A–B. Broken-open flint nodule containing conifer leafy axes and echinoids. Ca, *Catopygus*; Fr, *Frenelopsis*; Ge, *Geinitzia*; Gl, *Glenrosa*. SIL_ARC_5.
Fig. 2. A–B. Fragment de nodules de silex contenant des axes feuillés de conifères et échinides. Ca, *Catopygus* ; Fr, *Frenelopsis* ; Ge, *Geinitzia* ; Gl, *Glenrosa*. SIL_ARC_5.

and the Université Rennes 1 under the collection numbers SIL_ARC_1 to SIL_ARC_40. Six specimens were scanned using propagation phase-contrast X-ray synchrotron tomography (PPC-SRμCT) on beamlines ID19 and BM05 at the European Synchrotron Radiation Facility (ESRF), Grenoble, France (Tafforeau et al., 2006). Because of large sizes and high densities of the samples, high energy and long propagation distance between the sample stage and the source were combined. Acquisition and reconstruction protocol were explained in detail by Moreau et al. (2014b). We localized fossils contained inside the flint nodules using the 2D virtual sections and virtually removed 3D images of some of them. The voxels are 13 and 30 μm side. The 3D reconstructions of fossil specimens were performed with the software VG Studio Max 2.2 (Volume Graphics, Heidelberg, Germany).

4. Hidden biodiversity of the flints and exceptional preservation

4.1. Microorganisms and invertebrates from the flints

All studied flint nodules contain fossils and show a diverse assemblage of plants, microfossils and invertebrate remains (Figs. 2–6). These organisms are variously assembled inside the siliceous matrix. Invertebrates are exclusively marine, and consist of echinoids, bryozoans, bivalve fragments and abundant microfossils. Echinoids consist of about 1 cm long complete egg-shaped tests with pointed posterior margins, ascribed to the cassiduloid *Catopygus carinatus* Goldfuss (Figs. 2 and 3E–F).

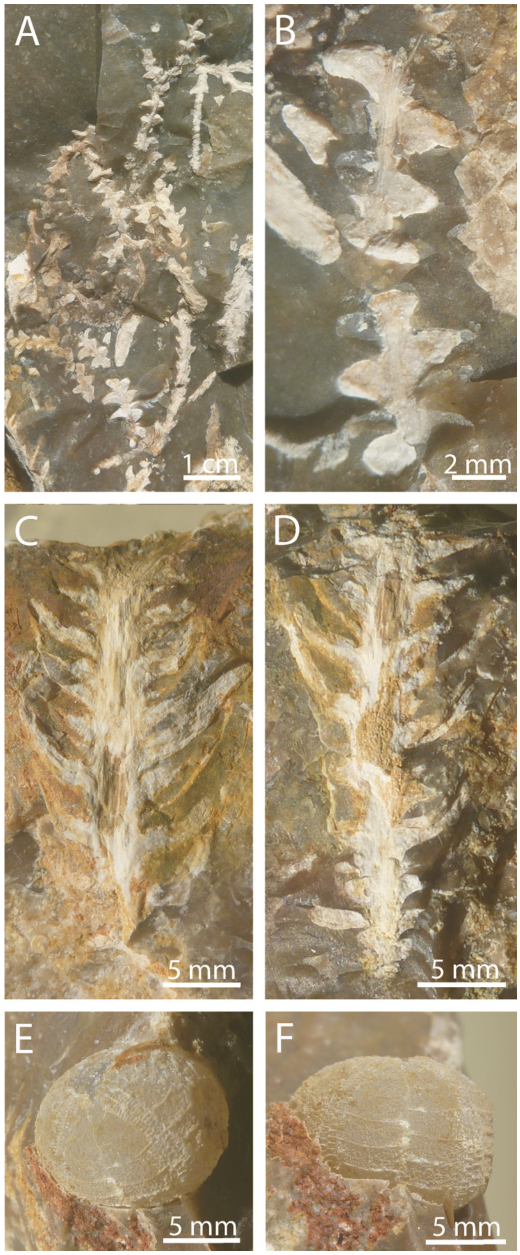

Fig. 3. A–B. Leafy axes of *Glenrosa*. C–D. Leafy axes *Geinitzia*. E–F. Echinoid *Catopygus*. A, SIL_ARC_3; B, SIL_ARC_6; C, E–F, SIL_ARC_5; D, SIL_ARC_1.
Fig. 3. A–B. Axes feuillés de *Glenrosa*. C–D. Axes feuillés de *Geinitzia*. E–F. Échinide *Catopygus*. A, SIL_ARC_3 ; B, SIL_ARC_6 ; C, E–F, SIL_ARC_5 ; D, SIL_ARC_1.

Other irregular echinoid fragments with large petaloid and slightly sunken ambulacra were ascribed to *Mecaster* Pomel. Regular echinoid spines can be also found in some flints. Microfossils consist of foraminifers and sponge spicules. Large benthic foraminifers were ascribed to *Orbitolina conica* d'Archiac. The co-occurrence of *Orbitolina conica* and *Catopygus carinatus* suggests a Cenomanian age. Locally, in the siliceous matrix, complete and fragmented sponge spicules form dense accumulations (Fig. 6). Sponge spicules are abundant both in flint nodules

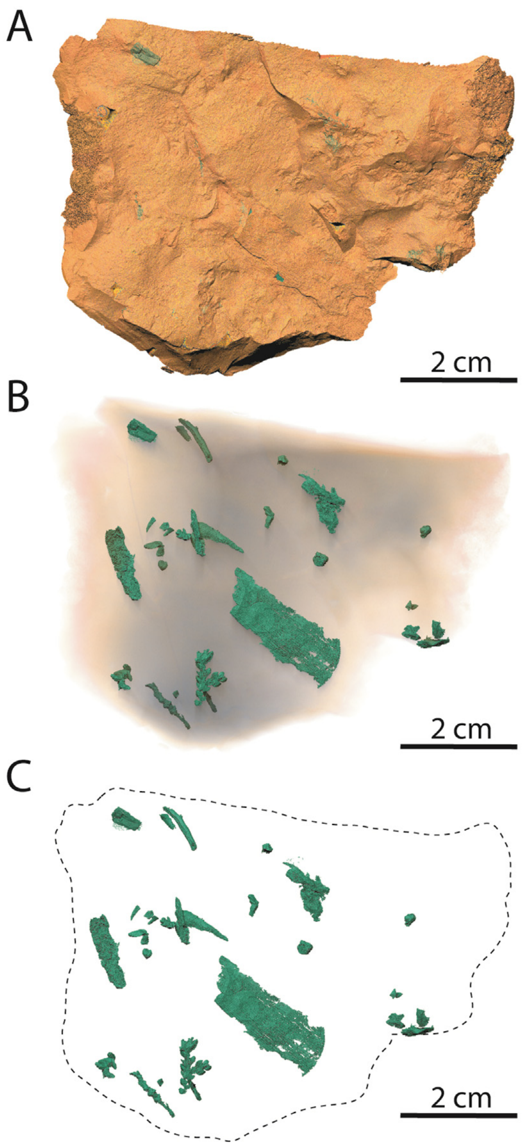

Fig. 4. A–C. PPC-SRμCT, 3D renderings of a whole flint nodule showing megafossil plant remains hidden inside. Voxel side = 30 μm. SIL_ARC_4.
Fig. 4. A–C. PPC-SRμCT, modèle 3D d'un fragment de nodule siliceux montrant les mégarestes de plantes à l'intérieur. Arête des voxels = 30 μm. SIL_ARC_4.

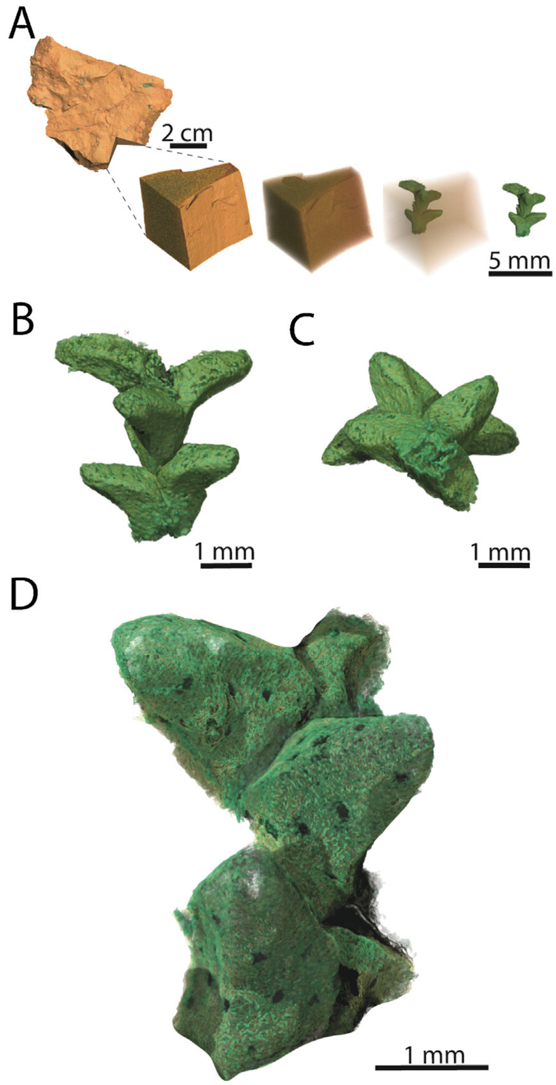

Fig. 5. PPC-SRμCT, 3D renderings. A. Isolated volume of silica-rich matrix containing a specimen of *Glenrosa* leafy axis. B. Lateral view of a *Glenrosa* leafy axis. C. Bottom view of a *Glenrosa* leafy axis. D. *Glenrosa* leafy axis and details of the cuticle showing the apertures of stomatal crypts (circular and dark marks on the leaf surface). Voxel side, A–C = 30 μm, D = 13 μm. A–C, SIL_ARC_4; D, SIL_ARC_3.
Fig. 5. PPC-SRμCT, modèle 3D. A. Volume de matrice siliceuse isolé et contenant un fragment d'axe feuillé de *Glenrosa*. B. Vue latérale d'un axe feuillé de *Glenrosa*. C. Axe feuillé de *Glenrosa*, vue de dessous. D. Axe feuillé de *Glenrosa* et détail de la cuticule montrant les ouvertures des cryptes stomatiques (marques rondes et sombres à la surface des feuilles). Arête des voxels, A–C = 30 μm, D = 13 μm. A–C, SIL_ARC_4 ; D, SIL_ARC_3.

containing *Orbitolina* and in nodules with plants, but no flint with a plant-*Orbitolina* association has been found. This indicates that two different silicified facies exist in the diachronic clay-with-flint: a typical Early Cenomanian facies, with *Orbitolina conica* (Vullo et al., 2003), and a slightly younger facies, similar to the early Late Cenomanian limestones with *Catopygus*, *Mecaster* and conifer remains (Moreau et al., 2014b).

4.2. Plants from the flints

Albian-Cenomanian plant fossils have been previously reported from several localities in Charente-Maritime: Archingeay–Les Nouillers (Font-de-Benon quarries), Fouras (Bois-Vert tidal flat), Aix Island (Bois-Joly tidal flat), Madame Island (Puits-des-Insurgés cliffs), and Tonnay-Charente (Les Renardières and Puy-Puy quarries) (Fig. 1; Coiffard et al., 2009; Gomez et al., 2004, 2008; Néraudeau et al., 2005, 2009). However, only plant impressions and compressions are preserved in clay. In palaeobotany, impressions usually provide the description of gross morphology only; the microscopic external and histological internal features are not preserved (Martín-Closas and

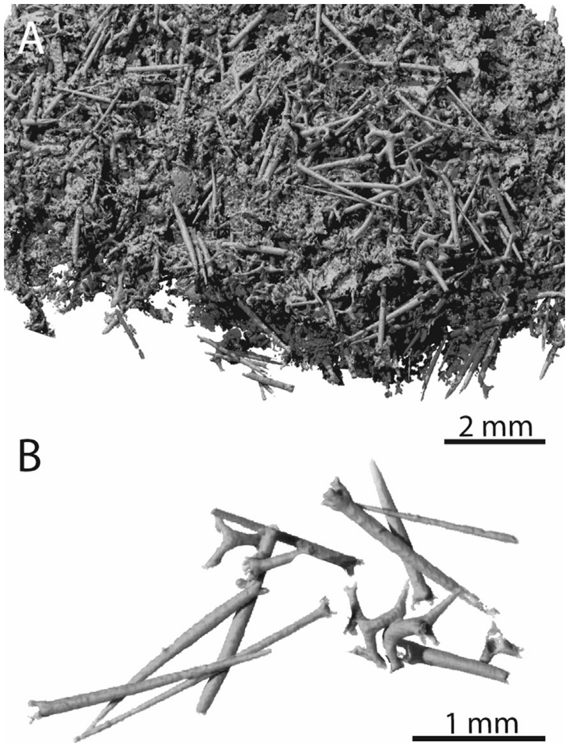

Fig. 6. PPC-SRμCT, 3D renderings. A. Accumulation of marine invertebrates including sponge spicules. B. Isolated sponge spicules. Voxel side = 13 μm. SIL_ARC_3.

Fig. 6. PPC-SRμCT, modèle 3D. A. Accumulation d'invertébrés marins incluant des spicules d'éponges. B. Spicules d'éponges isolés. Arête des voxels = 13 μm. SIL_ARC_3.

Gomez, 2004; Schopf, 1975). Compressions with cuticles preserved allow the description of microstructural details of the epidermis *sensu lato* including the stomatal apparatus. However, plant compressions rarely preserve their structures in three dimensions. In contrast, the plant fossils contained inside the flint nodules from Font-de-Benon quarry are preserved in three dimensions, and show exquisite internal histological details (Figs. 2, 3A–D, 5). Some of the plant specimens of the flints show vegetative and reproductive structures in anatomical connection. Such a connection is rare or even unknown in some deposits and taxa. Thus, the fragmentation and disarticulation of reproductive structures occur after maturation and dehiscence during the production. A too strong rinsing used to remove cuticles from clay may also increase the fragmentation of the most fragile anatomical connection. Thus, plant inclusions in silica-rich matrix provide unique information for associating different plant parts, relating structures and functions, and better understanding Cretaceous palaeoecosystems.

The plant assemblage consists only of fossil conifers (up to 5 cm long). They belong to the genera *Brachyphyllum* Brongn., *Frenelopsis* (Schenk) emend. J. Watson, *Geinitzia* Endl., and *Glenrosa* J. Watson & H.L. Fisher. *Brachyphyllum* shows spiral phyllotaxy, leaf free part shorter than the leaf cushion, and stomata arranged in rows of a single stoma wide. *Frenelopsis* shows leaf whorls without suture between leaves, very short free leaf tips, and stomata arranged in rows of a single stoma wide. *Geinitzia* shows spiral phyllotaxy, awl-shaped, leaves with long free leaf parts, and keeled abaxial surfaces. *Glenrosa* shows spiral phyllotaxy, long leaf free parts, and typical scattered stomatal crypts. Although *Brachyphyllum*, *Frenelopsis* and *Geinitzia* are frequently observed, *Glenrosa* appears to be the main plant within this assemblage. Some *Glenrosa* specimens also show leafy stems in connection with male cones (Moreau et al., 2014b). This is the first report of entire male cones bearing pollen sacs, though *Glenrosa* leafy stems have been reported from several Cretaceous localities of Asia, Europe and the United States (Gomez et al., 2012; Srinivasan, 1992; Watson and Fisher, 1984; Zhiyan et al., 2000). The silicified plants from the Font-de-Benon quarry show fine details of the external leaf surface such as stomatal crypts (Fig. 5D). Also, preliminary high-resolution X-ray microtomography tests show that cell walls of all internal tissues of stems, leaves, and male cone axes and scales are preserved. This exceptional preservation probably resulted from the silica microcrystallization on both the inner and outer surfaces of cell walls. Such permineralizations usually concern early silicification occurring during sedimentation or during the early stages of diagenesis (Eggert, 1974; Millay and Eggert, 1974; Remy et al., 1997; Taylor and Millay, 1977; Wellman, 2004). However, we cannot exclude that a first phase of silicification occurred earlier, though Moreau et al. (2014b) suggested that the main silicification phase of Cenomanian sediments occurred during the Eocene-Oligocene. The flint nodules of Font-de-Benon appear to be exceptional because plant fossils are entirely permineralized in 3D that provides both the gross morphology and the internal histological structures.

4.3. Silicification processes

A widespread silicification episode, associated with an extensive pedogenic alteration, occurred in western France (Grandin and Thiry, 1983; Turq, 2000) and other countries (Summerfield, 1983; Ullyott et al., 1998) under a warm climate during the Eocene-Oligocene interval. Exposed Cretaceous rocks were progressively decalcified under an intense leaching of soils by meteoric waters. Calcareous rocks from various regions and ages were progressively transformed in silica-rich duricrusts or clay-with-flints. This kind of post-sedimentary silicification was particularly important on limestones and marls interbedded in sandy series, or/and upon calcareous sediments containing siliceous sponge remains. Thus, Turonian (limestones with siliceous sponges) to Eocene (sandy limestones) deposits from different localities of Charentes were also affected by the same diachronic silicification (Daniou, 1978, 1979; Néraudeau, 2011).

As far as the Charentese flints are concerned, the silica may come from both from the rich sponge spicule content (Fig. 6) of the Cretaceous sediment and the Palaeogene dissolution of local Cenomanian sandstones (lithological units A, B2 and E *sensu* Néraudeau et al., 1997).

5. Depositional environment

The association of terrestrial plants and marine invertebrates suggests that the sediments were deposited proximally along the shoreline in brackish or shallow marine environment with both marine and continental inputs. This coastal palaeoenvironment was probably close to a conifer forest. Gomez et al. (2008) suggested that gymnosperm mangroves, mainly represented by the association of *Frenelopsis*, *Glenrosa* and *Nehvizdya*, settled along the coast line of the Charente-Maritime during the Albian-Cenomanian. Thus, *Brachyphyllum*, *Frenelopsis* and *Glenrosa* were previously reported from many coastal depositional environments opened to marine inputs (Gomez et al., 2004; Néraudeau et al., 2009). In contrast, in Charente-Maritime, *Geinitzia* was only reported from the Cenomanian clay of Puy-Puy quarry (Fig. 1), which is considered as a freshwater terrestrial environment (Gomez et al., 2004) or a brackish paralic deposit (Vullo et al., 2013). However, Cretaceous conifers display a large set of xerophytic features that might well accommodate them to a broad range of habitats or that some conifers were competing during environmental changes at the ecotones.

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