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Palaeontology of the upper Turonian paralic deposits of the Sainte-Mondane Formation, Aquitaine Basin, France

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| ABSTRACT |

The upper Turonian lignite deposits of Sainte-Mondane, Dordogne (Aquitaine Basin, SW France), consist of clays bearing translucent, orange to red, amber micrograins. The amber exhibits different types of microbial inclusions. The clays contain several conifers including the genera *Brachyphyllum*, *Frenelopsis* and *Glenrosa*, and a few leaf fragments of eudicot angiosperms. Among the plant meso-fossils the occurrence of *Costathea*, *Spermatites* and abundant, diverse, megaspores, including species of *Ariadnaesporites*, *Bacutritetes*, *Echitritetes*, *Erlansonisporites*, *Maexisporites*, *Minerisporites* and *Verrutritetes*, is noteworthy. Pollen grains of the Normapolles group are important components of the palynomorph assemblage. The clays were deposited in a calm, estuarine or lagoonal, muddy environment. The overlying lignitic sands contain large fossil wood pieces of the conifer *Agathoxylon*, small solitary corals, fragmentary oysters and pectinids, echinoid spines, a few teeth of marine selachians and bony fishes, but no amber is present. These sands were deposited in a high-energy coastal marine environment.

KEYWORDS | Amber. Plants. Palynomorphs. Turonian. Cretaceous. France.

INTRODUCTION

So far, Late Cretaceous ambers are mostly known from the Cenomanian (Martínez-Delclòs *et al.*, 2004; Penney, 2010). They have been reported from Ethiopia (Schmidt *et al.*, 2010), France (Néraudeau *et al.*, 2002; Gomez *et al.*, 2008; Perrichot *et al.*, 2010; Girard *et al.*, 2013), Germany (Schmidt *et al.*, 2001), Lebanon (Azar *et al.*, 2010), Myanmar (Ross *et al.*, 2010), Spain (Peñalver and Delclòs, 2010) and Russia (*e.g.*, Dolgan Formation; Savkevitch, 1974).

Post Cenomanian ambers are both uncommon and, in some cases, poorly studied. The most famous are from the Turonian of North America (*i.e.*, amber from Raritan, New Jersey; Grimaldi and Nascimbene, 2010) and Russia (Eskov, 2002). Santonian amber has been reported from Russia (*e.g.*, Kheta Formation; Savkevitch, 1974), France (Gomez *et al.*, 2003; Saint Martin *et al.*, 2012, 2013a), Hungary (Borkent, 1997), USA (Knight *et al.*, 2010) and Japan (Schlee, 1990). Campanian and Maastrichtian ambers have been reported from Canada (Carpenter *et al.*, 1937; McKellar and Wolfe, 2010), France (Lacroix, 1910; Nel *et al.*, 2004; Perrichot, 2005; Breton *et al.*, 2013) and Spain (Peñalver and Delclòs, 2010). Late Cretaceous amber has also been reported from New Zealand, but it was imprecisely dated (Lambert *et al.*, 1993).

A small amount of fossiliferous Turonian amber was recently discovered in southwestern Australia (Quinney *et al.*, 2015), but Turonian amber remains poorly documented out of the USA. In France, it was first recorded by Lacroix (1910) in the southeastern region. Several localities have been reported since then, for example La Mède and Roquevaire, Bouches-du-Rhône and Saint-Marcel-de-Carreiret, Gard, but they still need to be studied in detail (Nel *et al.*, 2004; Perrichot, 2005; Perrichot *et al.*, 2007). During World War II, numerous mines were developed in Cenomanian and Turonian lignites in the area around Sarlat-la-Canéda, Dordogne. The main bed is late Cenomanian in age (Fig.

1A) and contains very small amber grains (Arnaud, 1865; Saint Martin *et al.*, 2013b). In this paper, the sedimentary succession of an upper Turonian lignite mine near Sainte-Mondane (Figs. 1B; 2) is studied with regard to the plant meso-fossils and palynomorphs, and microorganisms included in amber grains. We also discuss the overlying sandy bed containing fragments of wood, debris of oyster and pectinid shells, corals, and small vertebrate remains including fish teeth. The depositional environments are interpreted according to the geological setting and the assemblages of fossil plants, palynomorphs, invertebrates and vertebrates, and the microbial inclusions in the amber.

GEOLOGICAL SETTING

The lignite mine of Sainte-Mondane is situated near the locality of La Bruyère, between the villages of Saint-Mondane and Veyrignac, around 10km to the southeast of Sarlat-la-Canéda and 2km to the west of Sainte-Mondane (Fig. 1B). The mine opening is located adjacent to the road, alongside the River Dordogne. The section consists of 10m of upper Turonian deposits (Fig. 2), the Sables et grès de Sainte-Mondane Formation of Cassoudebat and Platel (1973) and Platel (1989) (=Sainte-Mondane Formation in Platel, 1998) dated was by palynology (Fauconnier in Capdeville and Rigaud, 1987). The studied portion of the section, from the base to the top, is as follows (Fig. 3):

i) Unit I: 0.80 to 1.20m of laminated grey clays with plant cuticles and amber grains (Unit I-a), alternating at the top with fine sand laminations (Unit I-b); the base is not observed, so its thickness is probably greater.

ii) Unit II: 1.50 to 1.60m of cross bedded yellow, coarse sands (Unit II-a) with lenses containing cm- to m-sized wood fragments (Unit II-b) at the top. Fossil remains mainly consist of oyster fragments, small solitary corals, a few small selachian and bony fish teeth, and small turtle shell fragments. Animal macro-fossils are rare.

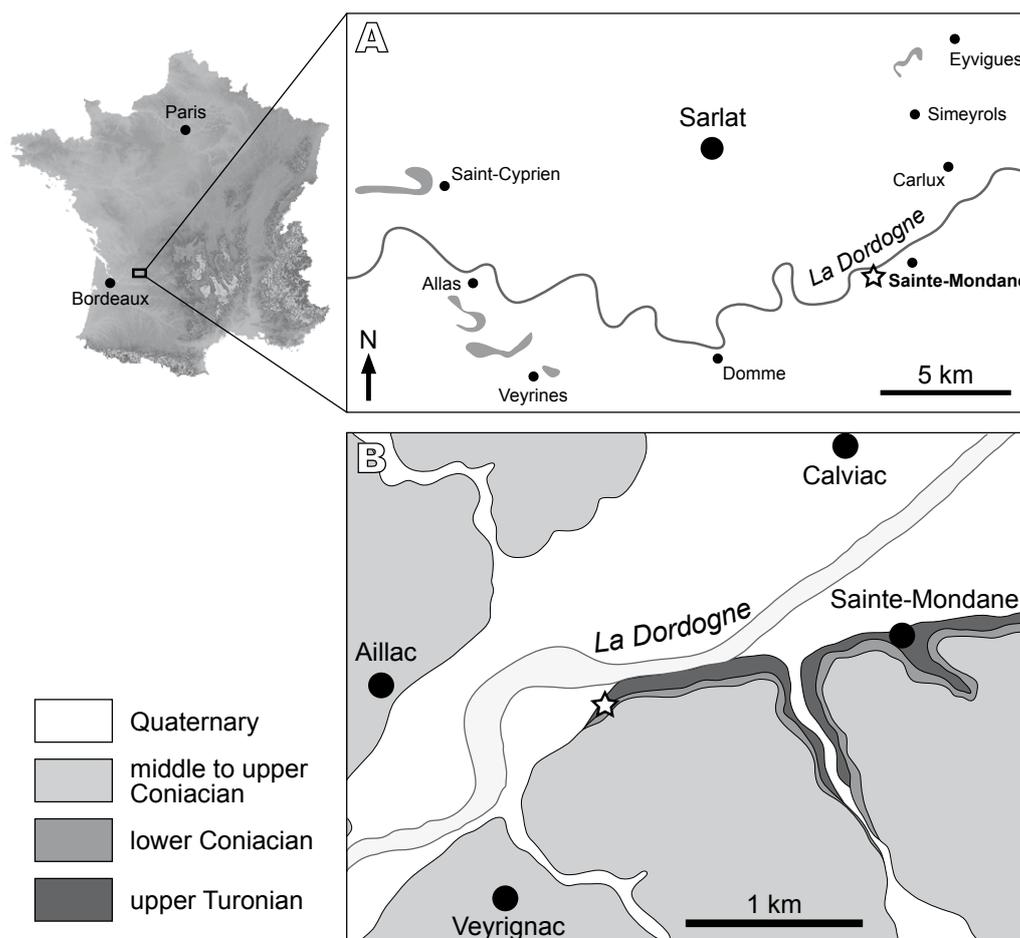


FIGURE 1. A) Geographical location and B) geological setting of the upper Turonian outcrop of Sainte-Mondane (Dordogne, Aquitaine Basin, SW France). Grey areas in (A) represent the upper Cenomanian lignite outcrops.

The unstudied portion of the section corresponds to Units III to V. Unit III consists of 2.20 to 2.50m of calcareous sandstones with siliceous nodules and cross bedding, fine-grained in its lower part (Unit III-a) and coarse grained and harder in its upper part (Unit III-b). This unit seems to be devoid of fossils. Units IV and V could not be examined because of their inaccessibility due to their height and dense vegetation cover.

MATERIAL AND METHODS

Units I and II were examined and sampled during four fieldtrips in April 2003 (D.N., J.-P.P.), May 2007 (V.G., D.N.), May 2008 (D.N.) and May 2011 (D.N., J.-P.S.M., S.S.M.).

From the lignitic clays of Unit I:

i) 100kg of sediment were washed and sieved at 0.35mm, and amber grains were picked out from the

residues. Both petrographic thin sections and polished sections were made. Polished sections were prepared from amber grains embedded in epoxy resin Araldite 2020. To avoid contamination by recent microorganisms, amber drops were washed with distilled water and then treated with H_2O_2 . Amber microinclusions were detected under a Zeiss Axioscope 40 light microscope. Very thin scraps of amber were mounted on glass slides in Eukit balsam and examined under this microscope at magnifications of x40, x63, and x100 (oil immersion). Preparations for scanning electron microscope (SEM) analysis were made by breaking small amber grains into pieces and immediately coating them with gold. This technique allows the exposure of fresh surfaces and minimizes the risk of contamination.

ii) 1kg of sediment was collected for palaeobotany. The rocks were bulk macerated in 30% of hydrogen peroxide for one day, and then washed through a 0.1-mm mesh sieve. Plant meso-fossils were sorted under an Olympus SZX 10 stereomicroscope. Photographs were taken with a Canon EOS 60D integrated digital camera at the Université

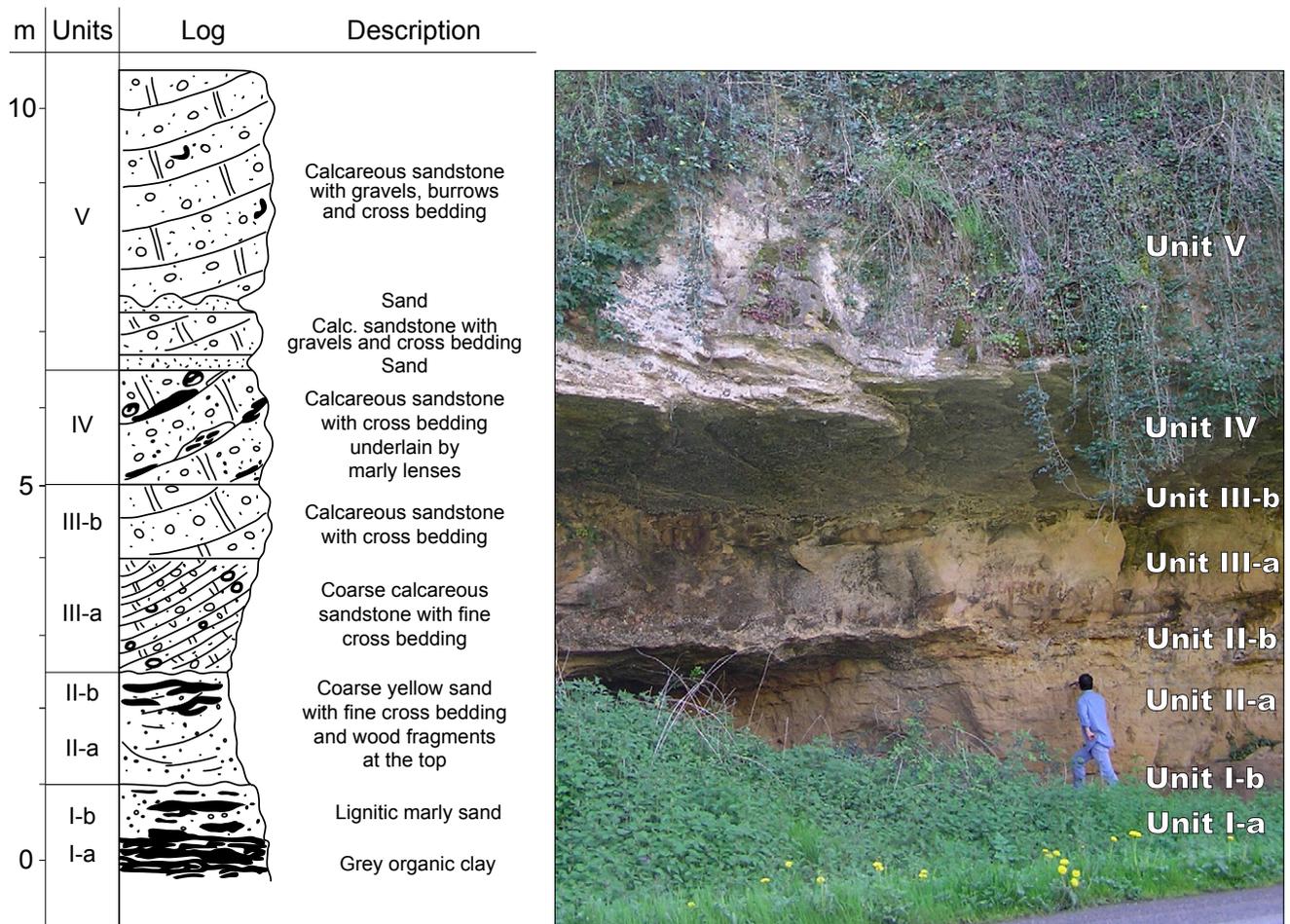


FIGURE 2. Stratigraphy of the upper Turonian Sainte-Mondane cliff section (Sainte-Mondane Formation): overall view of the outcrop with location of the five sedimentological units (I to V).

Lyon 1. Cuticles were treated using Schulze reagent. Untreated megaspores, seeds and cuticles were placed for a day in hydrofluoric acid to remove silicate remnants. Some slides were prepared for light microscopy by mounting the specimens in glycerine jelly or water.

iii) 2kg of the lignitic clays were set aside for micropalaeontological analysis. Processing for palynology was carried out using a standard procedure that involved immersion of 5g of sample in dilute HCl, followed by digestion in 58–62% HF and brief oxidation (30s) of the organic residue in fuming HNO₃, washing after each stage until the aqueous residue was neutral (for further details, see Batten, 1999). In addition 100g were processed for megaspores and other small meso-fossils. This involved initial soaking of the sample in a flask of warm water on a hot plate followed by further soaking in warm *ca.* 5% Na₄P₂O₇ and washing on a sieve with a mesh size of 85µm to reduce the bulk of the sample prior to subjecting the residue to acid digestion in HCl and HF as for the palynological sample.

50kg of sands of Unit II were washed and sieved at 0.5mm to remove wood, invertebrate and vertebrate microremains.

For the infrared analysis, 0.2mg of amber was crushed and mixed with KBr (FTIR grade; Merck, Germany) and pellets were prepared using a manual press. Transmission Fourier-Transform InfraRed (FTIR) spectroscopy was performed with a Bruker IFS 55 spectrophotometer. The spectrum was acquired between the 4000cm⁻¹ and 400cm⁻¹ range with 40 scans collected at 2cm⁻¹ resolution.

The material studied here is housed in several institutions: i) microorganisms preserved in amber in the micropalaeontological collections of the Muséum National d'Histoire Naturelle (MNHN), Paris, ii) palynological material in the plant microfossil collections of the Aberystwyth University, iii) palaeobotanical material in the collections of the Faculté des Sciences de Lyon, Université Claude Bernard Lyon 1 (UCBL-FSL), and iv) vertebrate material in the palaeontological collections of Institut de Géologie de Rennes (IGR), Université Rennes 1.

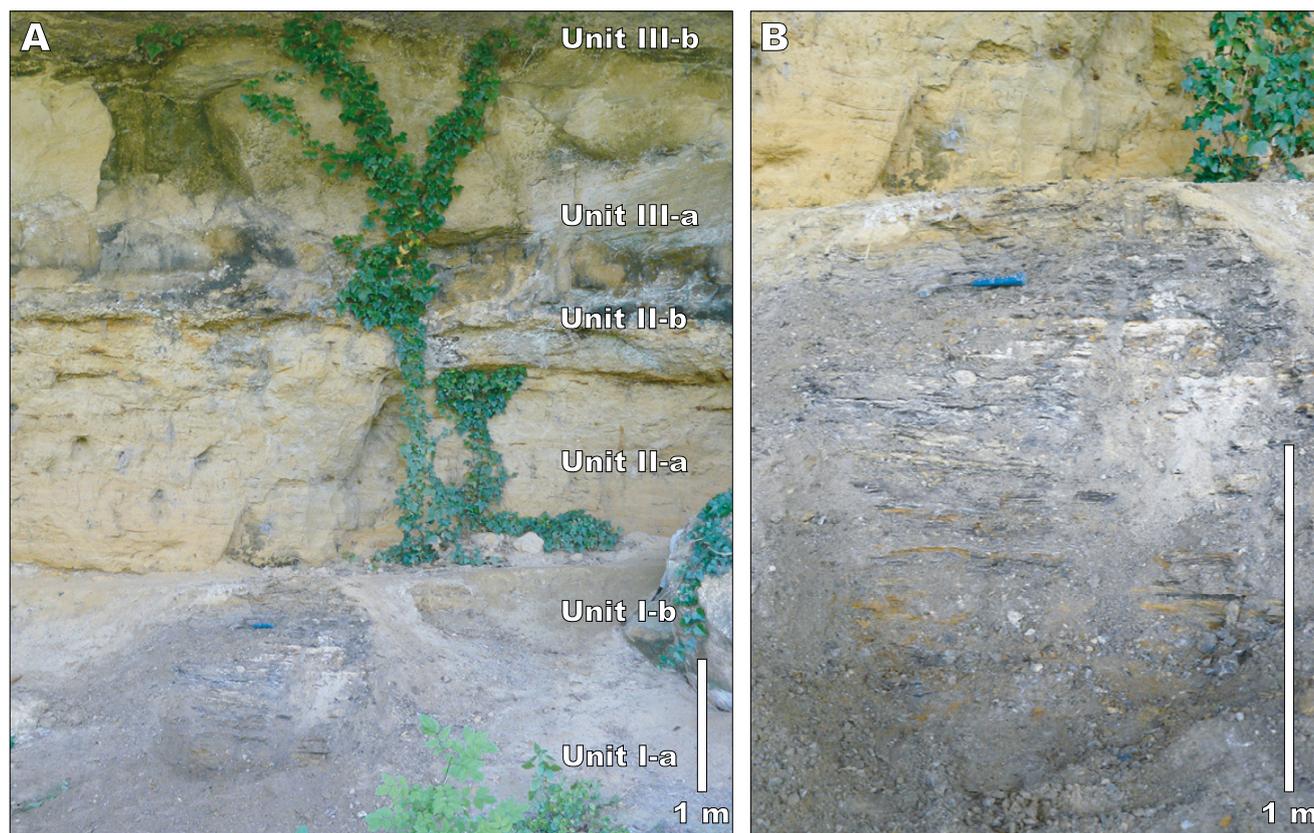


FIGURE 3. Studied portion of the upper Turonian Sainte-Mondane cliff section. A) Beds of Units I to III; the lignitic clayey facies with amber and plant remains is located in Unit I and the vertebrate and invertebrate marine remains are mainly located in the sands of Unit II. B) Lignitic beds of Unit I; note the alternation of thin sandy (white to yellow) and clayey laminations.

AMBER CHARACTERISTICS

Amber is abundant in the clayey beds exposed at the base of the section (Unit I), but only small grains up to 7mm in diameter are present (Fig. 4). The amber grains usually correspond to oval, elongated (Fig. 4A) or spherical, autotroph (Fig. 4B), resin drops. In some cases, amber is preserved as thin quadrangular scales. The colour ranges from dark red (the most common) to light yellow (a few grains). The surface is cracked and usually darker than the core. A few grains show a whitish to greyish crust (Fig. 4C), but totally opaque or milky grains are lacking.

The infrared spectrum of the Sainte-Mondane amber sample shows the typical profile of a fossilized resin spectrum (Fig. 5). The band assignments are represented in Table 1. The first part of the spectrum ($4000\text{--}1600\text{cm}^{-1}$) is common to all Cretaceous ambers, especially when compared to other French Cretaceous ambers dating from Albian to Santonian (Nohra *et al.*, 2015). However, the so-called fingerprint area of the spectrum ($1600\text{--}400\text{cm}^{-1}$) shows some differences with respect to other Cretaceous ambers, depending on their botanical origin (Langenheim and Beck, 1968). The

Dordogne amber shows some affinities with the early Late Cretaceous amber from Vendée (NW France) and with the Santonian amber from Provence (SE France), which have a more cupressaceous and araucarian origin according to their infrared spectra (Nohra *et al.*, 2015). When we compare the spectrum of Sainte-Mondane amber with the spectrum of recent resins (Tappert *et al.*, 2011), it is apparent that it has some affinities with the araucarian and cupressaceous resins. Thus, the resemblance between Turonian and Santonian French ambers can be explained by a similar palaeobotanical origin. However, the bands at 3040 , 1644 and 880cm^{-1} corresponding to exomethylene groups (Table 1) are relatively weak, which is a result of the depletion of these exomethylene groups by aromatization, reduction, and polymerization of the fossil resin (Langenheim, 1969). These exocyclic methylene groups are characteristic of some acids (communic and ozic), thus supporting the presence of the labdatriene polymeric structures in the amber studied (Grimalt *et al.*, 1988). Hence, according to these results, we suggest that the Sainte-Mondane amber might be a Class Ib amber (*sensu* Anderson, 1995) especially because the Baltic shoulder is absent in the spectrum.

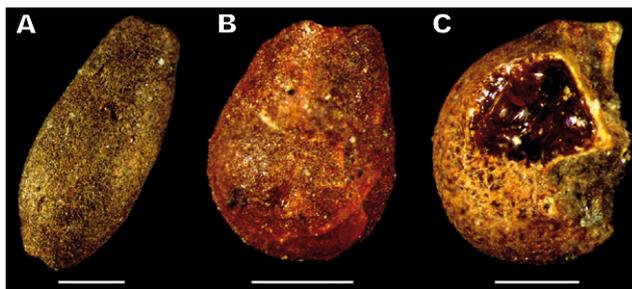


FIGURE 4. Automorph amber grains of reddish colour from the upper Turonian of Sainte-Mondane (Unit I). A) Elongated resin microdrop. B) “Water shape” resin drop. C) Red amber grain with a clear microbial crust. These amber grains were used for the preparation of sections and slides. Scale bars: 1mm (A), 500 μ m (B, C).

AMBER INCLUSIONS

Five main types of microbial inclusions have been observed under light and scanning electron microscopes:

i) Fine filaments 0.70–1.00 μ m in diameter branching dichotomously at angles of 70–80° and typically forked dichotomously at their tips (Fig. 6A–C). The size and way of filament development correspond to actinomycetes. When they are very abundant, they form a thin crust around the grains (Fig. 6A, B) with a possible bushy extension (Fig. 6B). The centripetal development of actinomycetes, probably when the resin was still soft, may explain the differences in colour and structure of the periphery of some grains. Thus, the density of filaments decreases from the periphery to the centre of the grains. Similar filaments have been described as “Actinomycetes type A” from the upper Albian and lower Cenomanian ambers of Charentes (Girard, 2010). Saint Martin *et al.* (2012, 2013a) have reported similar actinomycetes in the Santonian amber from southeastern France.

ii) Very fine filaments 0.60–0.80 μ m in diameter arranged in small clusters about 20–40 μ m in diameter, quite uncommon, scattered in the amber. The filaments show several branches (Fig. 6D) that can be derived from a single growth point, and straight or slightly curved endings. Dichotomies occur at a distance of about 2–4 μ m. The angle of the branches is often close to 90°. Similar filaments have been described as actinomycetes in *cf. Streptomyces* (Waggoner, 1994) in the Eocene amber of the USA, and in the Santonian amber from southeastern France (Saint Martin *et al.*, 2012, 2013a).

iii) Sheathed filaments 4–6 μ m in diameter (Fig. 7A, B). The filaments are up to 1mm long. They are regularly branched at angles of 50–90°. The sheath is translucent and the surface is finely granulated. The cell chain is not preserved, but a lumen of around 1 μ m in diameter is present.

The filaments grow from the surface to the centre of the amber grains. Their density decreases from the periphery to the centre. This type of filament is very similar to the sheathed bacterium *Leptotrichites resinatus* described from the Cenomanian Schliersee amber (Schmidt and Schäfer, 2005). Waggoner (1996) also described sheathed filaments as *cf. Leptothrix* from the Albian–Cenomanian amber of Ellsworth County, Kansas, USA. Ascaso *et al.* (2003) described mummified sheathed bacteria, which they assigned to *Leptothrix*, in some bubbles in the amber from the Lower Cretaceous of Álava, Spain. In France, filaments similar to *Leptotrichites resinatus* have also been reported from the Cenomanian (Girard *et al.*, 2009a, b, 2013), Santonian (Saint Martin *et al.*, 2012, 2013a) and Campanian (Breton *et al.*, 2013). Nevertheless, Breton and Tostain (2005) described filaments with very similar characteristics as belonging to cyanobacteria and gave them the name *Palaeocolteronema cenomanensis*. Girard *et al.* (2009a, b) emphasized the strong resemblance between these two taxa and suggested that phycocyanine measurements are needed to distinguish them. Owing to the very small size of the structures observed in our Turonian amber grains, it is not possible to apply such a method. However, the absence of clearly visible cells, the net dichotomy with a true branching angle of 60°, the structure of the sheath, and the dimensions of the sheath relative to the inner lumen (Schmidt and Schäfer, 2005) rather evoke the typical structures of *Leptotrichites*. Furthermore, Girard *et al.* (2009a, b) assumed that *Palaeocolteronema* developed in freshwater ponds when forest-fresh resin flowed into and trapped some filaments whereas *Leptotrichites* did not grow in ponds, but probably in forest litter or on the wet bark of trees. In our material the amber pieces correspond only to very small drops of resin suggesting an aerial origin more favourable to the occurrence of *Leptotrichites*. Lastly, it is worth noting that Speranza *et al.* (2015) have recently affirmed, on the basis of various analyses (using diverse techniques of microscopy and spectroscopy), a fungal origin for these types of resinicolous filaments.

iv) Frequent networks of apparently filamentous microstructures observed on the red peripheral layer of translucent red, drop-shaped amber grains (Fig. 7C). The apparent width of these microstructures is around 6 μ m all along their length. The extremities are rounded. No cell chains were observed. Similar structures were assigned by Girard (2010) to sheathed bacteria close to the genus *Sphaerotilus* in the Albian–Cenomanian ambers of Les Renardières, Fouras Bois-Vert and Fourtou. Later, Breton *et al.* (2013) observed the same features in the Campanian amber from Mas d’Azil (southern France) and noted that they cannot be identified as *Sphaerotilus natans*, the only modern species of the genus. Taking into account the features of the apparently filamentous structure in our material and the observations of Breton *et al.* (2013),

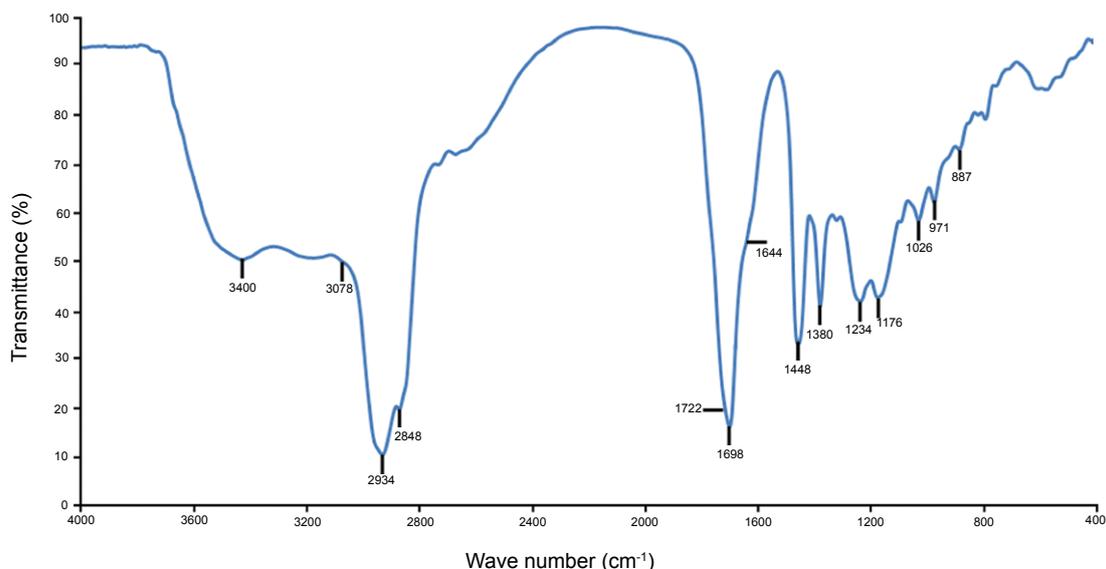


FIGURE 5. Infrared spectrum of Sainte-Mondane amber.

we think that an attribution to *Sphaerotilus* is highly questionable. Accurate identification will only be possible following a detailed analysis using appropriate techniques.

v) Septate filaments, yellow–orange coloured, of 2–4 μm in diameter (Fig. 7D). The filaments consist of chains of ovoid cells 8–15 μm in length. These features suggest a filamentous fungus. Similar septate hyphae have been reported in the Spanish Cretaceous amber (Martín-González *et al.*, 2009), the Albian–Cenomanian amber from southwestern France (Girard *et al.*, 2009b; Girard, 2010; Girard and Adl, 2011), and the Santonian amber from southeastern France (Saint Martin *et al.*, 2012, 2013a).

No animal inclusions have been found in the amber grains. Compared to other mid-Cretaceous (Albian and Cenomanian) French ambers (Néraudeau *et al.*, 2002, 2003) or to the contemporaneous Turonian Australian amber (Quinney *et al.*, 2015), the resin particles from

Sainte-Mondane differ by the lack or scarcity of pseudo-inclusions and protist-like inclusions (Girard *et al.*, 2011).

POLLEN, SPORES AND SEEDS

The clays of Unit I contains abundant and morphologically diverse plant microremains. During the preparation of the local geological map, Fauconnier (in Capdeville and Rigaud, 1987) recorded seven miospore taxa and three dinocyst species. The sample prepared for palynological examination for this paper yielded more than 40 species of miospores, taxonomically dominated by angiosperm pollen (*ca.* 27 species). The Normapollens are especially abundant, representing 94% of the angiosperm component and about 40% of the total assemblage. They include several species of *Complexiopollis* and *Trudopollis*, two and four of which, respectively, are illustrated in Figure 8. Less common are species referable

TABLE 1. Main Transmission Fourier-Transform InfraRed (FTIR) spectrum features of the Sainte-Mondane amber sample

Bands, wave number (cm^{-1})	Assignment
3400–	–OH stretching
3078	C–H stretching of exocyclic methylene groups
2950 – 2840	C–H stretching of alkyl groups
1722 – 1698	C=O stretching of carbonyl/carboxyl groups
1644	C=C stretching of exocyclic methylene groups
1448 – 1380	C–H bending vibration of alkyl groups
1250 – 1000	C–O stretching of aromatic ethers and phenols
887	C–H out of plane bending of exocyclic methylene groups

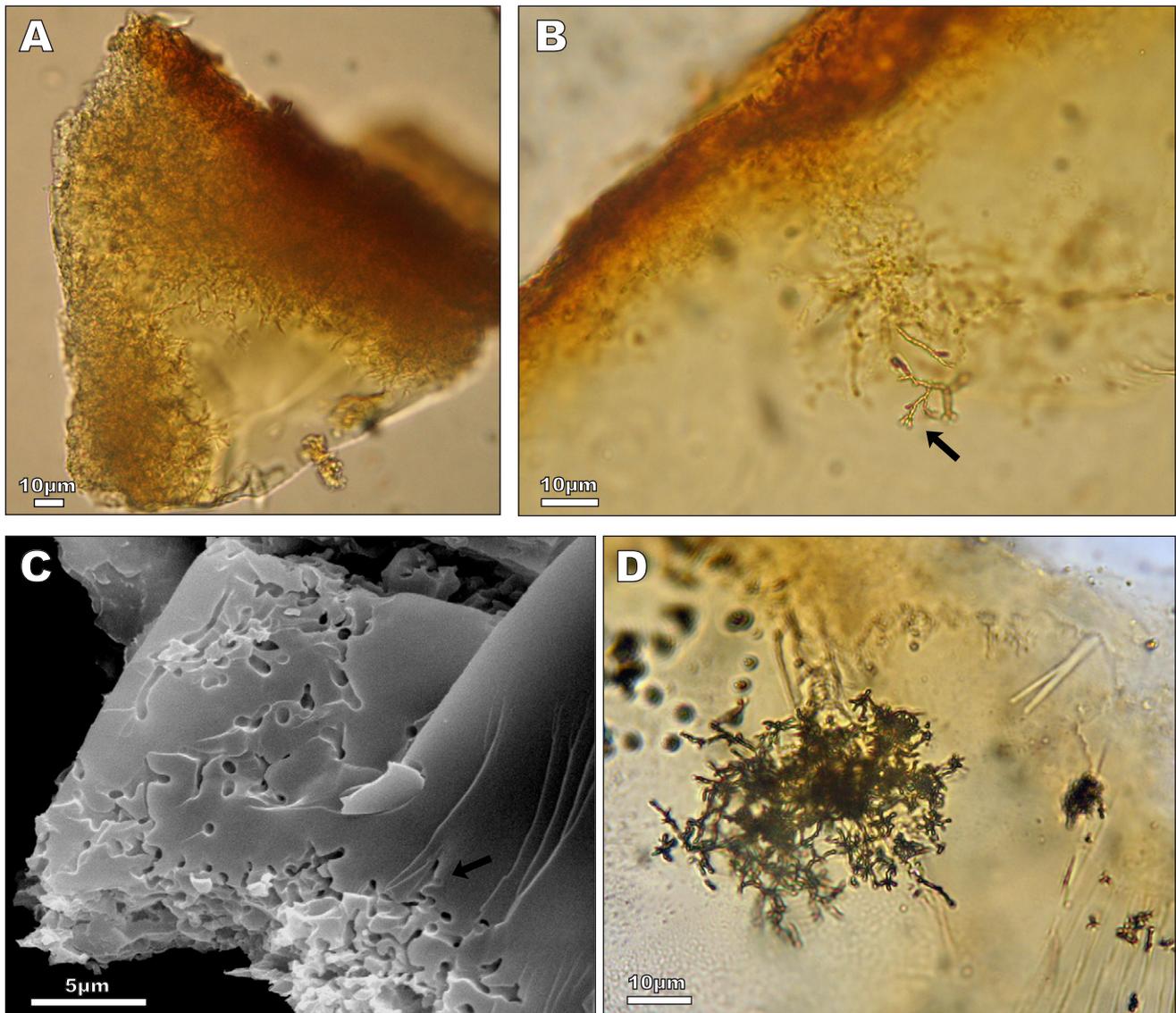


FIGURE 6. Microbial inclusions in amber from the upper Turonian of Sainte-Mondane (Unit I). A) Thin fragment of amber showing colonisation by Actinomycete A (MNHN.F.F62400). B) Detail of Actinomycete A; note the bushy development and the characteristic terminal forked dichotomy (arrow) (MNHN.F.F62401). C) SEM view of the peripheral crust of an amber grain showing the colonisation by filaments preserved as moulds of Actinomycete A with the characteristic terminal forked dichotomy (arrow) (MNHN.F.F62405). D) Cluster of fine filaments of *Streptomyces*-like actinomycete (MNHN.F.F62404).

to *Atlantopollis*, *Choanopollenites*, *Interporopollenites*, *Osculapollis*, *Plicapollis*, *Vacuopollis* and other genera (Fig. 8). Non-Normapollis angiosperm grains include monocolpate, tricolpate and periporate taxa represented by such forms as *Clavatipollenites hughesii* (not illustrated), *Tricolpopollenites minutus* (Fig. 8V) and *Echiperiporites* (Fig. 8D). Although ten species of fern spores were recorded, they comprise only 10% of the assemblage. Most are smooth-walled or weakly sculptured (*e.g.*, species of *Cyathidites* and *Dictyophyllidites*; Fig. 8S) but a few specimens of more strongly ornamented taxa such as *Microreticulatisporites* (*e.g.*, *Microreticulatisporites sacalii*; Fig. 8Y) were also encountered. By contrast,

although the gymnosperm component of the assemblage lacks diversity with only five species identified it comprises about 50% of the palynomorphs recorded: bisaccate grains (*e.g.*, *Podocarpidites* sp. cf. *P. potomacensis*; Fig. 8Z) dominate with common *Classopollis* (Fig. 8X) in association. Marine dinoflagellates are fairly common in the assemblage but a freshwater alga (*Tetraporina*) was also recorded.

Numerous types of seeds also occur including abundant *Spermatites*. Specimens referable to *Costatheca dakotaensis* (Schemel) Hall, 1967 were recovered from the preparation for megaspores and other small meso-fossils. Although it is possible that *C. dentata* and perhaps a few of the specimens

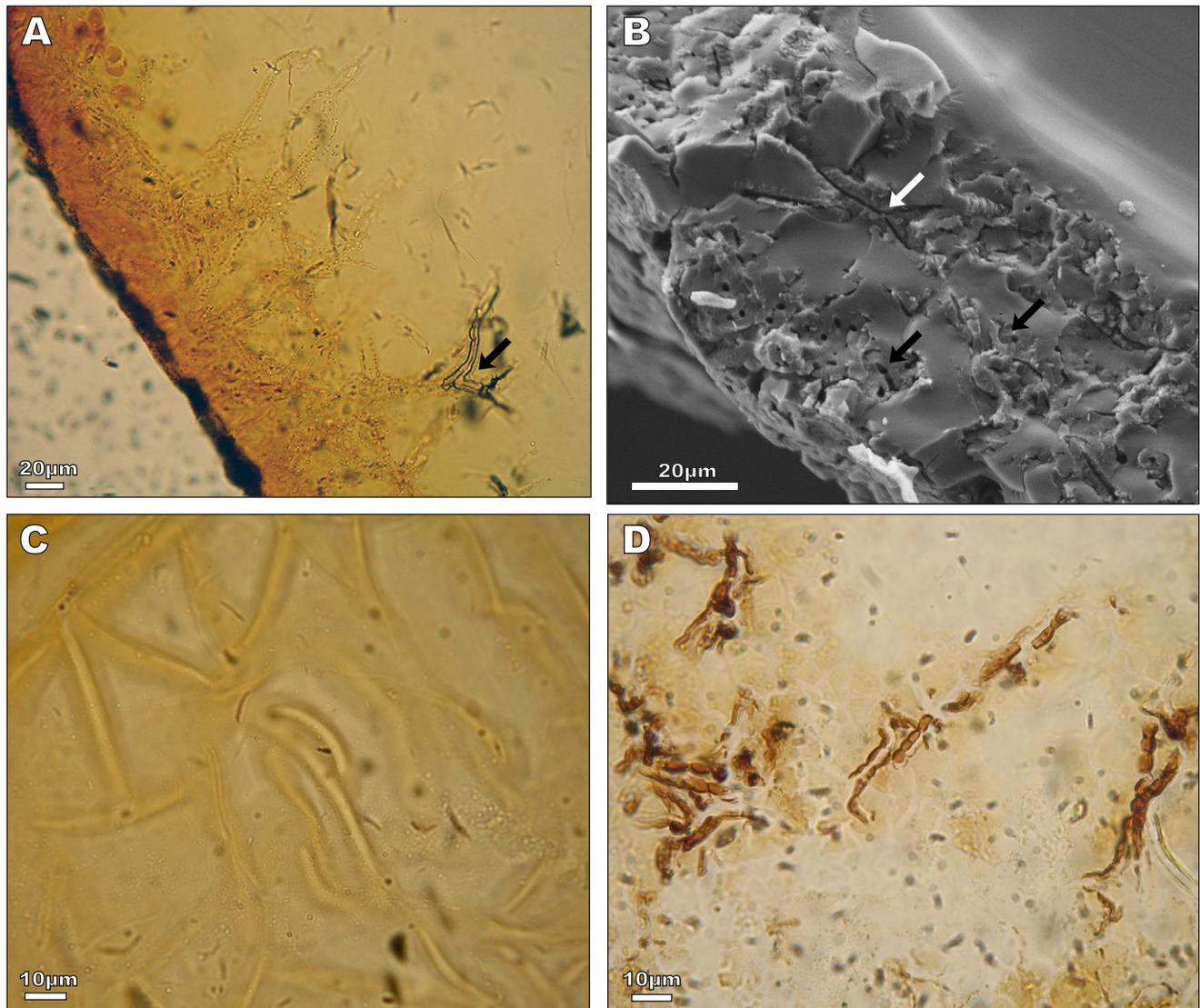


FIGURE 7. Microbial inclusions in amber from the upper Turonian of Sainte-Mondane (Unit I). A) Section of an amber drop showing colonisation by *Leptotrichites* tufts (arrow indicates the dichotomy and the sheath around the lumen) (MNHN.F.F62401). B) SEM view showing development of *Leptotrichites* network at the grain periphery (black arrows indicate the sheath and white arrow is directed at the true branching of a filament) (MNHN.F.F62405). C) Network of apparently filamentous microstructures observed on the periphery of a drop-shaped grain (MNHN.F.F62402). D) Septate hyphae of filamentous fungi (MNHN.F.F62403).

that have been identified in the past as *C. diskoensis* might be insect eggs (Batten and Zavattieri, 1995, 1996; Heřmanová *et al.*, 2013), in common with other species of *Costatheca*, *C. dakotaensis* is considered to be a seed cuticle. Colin (1973a, b, 1975) reported the same species from the Cenomanian of Dantou and La Malvie, also in Sarladais, but the specimens of *Costatheca* that he recovered from the upper Turonian of Saint-Cirq, about 30km northwest of Sainte-Mondane, were not identified to species.

The megaspore assemblage consists of some well to fairly well preserved specimens as well as numerous fragments of species referable to several genera

including *Ariadnaesporites*, *Bacutriteles*, *Echitriteles*, *Erlansonisporites*, *Maexisporites*, *Minerisporites* and *Verrutriteles*. Among these are *Echitriteles zemechensis* (Knobloch, 1984; Fig. 9A), *Minerisporites mercadensis* Lachkar in Floquet and Lachkar, 1979 and *Verrutriteles* sp. cf. *V. dubius* Potonié, 1956 *sensu* Colin, 1975. Representatives of *Bacutriteles*, such as *B. colinii* Lachkar in Floquet and Lachkar, 1979 (Fig. 9B), are the most common forms, although whole specimens are outnumbered by broken and fragmentary remains.

Notwithstanding identification problems associated with many of the mid-Cretaceous megaspore assemblages



FIGURE 8. Miospores from the upper Turonian of Sainte-Mondane (Unit I). Accompanying data are palynological preparation and slide numbers prefixed by QPR (Aberystwyth University palynological preparation identifier) followed by England Finder coordinates. Authors of taxa not otherwise cited in the text are not listed in the references. A) *Osculapollis aequalis* Tschudy, 1975; QPR3675.2, W43.0.B, I) *Vacuopollis microconcaus* Pacltová & Krutzsch, 1967 [also *Neotriangulipollis* sp. 1 *sensu* Azema *et al.*, 1981]; B, QPR3675.2, J23.0; I, QPR3675.3, N19.4. C) *Trudopollis* sp. cf. *T. conector* Pflug, 1953; QPR3675.2, U31.0. D) *Echiperiporites* sp.; QPR3675.2, P34.1. E) *Triangulipollis* sp. cf. *T. triangulus* Kedes & Diniz, 1981; QPR3675.2, L25.0. F) *Atlantopollis* sp. cf. *A. choffatii* Diniz, Kedes & Simonsics, 1977 (intermediate between *A. choffatii* and *A. reticulatu* Krutzsch in Goczán *et al.*, 1967); QPR3675.2, V27.4. G) *Trudopollis* sp. cf. *T. mechanicus* Pflug, 1953 [cf. *Trudopollis hemimechanicus* Pflug, 1953 in Médus, 1981]; QPR3675.2, X35.0. H) cf. *Trudopollis nonperfectus* Pflug, 1953 *sensu* Azema *et al.*, 1981; QPR3675.2, V36.0. J, Q) cf. *Extratropollenites hemiperfectus* Pflug, 1953 in Skarby, 1968 *sensu* Médus *et al.*, 1980 [*Subtrudopollis* sp. 2 in Azema *et al.*, 1981]; J, QPR3675.3, E31.2; Q, QPR3675.2, S25.2. K) *Complexiopollis patulus* Tschudy, 1973 *sensu* Azema *et al.*, 1981; QPR3675.2, W25.4. L) *Interporopollenites* sp. cf. *I. weylandii* Kedes & Hegedüs, 1975; QPR3675.2, D33.2. M) *Extratropollenites* sp. *sensu* Skarby, 1968; QPR3675.3, E22.3. N) *Plicapollis silicatus* Pflug, 1953; QPR3675.2, E29.4. O) *Complexiopollis praeatumesens* Krutzsch, 1959; QPR3675.2, J22.1. P) cf. *Plicapollis pseudoexcelsus* (Krutzsch, 1958) Krutzsch, 1961 *sensu* Azema *et al.*, 1981; QPR3675.2, X45.4. R) cf. *Vacuopollis semiconcaus* Pflug, 1953 in Pacltová & Krutzsch, 1967 *sensu* Médus *et al.*, 1980; QPR3675.2, K25.2. S) *Dictyophyllidites* sp.; QPR3675.2, R58.3. T) *Choanopollenites* cf. *discipulus* Tschudy, 1973 *sensu* Azema *et al.*, 1981 [cf. *Vacuopollis pyramis* Pflug, 1953 in Pacltová & Krutzsch, 1971 *sensu* Médus *et al.*, 1980]; QPR3675.3, S23.2. U) cf. *Trudopollis orthomechanicus* Pflug, 1953 *sensu* Azema *et al.*, 1981; QPR3675.2, K21.4. V) *Tricolpopollenites minutus* Brenner, 1963; QPR3675.2, O26.2. W) cf. *Conclavipollis* [= *Vacuopollis*] sp. 1 in Médus *et al.*, 1980; QPR3675.3, N28.4. X) *Classopollis torosus* (Reissinger, 1950) Couper, 1958; QPR3675.2, P35.4. Y) *Microreticulatisporites sacalii* (Deak & Combaz, 1967) Ravn, 1986; QPR3675.3, J20.2. Z) *Podocarpidites* sp. cf. *P. potomacensis* Brenner, 1963; QPR3675.2, N37.3.

that have been described hitherto, as noted previously by Batten *et al.* (2010), it is clear that the assemblage from Sainte-Mondane is at least partly comparable to that described by Colin (1975) from the upper Turonian of Saint-Cirq. Particularly significant is the specimen that he identified as *Echitriletes cf. lanatus* (see Colin, 1975: pl. 1, fig. 9). This appears to be very similar to a few of the spores recorded from Sainte-Mondane that are closely comparable, if not identical, to *Echitriletes zemechensis*, a species that should be placed in another genus in due course (Batten, 2012). His *Arcellites disciformis* (Colin, 1975: pl. 1, fig. 10) is probably a damaged *Ariadnaesporites*, which means that it is another taxon in common with the Sainte-Mondane assemblage.

PLANT CUTICLES AND WOOD

The plant cuticles from Unit I are well preserved showing clear details of epidermal cells and stomata (Fig. 10). The coniferalean cheirolepidiaceous genus *Frenelopsis* is represented by numerous fragmented leafy sheaths showing three leaf tips per whorl and well defined stomatal rows (Gomez *et al.*, 2002) (Fig. 10A, B). The conifer *Glenrosa* mostly consists of isolated leaves showing the typical stomatal hairy crypts of the genus (Gomez *et al.*, 2012) (Fig. 10C–E). This record is contemporaneous with that from the upper Turonian of La Mède, Bouches-du-Rhône (B. Gomez and V. Daviero-Gomez, unpublished data), and it demonstrates the broad age range of *Glenrosa* from the late Barremian to the late Turonian in Western Europe (Gomez *et al.*, 2001, 2012). Leafy stems bearing tiny, spirally arranged leaves and stomata randomly arranged are temporarily identified as *Brachyphyllum* (Fig. 10F, G). One aciculate, mucronate leaf tip probably belongs to a fourth type of conifer. A few cuticle fragments showing net venation clearly indicate the occurrence of eudicot angiosperms in the assemblage (Fig. 10H), but the small size of the fragments prevent any further identification. Only tiny fragments of wood are sorted.

The lignitic sands of Unit II-b contain large branches or trunks more than 1m long. They all belong to the conifer wood *Agathoxylon*.

INVERTEBRATE AND VERTEBRATE REMAINS

The clays of Unit I contain termite coprolites, hexagonal in section, corresponding to *Microcarpolithes hexagonalis* (Colin *et al.*, 2011). It is noteworthy that these coprolites are associated with the amber-bearing lignitic deposits from the Albian and Cenomanian of Charentes (Colin *et al.*, 2011), but also with some Early Cretaceous (Hauterivian–

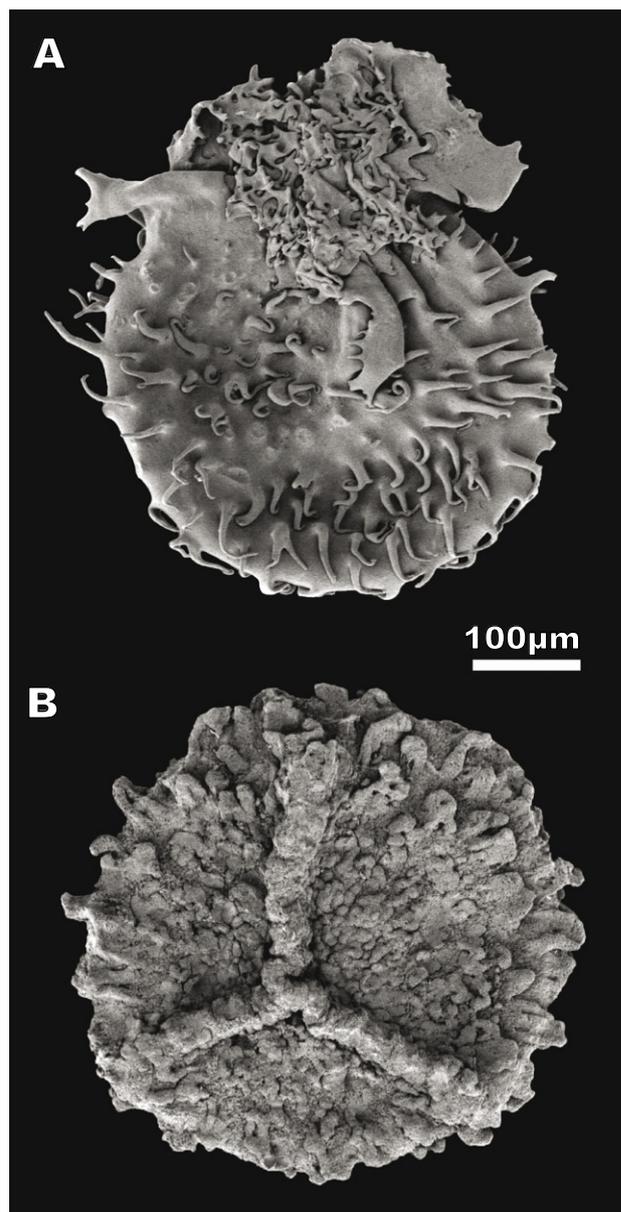


FIGURE 9. Examples of megaspores from the upper Turonian of Sainte-Mondane (Unit I). Preparation MFP509 (Aberystwyth University plant mesofossil preparation identifier), SEM stub number 2014/18. A) *Echitriletes zemechensis* Knobloch, 1984. B) *Bacutriletes colinii* Lachkar, in Floquet and Lachkar, 1979.

Barremian) lignitic deposits without amber such as the bone bed of Angeac-Charente (Néraudeau *et al.*, 2012). The Sainte-Mondane outcrop confirms its association with amber-rich lignites of southwestern France until the late Turonian as previously reported by Colin (1973a, b) at Saint-Cirq. No calcareous microfossils, such as ostracods or foraminifers, have been found in the clays.

The sands of Unit II-a contain small solitary corals, pectinid and oyster fragments, and broken echinoid spines.



FIGURE 10. Plant meso-fossils from the upper Turonian of Sainte-Mondane (Unit I). A) Whorl of three leaves of *Frenelopsis* sp. with short, distal free parts (UCBL-FSL 75132). B) Cuticle of half of the leafy whorl of *Frenelopsis* sp. showing parallel longitudinal rows of stomata (UCBL-FSL 75133). C) Leafy stem of *Glenrosa* sp. bearing spirally arranged stockey leaves (UCBL-FSL 75134). D) Lateral view of an isolated leaf of *Glenrosa* sp. showing numerous stomatal crypts on the abaxial cuticle (UCBL-FSL 75135). E) Top view of an isolated leaf of *Glenrosa* sp. showing several stomatal crypts on the adaxial cuticle (UCBL-FSL 75136). F) Leafy stem of *Brachyphyllum* sp. bearing spirally arranged scale-like leaves (UCBL-FSL 75137). G) Detail of (F) showing a leaf with randomly distributed stomata. H) Angiosperm eudicot leaf showing venation and numerous stomata (UCBL-FSL 75138). Scale bars: 1mm.

These invertebrate remains are too fragmentary to be identified more accurately, except the coral specimens that can all be assigned to *Aulosmilia compressa*, a species known from the upper Turonian of Uchaux, southeastern France (Roman and Mazeran, 1920). Vertebrate remains are rare and consist of a few selachian and osteichthyan teeth and very small fragments of turtle shells. The selachian teeth can be referred to the widespread anacoracid shark *Squalicorax* sp. and to the sclerorhynchid sawfishes *Ischyrhiza viaudi* (Fig. 11A) and *Ptychotrygon* sp. (Fig. 11B). Interestingly, *I. viaudi* was previously known only from the early Santonian deposits of Les Bardys in Vendée (Cappetta, 1981), where it was also found in association with *Ptychotrygon* sp. However, a latest Turonian or Coniacian age for the teeth found at Les Bardys cannot be totally discounted because they come from a sandy layer intercalated between a late Turonian erosion surface and an early Santonian clayey bed (Cappetta, 1981). The Late Cretaceous genus *Ischyrhiza* is mainly known from North America, whereas it is extremely rare in Europe (Cappetta, 2012). The teeth of *Ptychotrygon* from Sainte-Mondane and Les Bardys are morphologically similar and might be conspecific. They clearly differ from the teeth of *Ptychotrygon gueveli*, from the late Turonian of northwestern France (Cappetta, 2004), by a less developed ornamentation. The osteichthyan teeth can be assigned to cf. *Belonostomus* and cf. *Paralbula*. It is worth noting that the *Ischyrhiza*–*Belonostomus*–*Paralbula* association has been recorded from some Late Cretaceous coastal assemblages of North America (*e.g.*, Brinkman *et al.*, 2004).

PALAEOENVIRONMENTAL DISCUSSION

The clays of Unit I containing abundant and diverse plant meso-fossils, palynomorphs and amber grains were probably deposited in a low-energy environment: either an estuary or a muddy lagoon. Moreover the presence of filaments of *Leptotrichites* in some amber grains suggests that this resin was produced in a humid environment. Living sheathed bacteria inhabit permanent water bodies (Schmidt and Schäfer, 2005). The centripetal growth of the microbial inclusions suggests that actinomycetes and sheathed bacterial filaments in amber used the soft resin as a nutritional supply, and colonised the resin for as long as possible (Waggoner, 1994; Girard, 2010; Beimforde and Schmidt, 2011; Breton, 2011, 2012; Saint Martin *et al.*, 2012, 2013a; Breton *et al.*, 2013). This growth habit has also been described from other French ambers (Girard, 2010). The development of cyanobacteria and mycelia in amber probably occurred in a coastal forest before the sedimentation of the fossil resin, as previously suggested for the amber from the Albian–Cenomanian of Charentes (Girard, 2010). The absence of calcareous microorganisms is difficult to explain. It can be either an ecological



FIGURE 11. Batoid teeth from the upper Turonian of Sainte-Mondane (Unit II). A) Oral tooth of *Ischyrhiza viaudi* in occlusal view (IGR-PAL-2664). B) Oral tooth of *Ptychotrygon* sp. in occlusal view (IGR-PAL-2665). Scale bar: 1mm.

indicator or a diagenetic artefact. However, the clays of Unit I correspond to an anoxic depositional environment. Pyritized oysters often occur in this kind of facies, as seen in the lignites from the Albian and Cenomanian of Charentes (Néraudeau *et al.*, 2002; Videt and Platel, 2005). Hence, their absence in the clays of Unit I may be simply because they did not inhabit muds in which plant remains and amber grains accumulated. If so, these clays were deposited in a confined, very reducing environment rich in organic matter that was rarely connected to the sea.

The sands of Unit II containing corals, oysters, echinoids and fish teeth are clearly coastal marine deposits. However, the presence of several successive lignite lenses suggests repeated continental input. The cross-bedding structure and the coarse and irregular granulometry of the sands indicate that they were deposited in a high-energy, shallow-water environment during a major regressive event (Platel, 1989, 1996). They are clearly more marine than the lignitic limestones and clays with oysters and

amber from the Cenomanian of Sarlat-la-Canéda in the Dordogne (Videt and Platel, 2005; Saint Martin *et al.*, 2013b). Thus, the Cenomanian lignites of the same area that contain paralic oysters (*Acutostrea lingularis*) are devoid of stenohaline marine invertebrates, whereas the abundance of corals and the presence of echinoid spines at Sainte-Mondane indicate fully marine conditions.

CONCLUSIONS

The upper Turonian lignites of Sainte-Mondane constitute one of the rare Turonian amber deposits known in Europe. In the lignitic clays, amber is associated with wood (*Agathoxylon*), foliage (*Frenelopsis*) and abundant bisaccate and *Classopollis* pollen grains. The meso- and macro-fossil assemblage was previously found in the Albian and Cenomanian lignites of France and Spain (Gomez *et al.*, 2002, 2004; Najarro *et al.*, 2009, 2010; Colin *et al.*, 2011). Hence, the *Agathoxylon–Frenelopsis* association may have been typical of mid-Cretaceous amber-producing forests. In the overlying coastal marine sands, the presence of the sawfish genus *Ischyrhiza* is noteworthy.

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