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Published in:
Cretaceous Research

DOI:
[10.1016/j.cretres.2016.10.001](https://doi.org/10.1016/j.cretres.2016.10.001)

Publication date:
2017

Citation for published version (APA):

Néraudeau, D., Perrichot, V., Batten, D., Boura, A., Girard, V., Jeanneau, L., Nohra, Y. A., Polette, F., Saint Martin, S., & Thomas, R. (2017). Upper Cretaceous amber from Vendée, north-western France: Age dating and geological, chemical, and palaeontological characteristics. *Cretaceous Research*, 70, 77-95.
<https://doi.org/10.1016/j.cretres.2016.10.001>

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Accepted Manuscript

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PII: S0195-6671(16)30247-6

DOI: [10.1016/j.cretres.2016.10.001](https://doi.org/10.1016/j.cretres.2016.10.001)

Reference: YCRES 3459

To appear in: *Cretaceous Research*

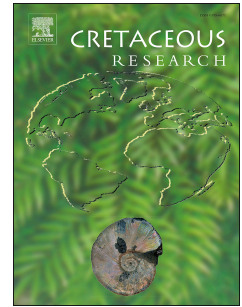
Received Date: 7 July 2016

Revised Date: 30 September 2016

Accepted Date: 3 October 2016

Please cite this article as: Néraudeau, D., Perrichot, V., Batten, D.J., Boura, A., Girard, V., Jeanneau, L., Nohra, Y.A., Polette, F., Martin, S.S., Saint Martin, J.-P., Thomas, R., Upper Cretaceous amber from Vendée, north-western France: Age dating and geological, chemical, and palaeontological characteristics, *Cretaceous Research* (2016), doi: 10.1016/j.cretres.2016.10.001.

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Upper Cretaceous amber from Vendée, north-western France: age dating and geological, chemical, and palaeontological characteristics

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ABSTRACT

The Upper Cretaceous lignite deposits of La Garnache, Vendée (western France), consist of two lignitic clay series, Garnache 1 and Garnache 2, separated by a fault. The first series cropped out to the south of the fault during road works until 2002 but is now covered by an embankment. It has provided numerous pieces of amber containing arthropod and micro-organism inclusions. The second lignitic series, exposed to the north of the fault, is rich in fossil wood but devoid of amber. Palynological analysis of Garnache 1 revealed several Normapolles species belonging to the genera *Atlantopollis*, *Complexiopollis*, *Osculapollis*, *Plicapollis* and *Trudopollis*, but larger forms typical of Senonian deposits are absent. By contrast, Garnache 2 proved to be dominated taxonomically and numerically by spores (*Appendicisporites*, *Camarozonosporites*, *Gleicheniidites*, *Patellasporites*, *Stereisporites*), associated with a few gymnosperm (*Cerebropollenites*, *Phyllocladidites*, *Classopollis*) and angiosperm (*Liliacidites*, *Retitricolpites* and a single specimen of the Normapolles *Complexiopollis*) taxa. Garnache 1 is, therefore, younger than Garnache 2, the latter being clearly Cenomanian in age whereas Garnache 1 is more likely to be Turonian. Lignitic clay of Garnache 1 contains numerous translucent, orange to red, pieces of amber. Vendean amber is rich in aquatic arthropods, such as tanaids and epicarideans (Crustacea), as well as marine or brackish siliceous micro-organisms such as diatoms and sponge spicules. These aquatic inclusions indicate that resin-producing trees grew along and close to the seashore. The amber-bearing clay was deposited in a calm, estuarine or lagoonal, muddy environment.

Keywords: Amber, Arthropods, Micro-organisms, Palynology, Turonian, Vendée, Western France

1. Introduction

Many Cretaceous amber-bearing deposits have been known in western France since the beginning of the 19th Century. The main localities are in Charentes (Lacroix, 1910; Schlüter, 1978; Néraudeau et al., 2002, 2003, 2005, 2008; Perrichot et al., 2007, 2010), Sarthe (Lacroix, 1910; Girard et al., 2013), Maine-et-Loire (Lacroix, 1910; Néraudeau et al., 2013), and Dordogne (Saint-Martin et al., 2013). Lacroix (1910) mentioned that amber had been reported from Carboniferous and Cretaceous lignites in Vendée by several authors (Cavoleau, 1818; Rivière, 1840, 1842; De la Fontenelle de Vaudoré, 1844) but even the precise descriptions of Cenomanian lignites from the south of Challans by Rivière (1842) and Louail (1984, p. 226) made no mention of amber despite noting the presence of very small crystals of gypsum and pyrite. Similarly, the mineral inventory of the department of Vendée by Cavoleau (1818), supplemented by De la Fontenelle de Vaudoré (1844), listed many things including fossil plants (lignite,

coal) and ambergris from cetaceans, but not amber or its equivalents “succin” and “retinasphalt”. Hence, amber in Vendée was effectively unknown until 2002 when many small pieces were found in a deposit exposed during a period of road works near the village of La Garnache. Although mainly consisting of mm- to cm-sized pieces, they are among the most fossiliferous of Cretaceous ambers from France.

The physical, chemical, and palaeontological characteristics of the amber that was recovered are described and, combined with consideration of the geological background (Figs 1, 2, 4) and the recovery of palynomorphs from the associated sediments, its age and palaeoenvironmental significance are discussed in this paper.

2. Material and methods

2.1. Locality

The amber-bearing deposit is located at La Robinière, near the village of La Garnache in Vendée (Fig. 1). Amber was collected during 2002 and 2003 (mainly by F. Dupé and D. Graves) from a first outcrop named “Garnache 1”. This consisted of grey clay with lignitic lenses (Anfray, 2004) and was limited to a few decimetres temporarily exposed by works along departmental road D32 between La Garnache and Challans (Fig. 2A, B). The exposure was on the right-hand side of the road to Challans at around 300 m from a bridge over it. The few observable *in situ* strata occurred in a trench dug into the road embankment (Fig. 2B). Amber and fossil wood were collected from the lignites (Fig. 2C, D).

Further field work was realized between 2005 and 2014, although by then the amber-rich layer had been removed by the road works or was covered by vegetation, the embankment and the road itself. In collaboration with the Departmental Road Agency of Challans, five excavations were carried out using a mechanical shovel in June 2011, along a 300-m-long transect from Garnache 1 to a second outcrop named “Garnache 2” (a few metres from the bridge mentioned above) at the base of the road embankment (Fig. 2E). No additional amber was found, nor could the amber-bearing bed be identified. Only more or less disturbed sand and lignites were encountered.

Currently the right-hand side of the road to Challans only exposes lignitic sand in the upper-middle parts of the embankment, corresponding to Garnache 2 (Fig. 2F, G), which is entirely devoid of amber.

For palynological, micropalaeontological, and palaeobotanical analyses and a further search for amber, a total of 10 kilograms of lignitic sand and clay from Garnache 2 were collected and analyzed. By comparison, only a few dozen grams of lignitic sand and clay coating amber and wood were available from Garnache 1 for palynological analysis.

2.2. Preparation and analytical techniques

2.2.1. Amber

The amount of material from Garnache 1 provided by the collectors comprises 5700 pieces of amber totalling 305 g only. Most of the pieces are 3 to 10 mm in size, but rare larger pieces up to 35 mm were also found. They are clear yellow to orange in colour (Fig. 3), with only a thin weathered surface and no cortex of alteration, in common with most Albian–Cenomanian French ambers (Girard et al., 2009a).

The amber fragments were ground and polished using a series of decreasing grits (1500, 2400) of silicon carbide papers on a water-fed lapidary wheel. Two pieces containing insect inclusions were embedded in Canada balsam between cover glasses using established techniques (Azar et al., 2003), but the balsam penetrated the amber matrix in a very unusual way and caused irreversible damage to the fossil inclusions (lightening and degrading the insect cuticle). Instead, fragile specimens were embedded in clear EpoxyCure resin using standard techniques (Nascimbene and Silverstein, 2000). The resulting blocks of epoxy were polished for an optimal view of the

arthropod specimens under various stereomicroscopes at magnifications of $\times 10$ to $\times 110$. The screening for micro-organisms was performed on small fragments that were mounted on slides with Canada balsam and observed directly under a Leica DMLP microscope (see methods in Girard, 2010). Polished sections were made by embedding pieces of amber in the epoxy resin Araldite 2020. Both petrographic and polished sections were photographed under a Zeiss Axioscope 40 optical microscope at magnifications of $\times 40$, $\times 63$ and $\times 100$ (oil immersion).

2.2.2. Wood remains

Wood remains were abundant in Garnache 1 and scarce in Garnache 2, but only fragments from the first outcrop (Fig. 2E) have been studied, to provide xylological data that could be combined with the resin data (amber is absent in Garnache 2).

The fragments are preserved as lignite and their maximum dimensions vary from a few centimetres to several decimetres. We examined 42 samples of secondary xylem under both scanning electron and light microscopes (SEM and LM) after standard preparation.

2.2.3. Palynomorphs

Two samples of sediment collected from Garnache 1 in 2002, and two from Garnache 2 in 2011, were examined for their palynological content.

Processing of the material was carried out using a standard procedure that involved immersion of 10 g of sample in dilute HCl, followed by digestion in 58-62% HF and brief oxidation (30 s) of the organic residue in fuming HNO₃, washing after each stage until the aqueous residue was neutral (for further details, see Batten, 1999, p. 15).

2.3. Repository

All the mesofossil material discussed herein is deposited in the Geological Department and Museum of the University Rennes 1 (France), under collection numbers IGR.GAR-001 to IGR.GAR-129 for pieces of fossiliferous amber, and IGR.PAL.9000 to IGR.PAL.9041 for analyzed samples of fossil woods. The palynological slides are currently housed in the palynological collection of Aberystwyth University, Wales, under slide numbers QPR3666.2, 4 and 5 and QPR3667.2. Thin sections of amber are housed at the Muséum National d'Histoire Naturelle, Paris, under collection numbers MNHN.F.F63106 to MNHN.F.F63109.

3. Geological background

Precise dating of the lignites and their associated amber in Garnache 1, as well as the lignite in Garnache 2, has been difficult because:

- (1) there is no longer any exposure of the series comprising Garnache 1 to enable further sampling to add to the limited material available for analysis;
- (2) previous interpretations of the complex geology of the Challans-Commequiers Basin, including La Garnache deposits, are confusing (Fig. 4): the most recent geological studies record lignitic deposits from Cenomanian (e.g., Viaud et al., 1979), Turonian (Ters and Viaud, 1983), Santonian (Azema and Viaud, 1979), and Eocene (Azema et al., 1978) successions (Fig. 4).

From the beginning of the 19th Century (Rivière, 1840, 1842) to the middle of the 20th (Ters, 1958, 1961), Cretaceous deposits in the Challans Basin were considered to be Cenomanian in age (e.g., Ters, 1961, fig. 10, p. 116). Thus, lignites of the region previously referred to as “Argiles à Lignite et sperkise” by Rivière (1842) were attributed to the base of the Cenomanian “Sables et argiles de Challans” by Louail (1984) (L1 in Fig. 4). These early age interpretations were applied to the first edition of the 1/80,000 Palluau geological map (Wallerant, 1902).

Turonian and Senonian deposits were recognized in the second edition of the geological map (Ters et al., 1972). The former consist of limestones containing oysters and inoceramids (*Inoceramus labiatus*) or ammonites (*Mammites* sp.), indicating an early Turonian age (Fig. 4). The Senonian was a poorly defined formation of limestones with rudists (*Praeradiolites cylindraceus*), sands with sponges, and a microfauna that indicated a post-Turonian age (Fig. 4). At this stage of knowledge, the only known lignitic clay in the Challans Basin was located at the base of the Cenomanian, with black clay containing fossil plants of the “Argiles et Sables de Challans” formation located at the middle/upper Cenomanian boundary.

At the end of the 20th Century, the Challans map at 1/50.000 (Ters and Viaud, 1983) identified three levels of lignitic clays in the regional Cretaceous stratigraphy (Fig. 4): (1) black clays of the “Argiles et Sables de Challans” at the middle/upper Cenomanian boundary (L1 in Fig. 4) (Louail, 1976; Louail and Viaud, 1977; Viaud, 1981), reported to the south and west of Challans but not to the north where La Garnache is located; (2) grey to black clays with early Turonian palynofloras (L2 in Fig. 4) from the south of Challans (“Creux jaune en Commequiers”) and from a borehole to the north at Petite Robinière near La Garnache (Ters and Viaud, 1983); (3) a lower Santonian dark clay series (L3 in Fig. 4) at “Bardys en Notre-Dame-de-Riez” and 10 km north of Challans at “Pavillon en La Garnache” (Azema and Viaud, 1979).

Diverse palynological assemblages were reported from these lignite-rich clay beds (Durand and Ters, 1958; Durand et al., 1963) along with a few macrofossils such as small Cenomanian (*Rhynchostreon suborbiculatum*, *Ceratostreon flabellatum*) and Senonian (*Ceratostron pliciferum*) oysters (Freneix and Viaud, 1986). Although wood was abundant in the Cenomanian black clays (Durand and Ters, 1958; Ters et al., 1972) no amber was recorded.

Notwithstanding the recognition of three levels of lignite-rich clays in the Challans-Commequiers Basin, their precise stratigraphic position has been difficult to determine because in several localities the sections consist of Santonian sand and dark clay overlying Cenomanian or Turonian sand and black clay (Freneix and Viaud, 1986). Confusion has increased since publication of the last edition of the regional geological guide, which indicated that all dark clay north of Challans (i.e., including the La Garnache deposits) is of Cenomanian age (Gabilly et al., 1997), contrary to the results of the earlier studies noted above. The combination of successions of sand, clay and oyster beds of similar general aspect where they crop out make it difficult to determine whether Cenomanian, Turonian or Senonian deposits are exposed, as has been the case with respect to the Garnache beds at La Robinière.

4. New observations and palynological analyses

4.1. Garnache 1

4.1.1. Age uncertainties

The sand and clay rich in lignite that can be seen in the embankment of the outcrop at Garnache 1 today do not yield amber. Being some 2–3 m above the amber-bearing bed exposed in 2002 they are probably a little younger, the older deposit either having been partly or totally removed or covered with asphalt by the road works. Therefore, dating of the amber and its animal and plant inclusions has to rely on analyses of the very limited material that was collected more than ten years ago.

According to the 1/80,000 geological map and the regional geological guide, the amber from Garnache 1 can be considered Cenomanian in age, whereas the most recent geological map at 1/50,000 indicates a Turonian or Santonian age (see section 3). Moreover, a borehole drilled at the locality Petite Robinière (Ters and Viaud, 1983), which is about 500 m from the amber locality, was found to contain Turonian black clay. On the other hand, one of the amateur palaeontologists (DG) collected a specimen of the oyster *Ceratostreon pliciferum* from the amber bed of Garnache 1, a species that is generally regarded as indicating a Coniacian age (Freneix and Viaud, 1983). Also in a palaeobotanical and palynological study of lignitic clay from Garnache 1, Legrand et

al. (2006) suggested that it was Senonian rather than Turonian in age. Based on these observations, there are two possible solutions regarding the age of the amber. (1) If the borehole drilled some 500 m distant from Garnache 1 is representative and the black clay encountered at a depth of 2 m under upper Turonian sand and sandy limestones (“Raillères faciès”) is early Turonian in age, the amber-bearing clay of Garnache 1 is probably also Turonian. It is noteworthy that the black clay in the borehole directly overlies schistose basement, which excludes the local presence of Cenomanian black clays. (2) If it is accepted that the geological map showing only Senonian strata (Ters and Viaud, 1983) is correct and that the find of a single shell of *Ceratostreon pliciferum* on the surface of the clay removed by the road works indicates a Coniacian–early Santonian age, then a third regionally significant lignitic bed, is probable.

4.1.2. New palynological analysis

One of the samples from Garnache 1 that was processed for its palynological content yielded a small assemblage of c. 70 palynomorphs. Specimens referable to the Normapolles group are dominant, comprising two-thirds of the taxa identified. They include several species of *Trudopollis* (Fig. 5H, N, T, Y), *Plicapollis* (Fig. 5I, J), *Complexiopollis* (Fig. 5M, O, U) and *Osculapollis* (Fig. 5P, V). Other genera such as *Atlantopollis* (Fig. 5K), *Neotriangulipollis* (Fig. 5L), *Extratropopollenites* (Fig. 5W) and *Subtrudopollis* (Fig. 5X) are only represented by one species each.

The assemblage also includes a few specimens of *Classopollis* (Fig. 5A–C), a bisaccate pollen grain (not illustrated) and several other non-Normapolles, angiosperm taxa. The latter are represented by tricolpate and tricolporate forms such as *Retitricolpites virgeus* (Groot, Penny et Groot) Brenner sensu Singh, 1971 (Fig. 5R, S), *Tricolpites* sp. cf. *T. barrandei* Pacltová, 1971 (Fig. 5Q), *Tricolpites* sp. (Fig. 5D, E) and *Tricolporopollenites distinctus* Groot et Penny (Fig. 5F, G). Very few spores were encountered.

According to Goczan et al. (1967), the stratigraphic range of the genus *Atlantopollis* extends from the middle Cenomanian to the middle Turonian. Azema et al. (1981) indicated in their fig. 5 that the recorded range of *Atlantopollis* species extends into the lowermost Santonian, but only Cenomanian and Turonian species were mentioned in the paper. Except for Stanley and Kedves (1975) who just referred to the material they examined as being from the “Upper Cretaceous”, all specimens identified as *Atlantopollis microreticulatus* Krutzsch in Goczan et al. (Fig. 5K) have been found in Cenomanian–Turonian sediments (Groot and Groot, 1962; Durand and Louail, 1976).

Complexiopollis praetumescens Krutzsch (Fig. 5M) is also regarded by most authors as an early form of the Normapolles group, being largely confined to upper Cenomanian–lower Turonian deposits (Krutzsch, 1959; Leopold and Pakiser, 1964; Van Amerom, 1965; Médus, 1970; Kedves, 1980, 1983; Herngreen and Chlonova, 1981). Médus and Ipert (1977) noted its presence in Santonian sediments but neither described nor illustrated it; as a result, it is not possible to verify their identification.

The occurrence of *Atlantopollis microreticulatus* and *Complexiopollis praetumescens* combined with the absence of larger forms typical of Santonian deposits, such as *Santonipollis*, *Papillopollis* and *Megatriopollis*, suggest that the sediments from Garnache 1 are more likely to be Turonian than Santonian in age.

4.2 Garnache 2

As mentioned above, the lignitic series of Garnache 2 are separated from those of Garnache 1 by a fault, so that their ages are not necessarily the same despite their close proximity.

Unlike the palynological sample from Garnache 1, that examined from Garnache 2 yielded thousands of specimens. Of the 500 recorded, 47 species have been identified (see detailed list in Table 1), of which only a few are illustrated here (Fig. 6). The assemblage is clearly dominated taxonomically (36 species) and numerically (78% of the assemblage) by spores. They include numerous schizaeaceous specimens (several

species of *Appendicisporites* and *Camarozonosporites*: (6A, B) and an abundance of essentially smooth-walled spores including *Stereisporites psilatus* Ross (Fig. 6I), *Gleicheniidites circinidites* (Cookson) Dettmann (Fig. 6K) and *Laevigatosporites ovatus* Wilson et Webster (Fig. 6J). Specimens referable to the genus *Patellasporites* are the most abundant, representing 20% of the assemblage (Fig. 6H). Other spores include *Crybelosporites* sp. (Fig. 6D).

Gymnosperm pollen comprise 5% of the assemblage with only four species encountered (*Cerebropollenites mesozoicus* (Couper) Nilsson (Fig. 6L); two species of *Phyllocladidites*; and a few specimens of *Classopollis*). Although the angiosperm component of the assemblage lacks diversity with only seven species identified, it amounts to about 15% of the palynomorphs recorded, including monocolpate, tricolpate, triporate and periporate grains represented by such taxa as *Liliacidites reticulatus* (Brenner) Singh (not illustrated), *Retitricolpites virgeus* (Groot, Penny et Groot) Brenner (not illustrated), *Tricolpites albiensis* Kemp, 1968 (Fig. 6E), and *Bohemiperiporis zaklinskaiae* Pacltová, 1968 (Fig. 6F, G) respectively. One specimen belonging to the Normapolles group has been identified as *Complexiopollis* sp. cf. *C. vulgaris* (Groot et Groot) Groot et Krutzsch (Fig. 6C), which suggests that this assemblage is unlikely to be older than mid Cenomanian (Azema et al., 1972).

No dinoflagellate cysts were recorded from either sample, rather the presence of the freshwater algae *Tetraporina* (in Garnache 1) and *Lecaniella* (in Garnache 2) was noted.

4.3 Conclusion

Based on these data the amber-bearing sediments of Garnache 1 are clearly younger than the deposits of Garnache 2. Although the palynomorph assemblage from the former is small and of limited diversity, overall it suggests a Turonian rather than a Santonian age (cf. Legrand et al., 2006). By contrast, the rich assemblage from Garnache 2 indicates a mid or possibly late Cenomanian age.

5. Palaeontological inclusions in the amber

The study of the available amber pieces revealed a diverse array of arthropods and micro-organisms. Most of the inclusions are exquisitely preserved, without taphonomic distortion or alteration (although they are sometimes fragmentary or partly concealed by debris or bubbles), therefore enabling detailed systematic studies to be carried out (e.g., Perrichot, 2014).

5.1. Arthropods

Arthropod inclusions are fairly abundant compared to similar amber deposits with a majority of small pieces. Ambers from the Triassic of Italy and the Santonian of south-eastern France, for example, are very similar in appearance but contain only a handful of arthropods each (Schmidt et al., 2012; Choufani et al., 2013). In contrast, 172 fossil arthropods were preserved in only 305 g of Vendean amber. They cover a broad diversity including the crustacean orders Isopoda and Tanaidacea; the millipede order Polyxenida; the arachnid orders Trombidiformes and Parasitiformes (Acari), Araneae, and Opiliones; and at least 30 families of hexapods in the orders Collembola, Blattaria, Coleoptera, Dermaptera, Diptera, Hemiptera, Hymenoptera, Isoptera, Neuroptera, Orthoptera, Psocodea, and Thysanoptera (see detailed list in Table 2).

These arthropods are mostly entombed in infra-cm stalactite-like or flat, multi-layered, amber slivers. As such, there has been an evident bias towards the selective trapping of tiny arthropods less than 2 mm in length, including mites (Acari; Fig. 7A), thrips (Thysanoptera), springtails (Collembola), biting, non-biting and gall midges (Diptera: Ceratopogonidae, Chironomidae, Cecidomyiidae; Fig. 7D), parasitic wasps (Hymenoptera: Mymaromatidae, Mymaridae, Platygasteridae), and a variety of insect larvae. Significant findings (Fig. 8) comprise a new family (Nasutiacaridae; Sidorchuk

et al., 2015) and the oldest record of the family Caeculidae within prostigmatid mites (Acari: Trombidiformes); the first fossil record of the extant spider genus *Baalzebub* Codrington (Araneae: Theridiosomatidae; Fig. 7B; Penney, 2014); the oldest record of a megaspilid wasp (Hymenoptera: Megaspilidae; Fig. 7E) and a mesopsocid booklouse (Psocodea: Mesopsocidae); and the infrequent geological record of prostigmatid mites (Acari: Erythraiae, Trombidiae; Fig. 7A) as well as the extant families Coniopterygidae in Neuroptera (Fig. 7C; Perrichot et al., 2014), Merothripidae in Thysanoptera, Compsocidae in Psocodea (Azar et al., 2014), Eriococcidae in Hemiptera and Crabronidae (Bennett et al., 2014) in Hymenoptera (Fig. 8). Also noteworthy is the occurrence of extinct taxa of parasitoid wasps, i.e. the Cretaceous *Serphites* Brues (Serphitidae; Engel and Perrichot, 2014) and *Archaeromma* Yoshimoto (Mymarommatidae; Fig. 7F), and of the fly *Microphorites* Hennig (Diptera: Dolichopodidae; Perrichot and Engel, 2014). Many arthropods remain to be studied before an assignment to family can be achieved: this may provide additional significant records.

The most striking feature is the unusually high number of aquatic arthropods, especially 28 individuals of very small isopod crustaceans found in 18 pieces of amber, and assigned to a larval stage of Bopyroidea or Cryptoniscoidea, together called Epicaridea within the suborder Cymothoidea (Fig. 9A). Epicarideans are ectoparasites of other crustaceans, but the larvae figured here represent a non-parasitic life stage which is probably part of the meiofauna, similar to that recently described from Miocene Mexican amber (Serrano-Sánchez et al., 2016). The present finding in Vendean amber is only the second, and the oldest, record of body fossils of epicarideans (Fig. 8), although evidence of parasitization of decapods by bopyrids extends back to the Jurassic (Williams and Boyko, 2012). These and the further findings of a tanaid (Sánchez-García et al., in press) and an undetermined water mite ('Hydracarina'; Fig. 9B) demonstrate the presence of wet, if not fully aquatic, conditions near the resin-producing trees. At this stage, however, a marine versus brackish or freshwater realm cannot be ascertained, and we cannot exclude the possibility that these arthropods lived in aquatic microhabitats on tree trunks or among the forest litter.

5.2. Micro-organisms

Vendean amber displays a variety of microscopic inclusions, among which are branched bacterial filaments and fungal hyphae, fern spores, but with rare protist-like inclusions (sensu Girard et al., 2011). We have also noted the outstanding presence of centric diatoms (unicellular siliceous microalgae; Fig. 9C) assignable to the marine Corethrales in two amber pieces (Saint Martin et al., 2015), and various sponge spicules (Fig. 9D) in more than 70 pieces. The sponge spicules comprise slightly curved oxea, and spiny and spherical acanthostyle elements. It is noteworthy that not only terrestrial but also aquatic siliceous remains are preserved in the amber, some of which together with the above-mentioned crustaceans. One diatom associated with epicarideans brings further support for the marine or brackish lifestyle of these crustaceans rather than freshwater microhabitats. The occurrence of marine or brackish organisms in amber has been recorded previously from Albian–Cenomanian amber from Charentes (Girard et al., 2008, 2009b; Masure et al., 2013) and Miocene Mexican amber (Serrano-Sánchez et al., 2016). This may be explained by the intervention of wind sprays which could bring marine organisms onto resin flows, or tides which could transport them into ponds near the resin-producing trees, as suggested by Girard et al. (2008, 2009b). This suggests a littoral forest.

Our microscopic analysis of petrographic thin sections revealed different types of micro-inclusions. Among these are apparently filamentous networks developed at the periphery of drop-like amber pieces (Fig. 10A, B), which are difficult to determine exactly as has already been pointed out for similar inclusions in Turonian amber from Dordogne (Néraudeau et al., 2016) and various fossil resins from Spain (Speranza et al., 2015). Also, at the periphery of some amber pieces, filaments with a branching pattern were observed: these exhibit two morphological classes: branched free filaments (Fig. 10C) and clumps of entangled filaments (Fig. 10D). Similar filaments in Eocene amber

from the USA were referred by Waggoner (1993) to the actinomycete cf. *Streptomyces* Waksman and Henrici, 1943. More recently, the same kind of filamentous structures were encountered in Santonian ambers from Martigues (Saint Martin et al., 2012) and Belcodène (Saint Martin et al., 2013). A network of septate filaments was observed in opaque-beige zones of some amber pieces. They are about 4 μm in diameter and are rarely branched (Fig. 10E, F). These characteristics correspond to fungal mycelium and the ovoid structures associated with these filaments represent conidiospores. With these features alone, it is difficult to identify the fungus precisely.

Polished samples of amber enabled further examination of this assemblage of micro-organisms. Many pieces contain hundreds of colonies of rod-shaped bacteria. Most of these represent cocci (Fig. 11), some germinating when they were fixed in the resin. Colonies of bacilli were also observed (not as common as cocci) (Fig. 11). Some of these are associated with bacterial filaments but there is no clear relationship between them. It is therefore impossible to determine whether the bacilli colonies originated from the fragmentation of the bacterial filaments or if they belong to another organism.

Filamentous bacteria observed in polished samples are mainly of three types: (1) Most abundant are peripheral filaments less than 1 μm in diameter. These are dichotomously ramified apically. They form spherical colonies up to 50–100 μm in diameter at the surface of the amber. The development of the colonies is sometimes so significant that all are joined to form an external layer of bacteria around some pieces. (2) A second type is preserved in the matrix of pieces of amber. The filaments are around 1 μm in diameter and in some cases, slightly orientated towards the flow of the resin. They ramify in a perpendicular orientation. A few of them include chains of round conidia about 1 μm in diameter. All of the specimens with conidia chains correspond to filaments that are orientated in the resin flow, showing that the reproductive structures were developed before they were trapped in the resin. (3) A third type corresponds to sheathed bacteria. The filaments form networks within the amber matrix. They are composed of a trichoma 1 μm in diameter surrounded by a sheath 4.5–5.5 μm in diameter. The sheath is clearly visible because it is marked by dust particles. Both the size and the morphological characteristics of these filaments correspond to the genus *Sphaerotilus*.

Fungi are represented by several specimens. Most abundant are mycelia on the surface of the amber. Only vegetative structures have been preserved, albeit poorly. They correspond to septate hyphae on which some clamps can be seen indicating they correspond to Basidiomycotyna. No reproductive structure is present to enable precise identification. Other fungal organisms correspond to translucent septate filaments (c. 2 μm in diameter) from which bunches of conidia emerge. All of these characteristics evoke a species close to some ascomycota of the genus *Botrytis* Micheli ex. Persoon, 1794.

One well-preserved fungus consists of networks of brown septate hyphae 4 μm in diameter associated with long chains of conidia that correspond to didymospores. A similar fungus in amber from Charentes was reported by Girard (2010) and putatively attributed to the genus *Cladosporium* Link, 1816. Saint Martin et al. (2012) encountered a similar specimen in Santonian amber from Martigues (SE France) and questioned Girard's identification. Both records suggest that this sort of fungus was quite common in Late Cretaceous forests of Western Europe. A more detailed investigation of the various specimens that have been found is required in order to identify more satisfactorily this higher fungus, Girard's (2010) determination almost certainly being erroneous.

Many other fungal remains have been observed in Vendean amber. They mostly correspond to conidia (didymospores and several kinds of phragmospores). Precise identifications have yet to be accomplished.

It has not been possible so far to identify a single record of another sort of filamentous micro-organism. This bacterium or fungus consists of a network of filaments 3.3–3.5 μm in diameter with an irregular and "spiny" surface. The filaments appear to be empty. Their diameter suggests that they are of fungal origin. The absence of a cell wall is problematic. It might have been completely destroyed during

fossilization. Alternatively, the remains might correspond to a coenocytic mycelium of Zygomycotina. However, the surface characteristics are not congruent with this conclusion.

Other micro-inclusions comprise fern spores (*Deltoidospora* sp. and indeterminate forms), arthropod faeces (coprolites), spider silk (Saint Martin et al., 2014), and abundant but taxonomically impoverished remains of terrestrial plants: wood fibres were recovered in many pieces and stellate hairs in a few.

6. Fossil woods and the resin-producing trees

Analyses of wood samples showed that their homoxylous anatomy is well preserved and revealed at least three distinct taxa of diverse affinities. Growth ring limits are indistinct or absent in all observed specimens.

6.1. Species 1

A few wood fragments show very large and numerous axial and radial resin canals (mean tangential diameter \times mean radial diameter: $100 \times 160 \mu\text{m}$) (Fig. 12A–D); both are entirely filled with tylosis; axial canals are frequently arranged in tangential groups of three or four; abietinean radial pits are exclusively uniseriate (Fig. 12E); rays are uniseriate (except those containing radial canals), low (5–15 cells high) and highly resinous; crossfields are composed of one or two taxodioid oculipores (Fig. 12E). All of the features occurring in these specimens are common, although generally intermingled, in genera belonging to Pinaceae. Several fossil taxa are defined for wood structures with affinities to this family. *Piceoxylon* Gothan is attributed to wood with normal resin canals showing thick walls, abietinean radial pits, oculipores in crossfields and ray tracheids. With the exception of the last feature, this description closely fits that of Species 1. Our wood samples also present affinities with *Pinuxylon* Gothan, *Pinoxylon* Knowlton, or *Pinites* Lindley et Hutton. However, these three genera always have oopores in crossfields, which is not the case in our material. Finally, our specimens share a lot of characters (especially axial resin canals with tylosis) with several Cretaceous woods (Holden, 1913; Mathiesen, 1924) attributed to the fossil genus *Pityoxylon* Kraus, although this genus has been regarded as illegitimate by Philippe and Bamford (2008).

6.2. Species 2

One third of the wood fragments show a typical homoxylous structure without normal resin canals (Fig. 12F); traumatic canals, however, may be present and arranged in long tangential bands (Fig. 12J); abietinean radial pits are exclusively uniseriate (Fig. 12H); axial parenchyma is abundant (Fig. 12G); rays are uniseriate and low (5–15 cells high); and crossfields are composed of one or two cupressoid to taxodioid oculipores (Fig. 12I). These features indicate affinities with the fossil genus *Taxodioxylon* Hartig.

6.3. Species 3

More than half of the remaining samples belong to a new taxon of uncertain affinity. The wood contains many axial parenchyma cells mixed throughout the tracheids (Fig. 13A–C); these cells are large (radial diameter \times tangential diameter: $40 \times 30 \mu\text{m}$) and conspicuous in both transverse and longitudinal sections because most of them are entirely filled with brown to red matter, probably of a resinous nature (Fig. 13A–C); normal and traumatic resin canals are lacking; rays are extremely low, often less than three cells high (Fig. 13D, E); and crossfields are composed of one (rarely two) cupressoid (rarely podocarpoid) oculipores (Fig. 13F–H). This type of crossfield pitting is frequently observed in wood of the Cupressaceae in which, however, pits are often more numerous. Also, some woods of the Podocarpaceae closely resemble the specimens studied in having axial parenchyma and a single oculipore per crossfield. Nevertheless, axial parenchyma is never as abundant as in our specimens. This last

original feature, as well as the aspect of the radial pits, is very similar to some of the angiosperms that present homoxylous wood structure: however, in these taxa the rays are very different and never as narrow and low. This very peculiar wood structure, between that of conifers and angiosperms, is clearly new and deserves a more thorough study.

The presence of amber in this rich accumulation of “coniferous” remains is not surprising as two of the species described show definitive resiniferous structures (canals or parenchyma) and the parenchyma of the third seems to be filled with resin. Based on the xylological results, the source of the Vendean amber may be the conifer families Pinaceae or Taxodiaceae (Cupressaceae s.l.), although a third, yet unknown family cannot be ruled out. However, all amber nodules at our disposal display the same yellow-orange colour, so it is unlikely that they originated from different sources. We complemented our study with spectroscopic analyses of the amber matrix in order to determine its origin more precisely.

7. Amber chemistry and the plant source

The chemical characterization of Vendean amber has been published elsewhere along with other Cretaceous and Eocene French ambers (Nohra et al., 2015). The infrared spectrum is typical of recent cupressaceous and araucarian rather than pinaceous resins (Tappert et al., 2011). The ^{13}C NMR spectrum corresponded to the class CA, which is typical of recent resins of Cupressaceae and Araucariaceae (Lambert et al., 2005). Finally, according to the Py-GC-MS results, Vendean amber belongs to the class Ib ambers as defined by Anderson et al. (1992). Its extract is composed of abietane-type terpenoids with significant callitrisate and its derivatives: dehydroabietin, dehydroabietic acid and labdanes are absent. This suggested a cupressaceous origin for the resin, even though cuparene and cedrene were not detected (Nohra et al., 2015). Since the publication of these results, we have carried out further investigations of the Py-GC-MS chromatogram and found two previously overlooked phenolic abietanes, 18-nortotarol and 18-norferruginol, which are cupressaceous biomarkers.

Finally, from the chemical characterization of amber and the wood analysis, we assume a Cupressaceae-related origin of the Vendean amber, with *Taxodioxydon* a possible source.

8. Palaeoenvironmental interpretations

When all of the lignitic clays of the Challans-Commequiers Basin were regarded as middle Cenomanian in age, they were typically interpreted as having been deposited in mangrove and coastal marsh environments in a warm, wet “tropical” climate, based on their palynoflora (Durand and Ters, 1958; Durand et al., 1963). Later, Azema and Viaud (1979) dated part of the black clay as Santonian based on palynomorph assemblages dominated by angiosperm pollen of the Normapolles group: 26 species of 13 genera (mainly *Extrapollis*, *Interporopollenites* and *Trudopollis*). Legrand et al. (2006) found foraminifers and marine dinoflagellates in clay from La Garnache, indicating a marine environment. These were associated with fern spores, conifer pollen (Cheirolepidiaceae, Cupressaceae/Taxodiaceae, Pinaceae, Podocarpaceae) and angiosperm pollen grains again dominated by representatives of the Normapolles group. They considered the palynomorph assemblage to reflect a sea-margin vegetation including mangroves in lagoons and brackish swamps under a subtropical to warm-temperate climate, the Vendée region being located at the edge of a continental land mass during the Late Cretaceous.

Viaud et al. (1979) indicated that well-dated Cenomanian lignites of the Challans area are devoid of microfauna. They found a few ostracods in the Turonian clay, but did not provide details of the palaeoenvironment during the Turonian transgression. The work of Legrand et al. (2006) implies that the presence of foraminifers in the Santonian lignitic clay indicates greater marine influence on these younger deposits.

In contrast to the above, no direct evidence for marine influence on the environment of deposition was encountered in either of the palynological assemblages recovered from La Garnache samples considered herein. However, the relative abundance of spores coupled with the low numbers of gymnosperm pollen recovered from Garnache 2 suggest a more proximal depositional environment than the small, angiosperm pollen-dominated assemblage from Garnache 1, perhaps reflecting the effects of the beginning of the Turonian transgression in western France. By contrast, the aquatic fossil content of the amber suggests a marine or brackish environment in the proximity of the resin-producing trees. The palynological and xylological data from Garnache 1 are insufficient for providing a detailed appraisal of the Vendean amber forest. However, it is worth noting that the cupressaceous origin of the amber and a marginal marine setting are consistent with the salt marsh or coastal swamp habitat suggested for other cupressaceous amber-producing forests known from the Cretaceous, e.g. in the Turonian of New Jersey (USA) and the Campanian of Canada (Grimaldi and Nascimbene, 2010; McKellar and Wolfe, 2010), and somewhat similar to present-day swamp forests dominated by the bald cypress, *Taxodium distichum*.

9. Conclusions

The Vendean amber inclusions add to our understanding of Turonian environments and ecosystems of the western European Archipelago and confirm that resin-producing trees grew close to the seashore, possibly in a salt marsh or swamp forest. As for other Cretaceous ambers in western France (Perrichot, 2005; Girard et al., 2009b), the biotic assemblage of the Vendean amber is surprisingly rich in aquatic species, such as tanaids and other crustaceans (see above) among the arthropods, and also diverse micro-organisms such as sponge spicules and diatoms. Although the diversity of fossil inclusions is outstanding considering the small amount of amber that was available for study, most are terrestrial arthropods of extant families having a widespread distribution and varied ecology today, and therefore of limited palaeoenvironmental value.

Acknowledgements

We are indebted to the following amateur palaeontologists who generously donated their amber material for investigation: Arlette Boulo, Thérèse Corgnet, Dominique Doyen, Fanny Dupé, Anne-Marie Guèdes, Gérard Guérineau, Alain Guillet and his brothers, Didier Graves, Luc Lucas, and Magali Weigandt. We dedicate this paper to the late André Dupé who also participated in amber collection with his wife Fanny, and passed away before it could be published. André and Fanny have been tireless in their support of, and interest in, the La Garnache fossil deposits. We thank the Conseil Général de Vendée for authorizing the excavation along the D32 road embankment, the Agence Routière Départementale de Challans, Fanny Dupé and Arnaud Schmitt for their kind assistance with the digging, and Serge Régnauld (Natural History Museum of Nantes) who brought this amber deposit to our attention and provided contacts with the amateur palaeontologists. We also thank colleagues who helped with identifying amber inclusions: Dany Azar, Vladimir Blagoderov, André and Patricia Nel, Alexander R. Schmidt, Ekaterina Sidorchuk, and Isabelle Véa. This paper is both a contribution to the program AMBRACE (coord. D. Néraudeau) from the National Agency of Research (ANR) and the program InterrVie NOVAMBRE (coord. D. Néraudeau) from the National Institute of Universe Sciences (INSU).

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Figure and table captions

Fig. 1. Simplified geological map of the Challans-Commequiers Basin showing the Cenomanian outcrops (in black) according to Ters (1961). The Turonian amber deposit (grey arrow) is very small and in contact with Cenomanian outcrops (A.O. = Atlantic Ocean).

Fig. 2. A, B, outcrop of La Garnache road works during the collection of amber by F. Dupé, D. Graves and their friends in the autumn of 2002. A, general view of the road works showing the road bridge (in La Garnache direction) and on the left-hand side the lignitic clay of Garnache 1 (red arrow), near the big tree, that was searched for its amber content by amateur palaeontologists (cf. Figs C, D); B, general view of the road works showing on the left side the section in the lignitic clay (Garnache 1) at the base of the embankment; C, close up of the amber deposit during the collection, with an excavation between the bridge and the big tree (Photograph, F. Dupé); D, close up of the amber deposit showing the amber collection in the lignitic clay (Photograph, D. Graves); E–G, views of the only lignitic outcrop (Garnache 2) still observable today, between the bridge and the big tree (white arrow on Fig. A): E, view of the outcrop at the base of the embankment; F, general view of the outcrop at the top of the embankment; G, view of the lignitic clay and sand sampled for palynology, palaeobotany and micropaleontology. Photographs, D. Néraudeau except where stated.

Fig. 3. Diversity of colour and shape of the Vendean amber. A, the most typical colour (orange to yellow) and size (5–10 mm) of the amber pieces. B, earthy and dark amber pieces relatively abundant. C, D, largest amber nodules, brown-red in colour. C, large polished nodules (15–22 mm); D, the largest nodule (34 × 22 mm). E–G, different shapes of Vendean amber pieces. E, subspherical drop (4 mm); F, subcylindrical stalagmite (10 mm); G, laminated scale (10.5 × 4.5 × 1.5 mm).

Fig. 4. Synthetic stratigraphical succession of the different Upper Cretaceous facies known in the La Garnache region, with location of the three main lignite occurrences: (1) L1 at the boundary between mid Cenomanian and upper Cenomanian; (2) L2 in the lower Turonian; (3) L3 in the Santonian part.

Fig. 5. Palynomorphs from the grey clay of Garnache 1. Accompanying data are palynological preparation and slide numbers prefixed by QPR (Aberystwyth University palynological collection identifier) followed by England Finder co-ordinates. Authors of taxa not otherwise cited in the text are not listed in the references. A, *Classopollis* sp. cf. *C. major* Groot et Groot, 1962; QPR3666.2, W20.0. B, C, *Classopollis torosus* (Reissinger, 1950) Couper, 1958; QPR3666.2, V49.0. D, E, *Tricolpites* sp.; QPR3666.4, P37.1. F, G, *Tricolporopollenites distinctus* Groot et Penny, 1960; QPR3666.4, R40.2. H, *Trudopollis hemimechanicus* Pflug, 1953; QPR3666.4, D48.2. I, *Plicapollis* sp. cf. *P. vacuus* Tschudy, 1975; QPR3666.4, P52.0. J, *Plicapollis* sp. cf. *P. excellens* (Pflug, 1953) Krutzsch in Goczán et al. 1967; QPR3666.4, Q20.2. K, *Atlantopollis microreticulatus* Krutzsch in Goczán et al., 1967; QPR3666.2, X37.0. L, *Neotriangulipollis* sp. 1 sensu Azéma et al., 1981; QPR3666.5, G29.0. M, *Complexiopollis praetumescens* Krutzsch, 1959; QPR3666.4, U44.0. N, T, Y, *Trudopollis* sp. cf. *T. pertrudens* (Pflug in Thomson and Pflug, 1953) Pflug, 1953; QPR3666.4, lost specimen. O, U, *Complexiopollis vancampoeae* Diniz, Kedves et Simoncsics, 1974; QPR3666.4, O28.0. P, *Osculapollis* sp. A sensu Christopher, 1979; QPR3666.5, O23.4. Q, *Tricolpites* sp. cf. *T. barrandei* Pacltová, 1971; QPR3666.4, J20.0. R, S, *Retitricolpites virgeus* (Groot, Penny et Groot, 1961) Brenner 1963 sensu Singh, 1971; QPR3666.4, N19.3. V, *Osculapollis* sp.; QPR3666.2, J34.4. W, *Extratropopollenites emaciatus* Skarby, 1968 sensu Médus et al., 1980 [cf. *Pseudoplicapollis longiannulata* Christopher, 1979]; QPR3666.2, X46.1. X, *Subtrudopollis* sp. 2 sensu Azéma et al., 1981; QPR3666.2, P23.1. Scale bar represents 10 µm.

Fig. 6. Palynomorphs from the clay of Garnache 2. Slide number: QPR3667.2. Accompanying data are followed by England Finder coordinates. Authors of taxa not otherwise cited in the text are not listed in the references. A, *Appendicisporites* sp. cf. *A. potomacensis* Brenner, 1963; T45.1. B, *Camaronosporites semilevis* Krutzsch, 1963; M50.4. C, *Complexiopollis* sp. cf. *C. vulgaris* (Groot et Groot, 1962) Groot et Krutzsch in Goczán et al., 1967; M18.4. D, *Crybelosporites* sp.; K42.0. E, *Tricolpites albiensis* Kemp, 1968; N25.0. F, G, *Bohemiperiporis zaklinskaiae* Pacltová, 1968;

P20.0. H, *Patellasporites tavadensis* Groot et Groot, 1962; J17.4. I, *Stereisporites psilatus* (Ross, 1949) Pflug in Thomson and Pflug, 1953; M12.0. J, *Laevigatosporites ovatus* Wilson et Webster, 1946; W19.0. K, *Gleicheniidites circinidites* (Cookson, 1953) Dettmann, 1963; U14.3. L, *Cerebropollenites mesozoicus* (Couper, 1958) Nilsson, 1958; U43.0. Scale bar represents 10 μm .

Fig. 7. Diverse terrestrial arthropods fossilized in Vendean amber (Photographs, V. Perrichot). A, prostigmatid mite (Acari, Parasitengona, Trombididae; IGR.GAR-88). B, ray spider (Araneae, Theridiosomatidae: Baalzebub sp.; IGR.GAR-91). C, dustywing (Neuroptera, Coniopterygidae; IGR.GAR-2). D, gall midge (Diptera, Cecidomyiidae; IGR.GAR-87.1). E, megaspilid wasp (Hymenoptera, Megaspilidae; IGR.GAR-115). F, false fairy wasp (Hymenoptera, Mymarommatidae: Archaeoromma sp.; IGR.GAR-11).

Fig. 8. Diagram summarizing known arthropod fossils with a significant record from Turonian Vendean amber.

Fig. 9. Diverse aquatic inclusions fossilized in Vendean amber (Photographs A and B, V. Perrichot; C and D, A. Schmidt). A, epicaridean larva (Crustacea, Cymothoidea IGR.GAR-08). B, fragmentary water mite ('Hydracarina', family indet.; IGR.GAR-45). C, centric diatom (Corethrales: Corethraceae; IGR.GAR-33). D, polyaxon sponge spicule ("spheraster"; IGR.GAR-19).

Fig. 10. Micro-inclusions observed in petrographic thin sections (photographs JP and S Saint Martin). A, network of apparently filamentous microstructures observed on the periphery of drop-shaped grains (MNHN.F.F63106). B, detail of microstructures figured in A (MNHN.F.F63106). C, Streptomyces-like actinomycete showing branching pattern (MNHN.F.F63107). D, Streptomyces-like actinomycete showing clumps of entangled filaments (MNHN.F.F63108). E, network of fungal mycelium exhibiting septa (arrow-heads) and conidia (arrows) (MNHN.F.F63109). F, detail of fungal mycelium with very distinctive septa (arrow-heads) (MNHN.F.F63109).

Fig. 11. Association of cocci (co) and bacilli (ba) observed in a fragment of Vendean amber. Scale bar = 10 μm .

Fig. 12. Wood anatomical features of Species 1 (A–E) and 2 (F–J) described from lignitic material of Garnache 1. A, B, transverse section, numerous and large axial resin canals, sometimes arranged in short tangential bands. C, longitudinal tangential section, axial canals filled with tylosis. D, longitudinal tangential section, low rays. E, SEM, one or two oculipores per crossfield and abietinean radial pits. F, transverse section, absence of normal axial canal. G, longitudinal tangential section, axial parenchyma. H, longitudinal radial section, abietinean radial pits. I, longitudinal radial section showing crossfield. J, transverse section, traumatic resin canals arranged in long tangential bands. Scale bars: A = 2 mm; B–D, F, J = 500 μm ; E = 100 μm ; G = 200 μm ; H, I = 50 μm .

Fig. 13. Wood anatomical features of Species 3 described from lignitic material of Garnache 1. A–C, SEM, transverse section, abundance of axial parenchyma cells filled with a brown matter. D, E, longitudinal tangential section, axial parenchyma cells and very low rays. F (SEM), G, H, longitudinal radial section, one or two cupressoid oculipores per crossfield. Scale bars: A, B, D, E = 500 μm ; C = 100 μm ; F–H = 50 μm .

Table 1. Spores and pollen grains recorded from the lignites of Garnache 1 and Garnache 2.

Table 2. Arthropod taxa recorded from Vendean amber.

| Spores | Garnache 1 | Garnache 2 |
|--------------------------------------------------------------|------------|------------|
| <i>Appendicisporites</i> sp. cf. <i>A. potomacensis</i> | | • |
| <i>Appendicisporites potomacensis</i> | | • |
| <i>Appendicisporites punctatus</i> | | • |
| <i>Appendicisporites</i> sp. | | • |
| <i>Appendicisporites dentimarginatus</i> | | • |
| <i>Biretisporites potoniaei</i> | | • |
| <i>Camazonosporites hammenii</i> | | • |
| <i>Camazonosporites rudis</i> | | • |
| <i>Camazonosporites semilevis</i> | | • |
| <i>Camazonosporites</i> sp. | | • |
| <i>Camazonosporites</i> sp. cf. <i>Retiriletes annulatus</i> | | • |
| <i>Cicatricosporites</i> sp. | | • |
| <i>Cingulatisporites tavadensis</i> | | • |
| <i>Concavisporites jurienensis</i> | | • |
| cf. <i>Concavissimisporites penolaensis</i> | | • |
| <i>Crybelosporites</i> sp. | | • |
| <i>Cyathidites minor</i> | | • |
| <i>Cyclogranisporites leopoldii</i> | | • |
| <i>Deltoidospora</i> sp. | • | • |
| <i>Densoisporites</i> sp. | | • |
| <i>Dictyophyllidites</i> sp. sensu Brenner, 1963 | | • |
| <i>Distaltriangulisporites perplexus</i> | | • |
| <i>Foveotriletes subtriangularis</i> | | • |
| <i>Gleicheniidites circinidites</i> | | • |
| <i>Gleicheniidites senonicus</i> | | • |
| <i>Granulatisporites dailyi</i> | | • |
| <i>Laevigatosporites ovatus</i> | | • |
| <i>Laevigatosporites</i> sp. | • | • |
| <i>Patellasporites</i> sp. cf. <i>P. fuscus</i> | | • |
| <i>Patellasporites distaverrucosus</i> | | • |
| <i>Patellasporites</i> sp. | | • |
| <i>Patellasporites tavadensis</i> | | • |
| <i>Peromonolites</i> sp. | • | • |
| <i>Perotriletes pannuceus</i> | | • |
| <i>Reticulosporis gallicus</i> | | • |
| <i>Sestrosporites</i> sp. cf. <i>S. pseudoalveolatus</i> | | • |
| <i>Stereisporites psilatus</i> | | • |
| <i>Verrucosisporites</i> sp. | | • |
| Gymnosperm pollen | | |
| <i>Cerebropollenites mesozoicus</i> | | • |
| <i>Classopollis</i> sp. | | • |
| <i>Classopollis</i> sp. cf. <i>C. major</i> | • | • |
| <i>Classopollis torosus</i> | • | • |
| <i>Phyllocladidites</i> sp. cf. <i>P. minimus</i> | | • |

| | | |
|------------------------------------------------------------------------------|---|---|
| <i>Phyllocladidites inchoatus</i> | | • |
| Undetermined bisaccates | • | |
| Angiosperm pollen | | |
| <i>Atlantopollis microreticulatus</i> | • | |
| <i>Bohemiperiporis zaklinskaiae</i> | | • |
| <i>Complexiopollis praetumescens</i> | • | |
| <i>Complexiopollis</i> sp. cf. <i>C. vulgaris</i> | | • |
| <i>Complexiopollis vancampoeae</i> | • | |
| cf. <i>Echimonocolpites acanthus</i> | | • |
| <i>Extratropipollenites emaciatius</i> Skarby, 1968 sensu Médus et al., 1980 | • | |
| <i>Liliacidites reticulatus</i> | | • |
| <i>Neotriangulipollis</i> sp. 1 sensu Azema et al., 1981 | • | |
| <i>Osculapollis</i> sp. | • | |
| <i>Osculapollis</i> sp. A sensu Christopher, 1979 | • | |
| <i>Plicapollis</i> sp. cf. <i>P. excellens</i> | • | |
| <i>Plicapollis</i> sp. cf. <i>P. vacuus</i> | • | |
| <i>Retimonosulcites ellipticus</i> | | • |
| <i>Retitricolpites virgeus</i> | • | • |
| <i>Subtrudopollis</i> sp. 2 sensu Azema et al., 1981 | • | |
| <i>Tricolpites albiensis</i> | | • |
| <i>Tricolpites</i> sp. | • | |
| <i>Tricolpites</i> sp. cf. <i>T. barrandei</i> | • | |
| <i>Tricolporopollenites distinctus</i> | • | |
| <i>Trudopollis hemimechanicus</i> | • | |
| <i>Trudopollis</i> sp. cf. <i>T. pertrudens</i> | • | |

Table 1. Species of spores and pollen grains encountered in the La Garnache samples.

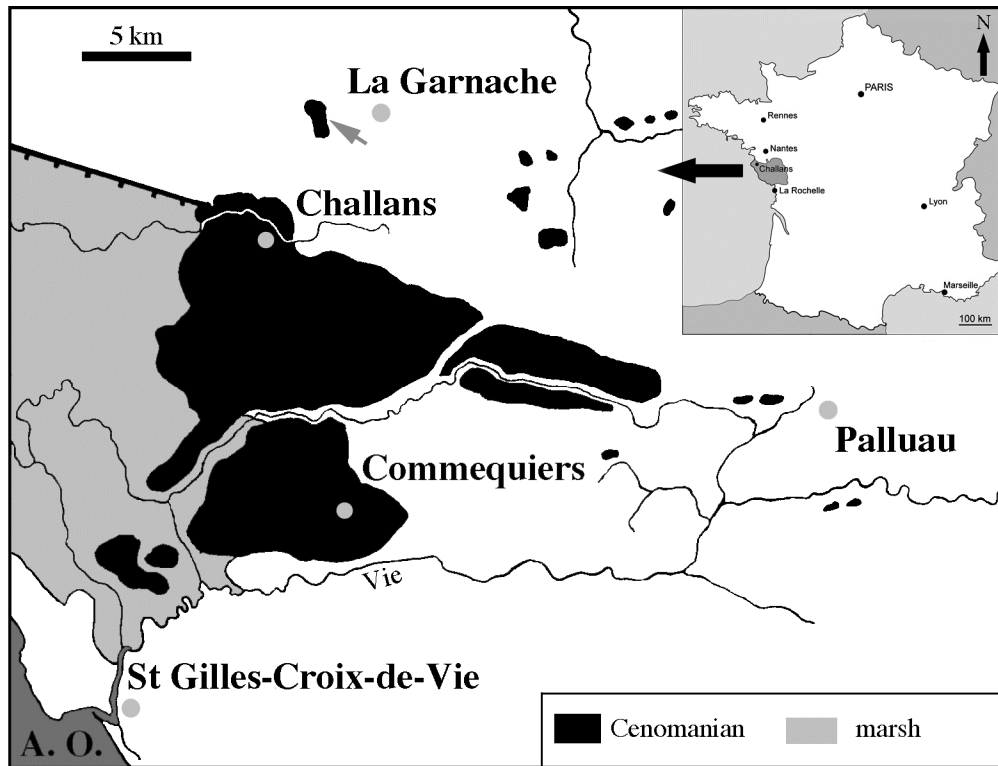
| Class | Order | Suborder/Family | Figures |
|-------------------|--------------|-------------------|---------|
| Crustacea | | | |
| | Isopoda | indet. | 28 6A |
| | Tanaidacea | Alavatanaidae | 1 |
| Diplopoda | | | |
| | Polyxenida | Polyxenidae | 1 |
| Arachnida | | | |
| | Acari | Mesostigmata | 2 |
| | | Prostigmata | 8 5A |
| | | Hydracarina'? | 1 6B |
| | | indet. | 17 |
| | Araneae | Theridiosomatidae | 1 5B |
| | | indet. | 8 |
| | Opiliones | indet. | 1 |
| Entognatha | | | |
| | Collembola | indet. | 1 |
| Insecta | | | |
| | Blattaria | indet. | 1 |
| | Coleoptera | Ptinidae | 1 |
| | | Staphylinidae | 1 |
| | | indet. | 2 |
| | Dermaptera | indet. | 1 |
| | Diptera | Cecidomyiidae | 4 5D |
| | | Ceratopogonidae | 10 |
| | | Chironomidae | 5 |
| | | Dolichopodidae | 1 |
| | | Anisopodidae | 3 |
| | | indet. | 9 |
| | Hemiptera | Eriococcidae | 1 |
| | | Fulgoromorpha | 2 |
| | | Indet. | 2 |
| | Hymenoptera | Crabronidae | 1 |
| | | Megaspilidae | 1 5E |
| | | Mymaridae | 4 |
| | | Mymarommatidae | 5 5F |
| | | Platygastridae | 8 |
| | | Serphitidae | 2 |
| | | indet. | 3 |
| | Isoptera | indet. | 1 |
| | Neuroptera | Berothidae | 1 |
| | | Coniopterygidae | 1 5C |
| | Orthoptera | indet. | 1 |
| | Psocodea | Archaeatropidae | 3 |
| | | Compsocidae | 1 |
| | | Mesopsocidae | 2 |
| | | indet. | 3 |
| | Thysanoptera | Merothripidae | 1 |
| | | indet. | 1 |

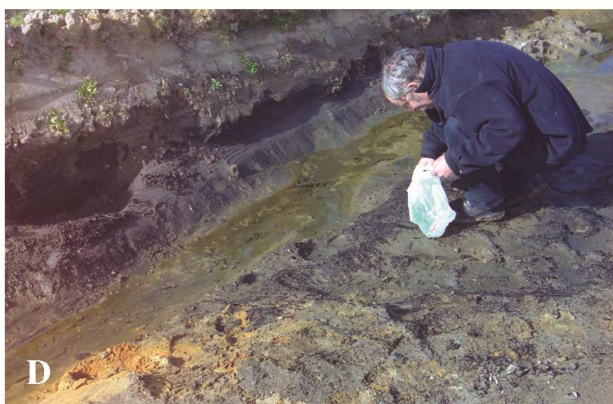
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| Indet. | | 14 |
| Arthropoda | indet. | 6 |

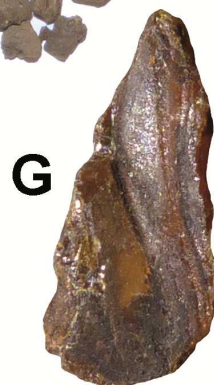
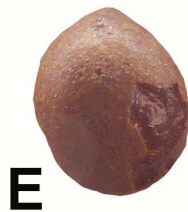
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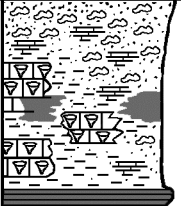

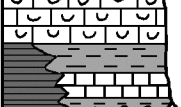
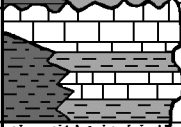
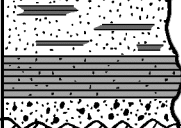
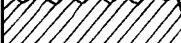
| | |
|-------------------|-----|
| TOTAL, ARTHROPODS | 171 |
|-------------------|-----|

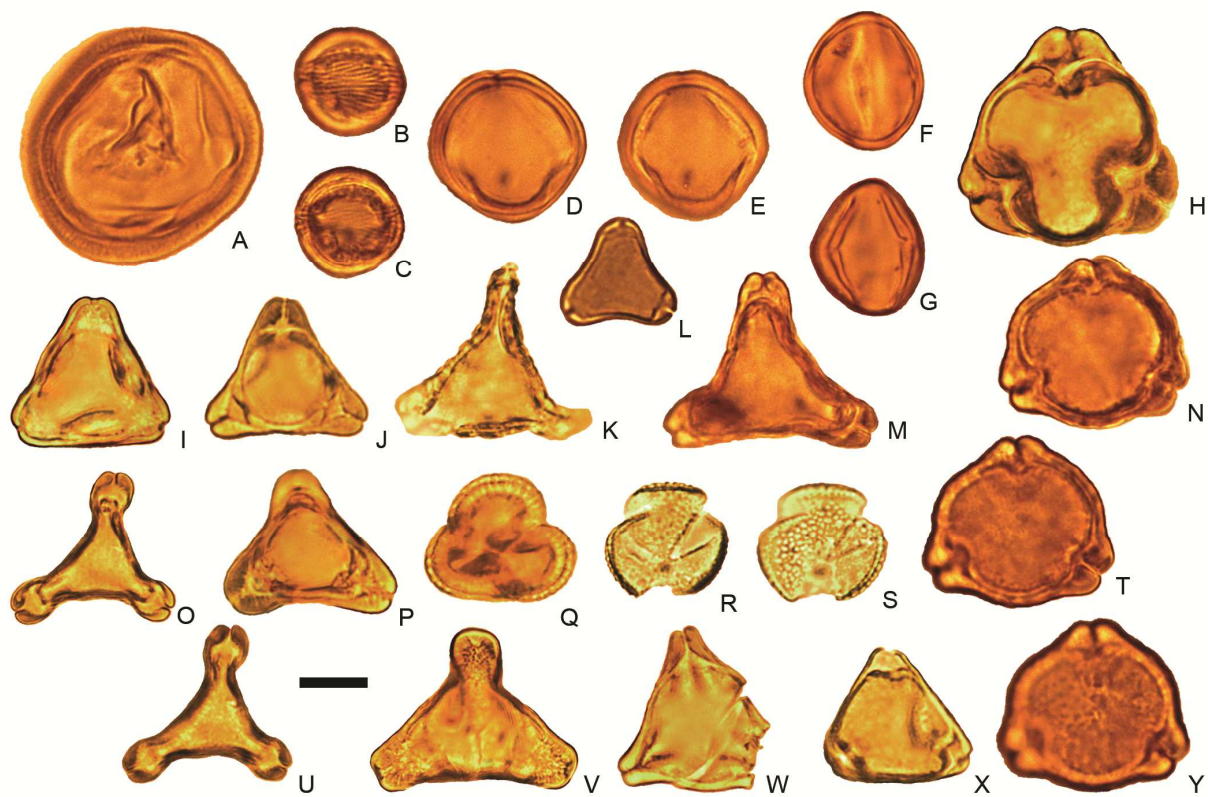
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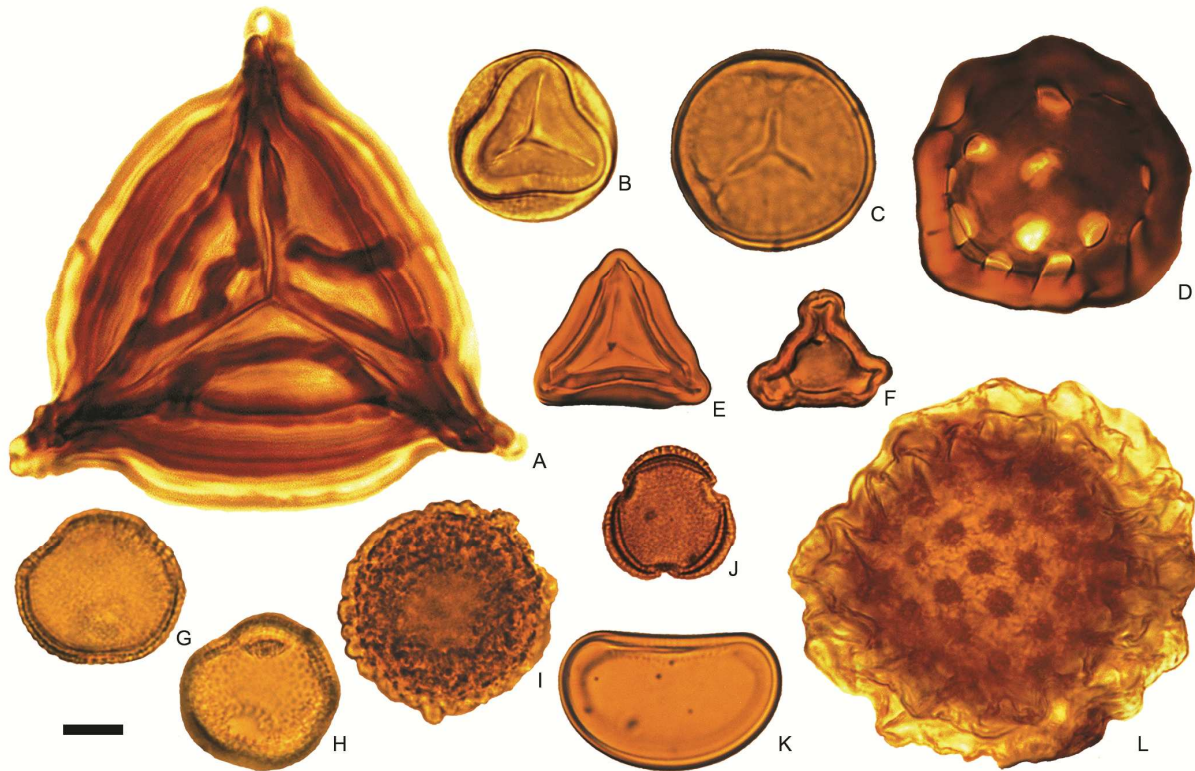






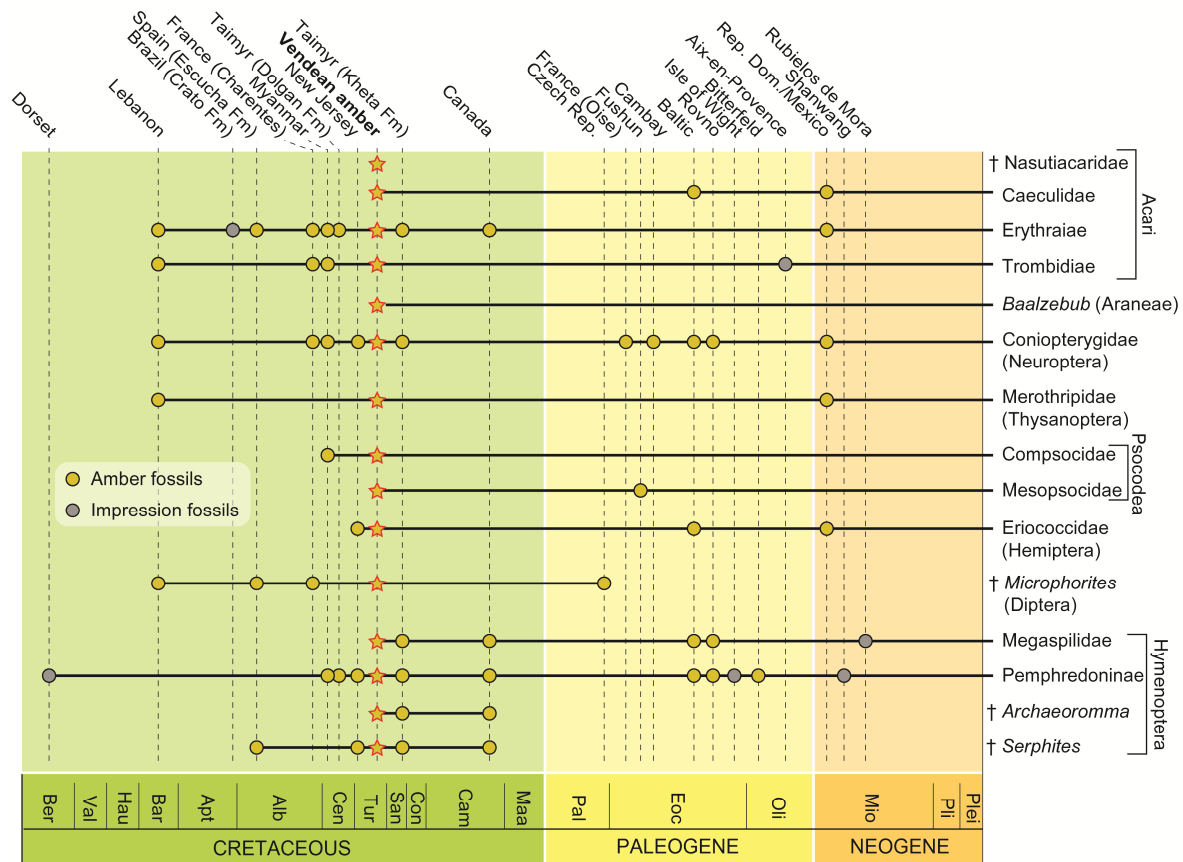
| | | | | |
|------------------------|----------|------------------------------------------------------------------------------------|------|-------------------------------------------------------------------------|
| Santonian to Campanian | C5 to C7 |  | L3 ● | Sand with sponges Marls and limestones with rudists Lignitic clay |
| Upper Turonian | |  | | Marls and sandy limestones with rudists |
| Lower Turonian | C3 |  | L2 ● | Glauconitic marls and lignitic clay |
| Upper Cenomanian | C2b |  | L1 ● | Alternation of marls and limestones, locally dominated by marls |
| Middle Cenomanian | C2a |  | | Alternation of coarse sand and lignitic clay |
| Metamorphic substratum | |  | | Schists and gneisses |

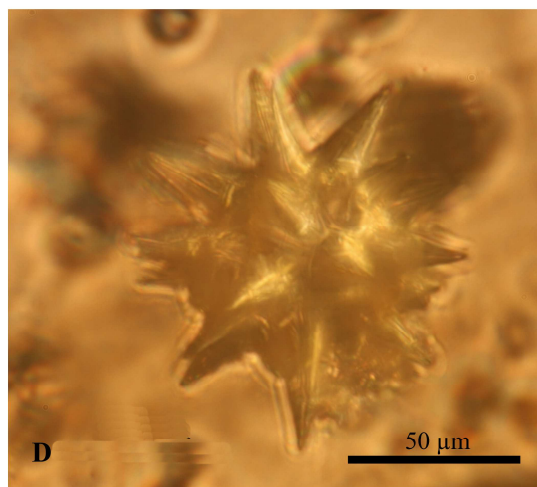
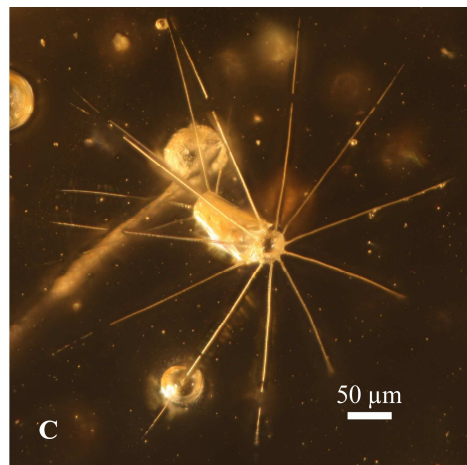




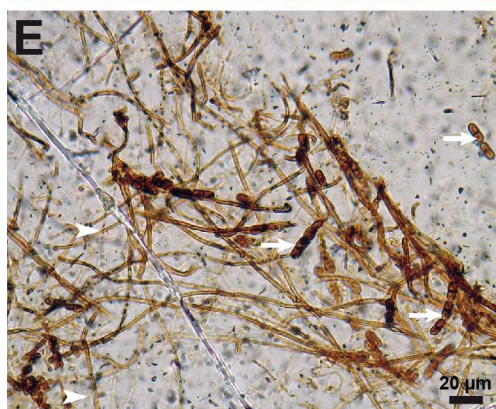
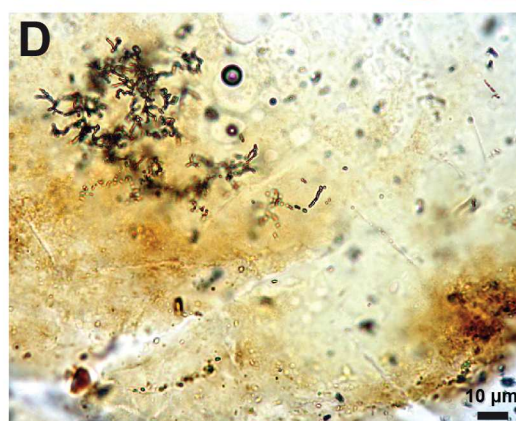
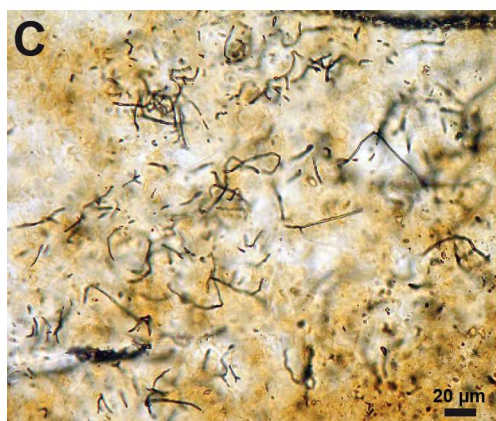
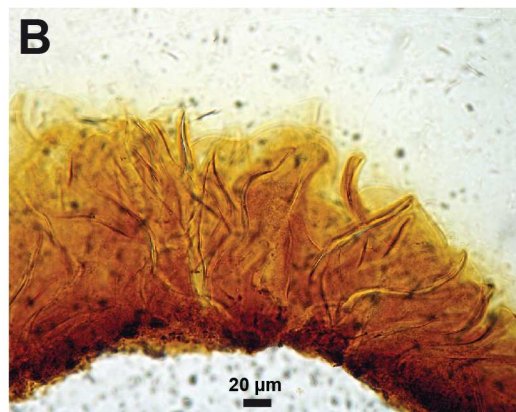
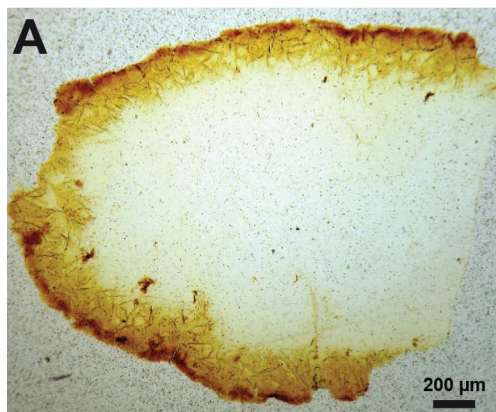
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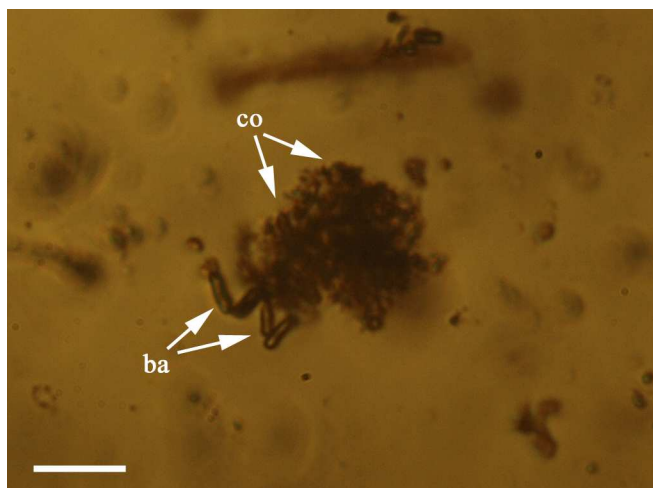




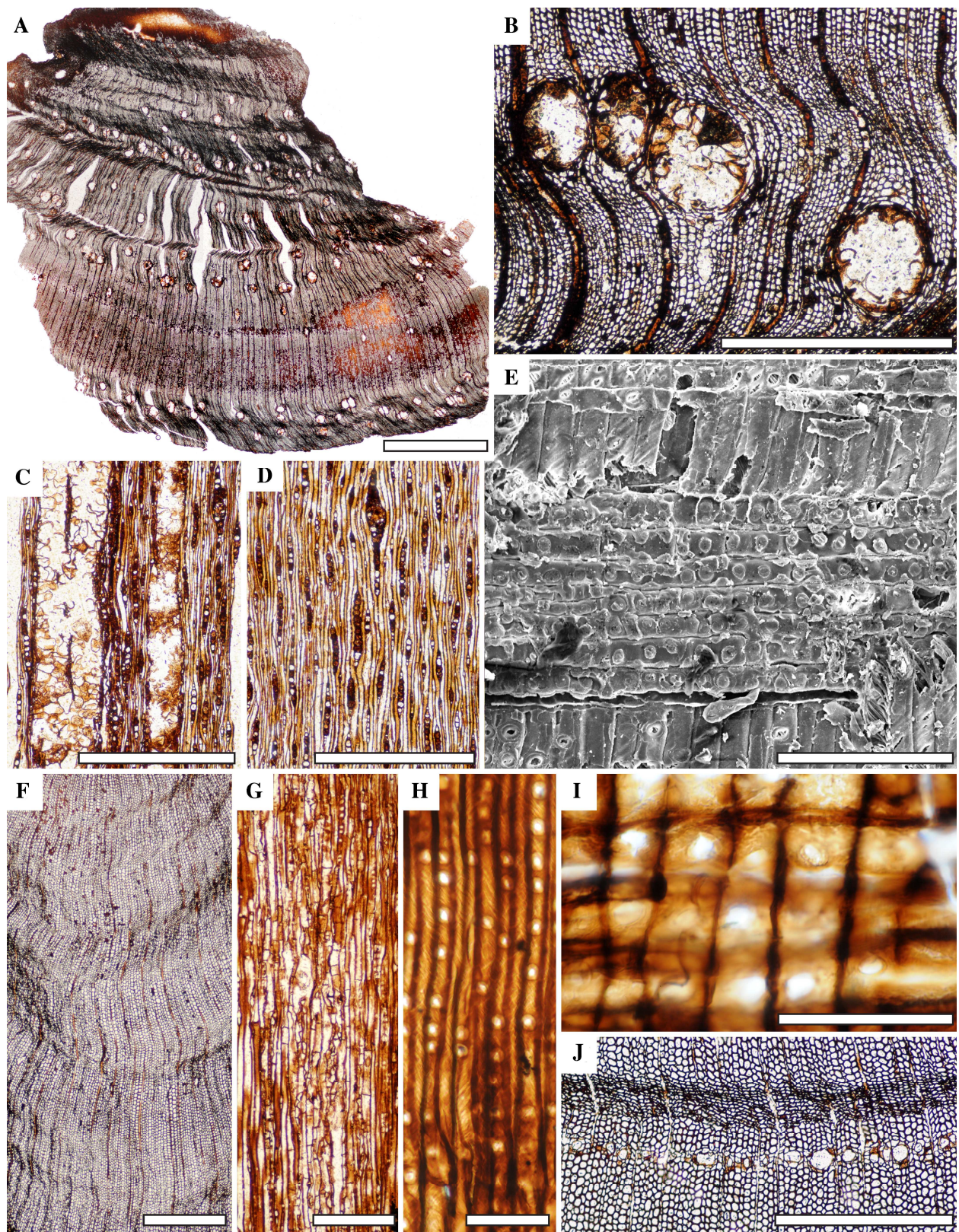


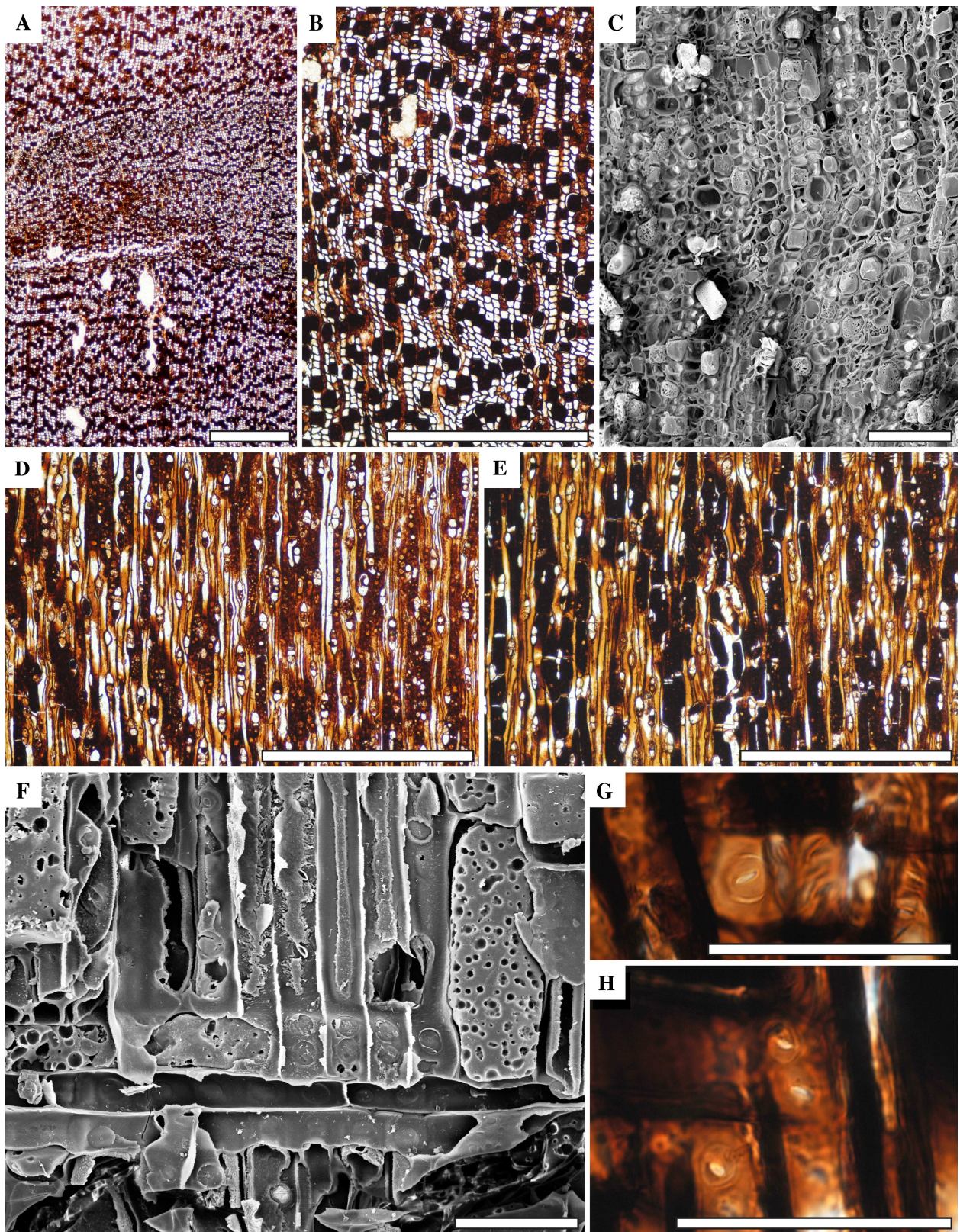
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Highlights

- A very fossiliferous amber is described from the Turonian of France.
- It consists of the first record of arthropods in Turonian amber from this part of Europe.
- Both terrestrial and marine macro- or micro-organisms are preserved in the amber.
- Palynological data from the amber deposit precise the Turonian age and characterize the amber forest.
- Wood analysis and amber chemistry identify for the first time Cupressaceae conifers for the fossil resin producers, when Araucariaceae and Cheirolepidiaceae are usually associated to French Mid Cretaceous ambers.