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Original article

# The Cenomanian amber of Fourtou (Aude, Southern France): Taphonomy and palaeoecological implications

## *L'ambre cénomanien de Fourtou (Aude, Sud de la France) : taphonomie et implications paléoécologiques*

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**Abstract**

The discovery of new amber outcrops in France in the last fifteen years and the reinvestigation of outcrops that had been forgotten provide new sources of palaeontological data. One of these forgotten localities is the Cenomanian outcrop of Fourtou in the Aude department, Southern France. Mentioned in old manuscripts since 1700, perhaps known and used since the Palaeolithic, the Cenomanian amber of Aude is still poorly studied. Here we present a synthesis of the data obtained on this amber, focusing on the outcrop of Fourtou that provided the largest quantity of amber in the area. Systematic and taphonomy of Fourtou amber inclusions are described and discussed in order to propose a hypothesis about the environment in which Cenomanian Fourtou amber was produced.


*Keywords:* Amber fossils; Cretaceous; Palaeoenvironment; Resiniferous forest; Taphonomy

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**Résumé**

Depuis une quinzaine d'années, de nouveaux gisements à ambre ou de gisements « oubliés » depuis longtemps ont été (re)découverts. Mentionné dans des écrits dès 1700, peut être connu et utilisé depuis le Paléolithique, l'ambre cénomanien de l'Aude (sud de la France) en est un bel exemple, tout particulièrement le gisement de Fourtou. Dans cet article, nous faisons une synthèse des données existantes sur l'ambre de ce gisement jusqu'alors peu étudié. La systématique et la taphonomie des inclusions ambrifères de Fourtou sont présentées et discutées afin de proposer une hypothèse sur le milieu de production de cet ambre cénomanien.


*Mots clés :* Crétacé ; Forêt résinifère ; Fossiles de l'ambre ; Paléoenvironnement ; Taphonomie

## 1. Introduction

Amber is widely present in France, especially within the Cretaceous deposits, and numerous localities were known as soon as in the 18th and 19th centuries. Most of these historical outcrops have been completely forgotten. Re-development of amber studies in France, since the end of the 20th century, allowed their rediscovery. In the present paper, we present one of them: the outcrop of Fourtou (Aude, Southern France).

Aude amber is known at least since the beginning of the 18th century. It is mentioned, indeed, in a "Mémoire sur l'ambre jaune" written by the Académie Royale des Sciences in 1705 (Cassini, 1723; Anonymous, 1730) that, in January 1701, the famous astronomers Jean-Dominique Cassini (1625–1712) and his son Jacques Cassini (1677–1756), together with Mr Maraldi, discovered a kind of yellow amber in a jet mine close to a mountain called Bugarach. This reference constitutes the first report of the Aude amber and probably the first from Fourtou. Indeed the mine debris of Fourtou, that contain the amber presented here, are located on the north side of the Mount Bugarach. According to Cassini and Maraldi, the amber was at that time burnt with coal and lignitic wood to serve as fuel by the local people and that the main activity of the mines was the extraction of jet, locally used in manufacturing jewellery (Anonymous, 1730). In November 1739, the botanist Le Monnier joined the Jacques Cassini's son, César-François Cassini, and visited again what he called the jet mine near Bugarach (Cassini de Thury, 1744). Le Monnier's description of the mine (a pile of coal against a high rock) evokes the outcrop in Fourtou, although Le Monnier suspected that several other mines existed in the vicinity. Gensanne (1778) mentioned that jet extraction had ceased, and no more evoked the use of amber. Later in the 1820s, some coal was extracted near Fourtou from different Late Cretaceous levels but these works were abandoned in 1830 (Vène, 1834).

In the present article, we focus on the locality of Fourtou that provided the greatest quantity of amber. In reality the name of Fourtou comes from the nearest town Fourtou built on a Turonian basement, but the so-called amber outcrop of Fourtou is located on the Cenomanian part of the Fourtou area, i.e. close to the Mont Burgarach. Historically, amber from this outcrop is called Fourtou amber, but it might be better to call it Bugarach amber. However to avoid any confusion with previous studies, we maintained the term of Fourtou amber. Here we present the different data available on the sedimentology of this locality and on the amber in order to propose a model of reconstitution of the Cenomanian amber forest of Aude. Comparisons with coeval amber forests

known in Southern France and Northern Spain are made to replace Aude amber forest into the geographical context of the Europe during the Cenomanian.

## 2. Geological setting

More recent studies on the Middle to Upper Cretaceous strata of the Corbières are those of Bilotte (1985) (Fig. 1). Southward, deposits representing an "open basin" with planktonic foraminifers are preserved in the tectonic unit called "lame de Camps-Peyrepertuse". This unit is overlapping northward the deposits of a middle to inner platform mostly composed of terrigenous and/or carbonaceous sediments dated from the Cenomanian and the Turonian.

During the Cenomanian, layers of lignitic clay with occasional amber progressively transgressed on the emerged landscape. At Fourtou, transgressive on the Aptian, lignitic clay with amber alternates with sandy limestones containing large foraminifers (*Orbitolina concava* Lamarck 1816, *O. conica* d'Archiac 1837, *Praealveolina cretacea* d'Archiac 1835). The end of the Cenomanian is marked by more carbonaceous deposits and by the establishment of bioconstructions with rudists (Caprinidae and Radiolitidae) (Bilotte, 1973).

Sénesse (1937) precisely mentioned Fourtou amber in the Middle Cenomanian lignitic clay of Roque-Rouge (dark marls with amber on Fig. 1B). Bilotte (1973), studying the sedimentological and micropalaeontological contents of the Cenomanian layers of the Corbières, also mentioned the presence of molluscs in the amber layers, indicating that the sedimentation took place in a brackish environment.

During several field trips in 2000s, we failed in locating the *in situ* layer; only picking into mine debris or dumps was possible. These field trips allowed the discovery of millimetric to centimetric translucent amber pieces of yellow to red colour, and totalling about 2 kg.

Mine dumps at Fourtou are composed of clays with plant debris (wood, cuticles). No shell or vertebrate debris was found. Lithology and fossils from this mine debris, as well as data from Sénesse (1937) and Bilotte (1973, 1985), argue for coastal perhaps lagoonal deposits.

## 3. Material and methods

Data about the sedimentological context were mainly obtained during field trips made by M.B. during his thesis and during a recent field trip of G.B., M.B. and Daniel Vizcaïno (Carcassonne) (July 2011).

Sediment was collected for bulk maceration in $H_2O_2$ and plant cuticles isolated. These were treated with the classical Schultze's maceration. About twenty wood samples were collected in 2003 by JLL and 2004 by MP, on two outcrops: Fourtou and Cubières-sur-Cinoble (Fig. 1A). Sorting under the microscope allowed us to select five specimens from Fourtou (M.P. 1468–1472 in Philippe's collection, Lyon 1 University) and one from Cubières (M.P. 1473). These specimens were studied using two different methods: razor blade thin sections and casts. Specimens were searched for a fresh fracture in radial plan or, in the absence of such a surface, gently split with a disposable razor blade. On the fracture plan thick Collodion® (cellulose acetate) was applied and allowed to dry for a day. The cast was then stripped off and studied with a normal transmitted light microscope.

The greatest part of the amber samples was collected from mine debris in Fourtou during one field trip by V.P., A.N. and a team of the MNHN in April 2004, and during two field trips by V.G. in August 2005 and July 2006 (Fig. 2). The amber pieces were washed and a first screening for arthropods made using a stereomicroscope. The pieces were then polished on a

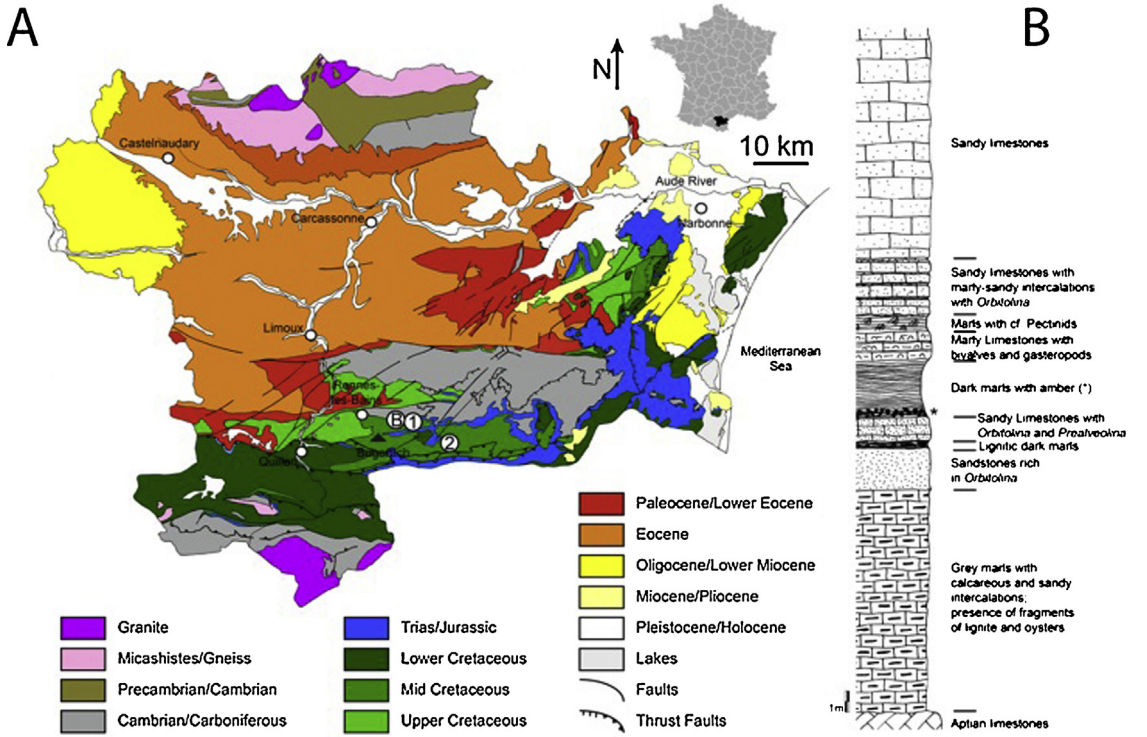


Fig. 1. Simplified geological map of Aude Department (A) and stratigraphic log observed at Roque-Rouge (B). 1- Locality of Fourtou. 2- Locality of Cubières-sur-Cinoble. Modified from Bilotte (1989).

*Carte géologique simplifiée du département de l'Aude (A) et coupe stratigraphique observée à Roque-Rouge (B). 1- Localisation de Fourtou. 2- Localisation de Cubières-sur-Cinoble (d'après Bilotte, 1989, modifié).*

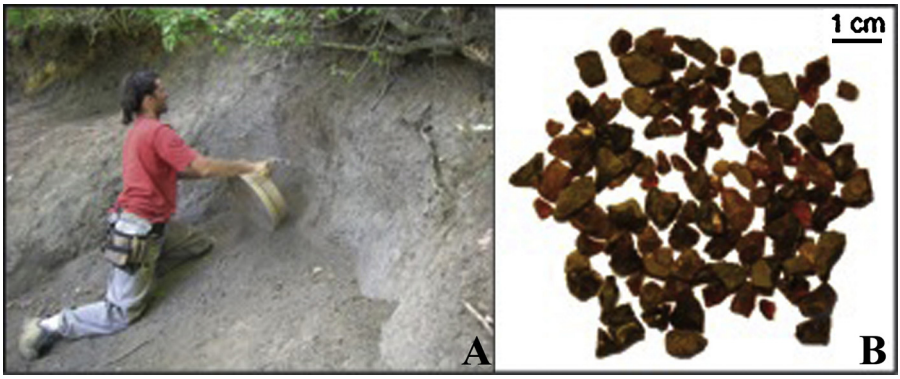


Fig. 2. Mine debris of Fourtou in which Romain Liard (Espéraza digger team 2005) is seeking for amber (A). This amber is mainly of red colour and can be translucent or totally opaque (B).
*Déblais de mines de Fourtou dans lesquels Romain Miard (équipe de fouilles d'Espéraza 2005) est en train de chercher de l'ambre (A). Cet ambre est généralement de couleur rouge, et peut être translucide ou totalement opaque (B).*

grinder using different abrasive discs, and pieces containing arthropod inclusions were cut and either included in Canada balsam or further polished for an optimal examination of the specimens under a stereomicroscope. The microfossils were studied following the method described by Girard et al. (2009b). Samples were first decontaminated using a three-step protocol (Girard et al., 2009b):

- an ultrasonic cleaning;
- an oxidation with 9–10% $H_2O_2$ and;
- an acid attack with 5% HF.

Then small fragments of amber were detached with a scalpel and mounted in Canada balsam on a slide. Preparations were then observed under a Leica DMLP microscope. Helicon Focus software was used to combine photos of an inclusion at different foci, which facilitates better illustration.

## 4. Amber and associated plant remains from Fourtou

### *4.1. Plant remains*

The fossil woods preserved in the middle Cenomanian mine debris of Fourtou correspond to lignite. This is quite diagenetically evolved, with several pieces being jet-like. Some other fragments are oxidised and looked like fusain, suggesting fossil charcoal. From a xylological point of view the xyloflora of Fourtou is homogenous, the wood assemblage being entirely composed of the conifer morphogenus *Agathoxylon* Hartig. Specimen M.P. 1471 (Fourtou) and M.P. 1473 (Cubrières) can be assigned more accurately to *Agathoxylon gardoniense* (Crié) Philippe, a fossil species commonly encountered in the Cenomanian of France (Néraudeau et al., 2002).

Plant cuticles are abundant and well preserved, although only conifers were recognised. Two fossil taxa are documented, *Frenelopsis alata* (K. Feistmantel) E. Knobloch with its characteristic three-leaved whorls and *Glenrosa* sp., readily recognised by its

deep stomatal crypts. The excellent preservation of cuticle evidences deposition in anoxic environment.

### 4.2. Amber

Fourtou amber corresponds to irregular nodules that range from few millimetres to 4–5 cm in diameter. They are mostly red in colour (being more or less translucent in that case), more rarely brown and completely opaque. These irregular nodules originated from the fragmentation of bigger samples and only few samples have kept an original surface. The latter corresponds to a dark peripheral cortex. Comparative thermal analyses on different Cretaceous French ambers by Ragazzi et al. (2009) showed that Fourtou amber has characteristics of other mid Cretaceous ambers, and the main differential thermogravimetric peak at 415 °C is consistent with a middle Cenomanian age. Ragazzi et al. (2009) also showed that Fourtou amber is characterised by a high concentration of sulphur as compared to most of Cretaceous amber, a concentration they interpreted as the result of a diffusion of the element from the embedding sediment into the resin. It may indicate reductive conditions in the depositional environment. We cannot confirm this hypothesis since no pyrite or sulphur minerals have been found in Fourtou. Another explanation can be the diffusion of sulphuric ion in the amber forest soil. The resin accumulated on the soil before its transportation by water until the depositional environment. Sulphurs are an important component in soil and thus their diffusion cannot be totally excluded.

The botanical origin of Fourtou amber is unclear yet, as only few data are available. FTIR analyses have yet not been performed on Fourtou amber. The presence of the araucaria-like wood *Agathoxylon* and Cheirolepidiaceous leave (mesorests of *Frenelopsis alata* foliage and putatively *Glenrosa* sp.) among the plant remains associated with the amber suggests the resin was produced by conifers such as the Araucariaceae and/or the Cheirolepidiaceae. Palaeobotanical evidences led to similar conclusion about the trees which were the probable sources of the Albian and Cenomanian amber from the surrounding areas like Charentes in France (Perrichot et al., 2010) and Basque-Cantabria in northern Spain (Peñalver and Delclòs, 2010).

#### 4.2.1. Microinclusions

##### 4.2.1.1. Bacteria.

*4.2.1.1.1. Rod-shaped bacteria.* Colonies of rod-shape bacteria were observed in many preparations (Fig. 3A). The colonies have a diameter of 30–50 μm and are composed of cocci to bacilli elements of 0.5–1.2 μm.

*4.2.1.1.2. Actinobacteria.* Dichotomously-branched actinobacteria. Colonies of dichotomously-branched actinobacteria are present in Fourtou amber (Girard, 2010; Breton, 2012) (Fig. 3B). These colonies are 10–20 μm in diameter and are composed of regularly dichotomously branched filaments (1 μm in diameter). These colonies are similar to those found in Charentes amber (Girard et al., 2009c; Girard, 2010) even if their diameter is smaller than those of Charentes amber.

Perpendicular-branched actinobacteria. Extensive nets of actinobacteria were observed in many preparations (Breton, 2012) (Fig. 3C). They have approximately the same diameter than the first kind of actinobacteria, but they are characterised by anisotomous perpendicular branching. Similar actinobacteria were reported in the Charentes amber (Girard et al., 2009c; Girard, 2010). In the Fourtou amber, such filaments are mostly located at the surface of the amber nodules where they form thin cortex.

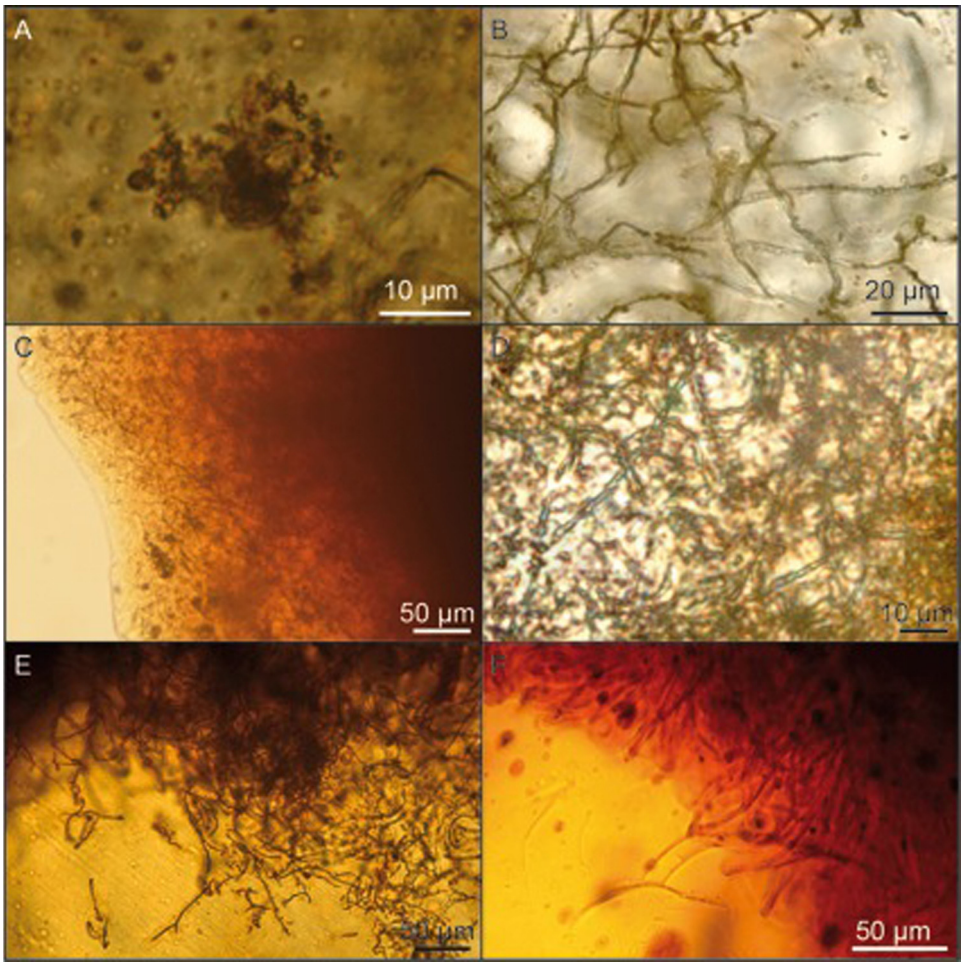


Fig. 3. Representative Bacteria in Fourtou amber. A. Rod shaped bacteria. B. Dichotomously-branched actinobacteria. C. Perpendicularly-branched actinobacteria. D. Twisted actinobacteria. E. cf. *Leptotrichites* filaments. F. cf. *Sphaerotilus* filaments.
*Inclusions de bactéries dans l'ambre de Fourtou. A. Bactéries en bâtonnets. B. Actinobactéries à subdivisions dichotomiques. C. Actinobactéries à subdivisions perpendiculaires. D. Actinobactéries torsadées. E. cf.* Leptotrichites *filamenteuses. F. cf.* Sphaerotilus *filamenteuses.*

Twisted actinobacteria. These filaments have a diameter of 1.0–1.3 µm and some of them are characterised by a twisted aspect (Breton, 2012) (Fig. 3D). They develop extensive net in the amber samples. Part of these filaments is parallel to the resin flow. Similar filaments were found in the Cenomanian amber of Salignac (Alpes-de-Haute-Provence, SE France) (Girard, 2010).

Sheathed Bacteria. Two kinds of sheathed filaments were identified in Fourtou amber. They can occur as syninclusions in the same amber pieces.

The first kind of sheathed bacteria is composed by a trichoma with a diameter of 0.9–1.4 µm protected by a sheath 6–7 µm in diameter (Fig. 3E). The sheath generally has a dusty aspect. Trichoma cells have a length comprised between 1.5 and 2.0 µm. The filaments dichotomously branch at regular intervals. It can be found in dark areas at the periphery of some red translucent

amber pieces. In such preservations, the filaments have a centripetal growth (it means from the outer part of the amber piece to the inner part). This organism is also present in opaque brown pieces in which the filaments entirely occupy the samples. It seems that these first sheathed filaments grew into the resin before its solidification and were probably resin colonisers. Morphologically, these filaments are very similar to those of two others taxa described from Cretaceous ambers: the cyanobacterium *Palaeocolteronema cenomanensis* Breton and Tostain, 2005 was described from Sarthe amber (France, Lower Cenomanian) (Breton and Tostain, 2005) and the sheathed bacterium *Leptotrichites resinatus* Schmidt, 2005 in Schmidt and Schäfer, 2005 from the Cenomanian amber of Schliersee (Germany) (Schmidt and Schäfer, 2005). Girard et al. (2009a) performed measurements of phycocyanin concentrations preserved into sheathed filaments from diverse Cretaceous ambers. Concerning Fourtou amber, they showed that the first kind of sheathed filaments lacks such blue pigments, indicating that it probably belongs to the species *L. resinatus*.

The second kind of sheathed filaments from Fourtou amber is less frequent (Girard, 2010; Breton, 2012) (Fig. 3F). It is always found at the periphery of the red translucent amber pieces of Fourtou in which they form a thin cortex. Sometimes these sheathed filaments of the second type are mixed with those of *L. resinatus*. They are composed of a trachoma, 0.9–1.1 μm in diameter (slightly smaller than those of *L. resinatus*), protected by a brown and smooth sheath, 6–7 μm in diameter. Trichoma cells are 1.5 to 1.7 μm in length. The filaments, centripetally oriented, are rarely branched and their diameter is more or less constant all along the filaments, excepted at their tips where the filaments become inflated and rounded (the diameter increase to 10–12 μm). Measurements of phycocyanin concentrations of the cortex composed by these sheathed filaments show that they also correspond to sheathed bacteria and not to cyanobacteria. The rounded ends of the filaments indicate that they probably belong to the genus *Sphaerotilus* Kützing, 1833.

*4.2.1.2. Fungi.* In a group of elliptical fungal spores were found (Fig. 4A). They have a length of 5.7 to 7.2 μm and a width of 4.4 to 5.7 μm. No ornamentation or aperture was observed at their surface. They are associated with decomposed organic matter, probable plant remains on which the fungus grew. Absence of mycelium makes the precise identification of the fungal spores difficult. Thus they are here reported as Fungi indet.

*4.2.2. Macroinclusions*

*4.2.2.1. Arthropods.* Arthropod inclusions are fairly infrequent, with only 35 specimens found among ca. 2 kg of amber collected to date (Fig. 4B–D). Yet they compose a rather diverse assemblage of insects, arachnids, myriapods, and crustaceans. Six of them were too partial or too degraded to be of systematically assigned. Surprisingly, the most abundant order is not the Diptera as in many amber deposits, but, it is the Hymenoptera, which account for 17% of all observed arthropods. All are parasitic wasps, and Scelionidae are common (Fig. 4B) as in all other Cretaceous ambers. A single chalcidoid was found, which is here tentatively assigned in the Eupelmidae before a more thorough study. Two specimens belong to extinct subfamilies of wasps: one in the Falsiformicidae (Fig. 4C)[1] and the other one in an undetermined ceraphronoid family with close affinities to the Stigmaphronidae. Diptera, and Hemiptera are each represented by three specimens each, most of which are too fragmentary or too poorly preserved for a precise assignment to any family. The only identifiable dipteran is a Chironomidae, the two other ones are undetermined

[1] Perrichot, V., Engel, M.S., Nel, A., Ortega-Blanco, J., Delclòs, X., Soriano, C., Tafforeau, P., (In Prep). In search of ant ancestors: ruling out the Falsiformicidae (Hymenoptera: Chrysidoidea). Systematic Entomology.

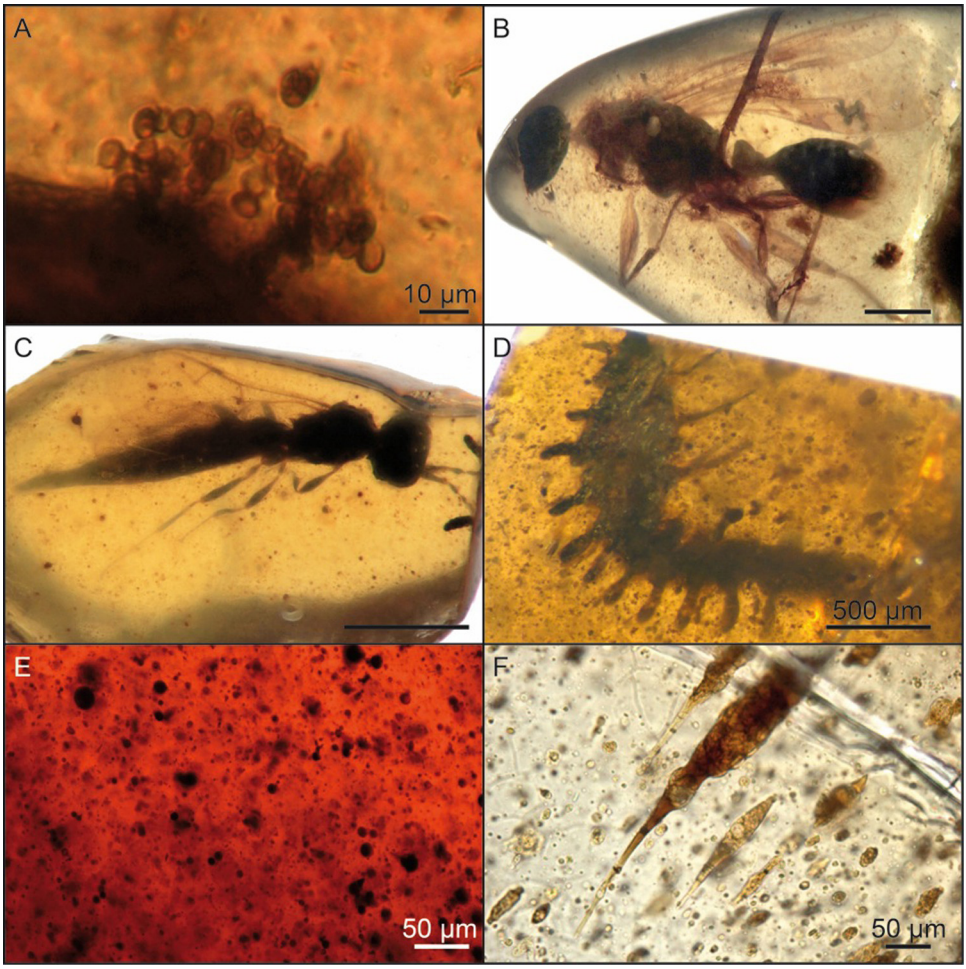


Fig. 4. Representative eukaryotes and protist-like inclusions in Fourtou amber. A. Fungal spores. B. One specimen of the extinct, Cretaceous wasp family Falsiformicidae (coll. MNHN no. F.A33607). C. One specimen of the common living wasp family Scelionidae (coll. Univ. Rennes 1 no. IGR.FOU-10.2). D. Larva of an undetermined Coleoptera or Neuropteroidea (Morel coll. no. IGR.FOU-106). E. First kind of protist-like inclusions. F. Second kind of protist-like inclusions.
*Inclusions d'eucaryotes et de protistes supposés dans l'ambre de Fourtou. A. Spores de champignons. B. Spécimen de la famille crétacée (éteinte) des guêpes Falsiformicidae (coll. MNHN n° F.A33607). C. Spécimen de la famille, vivant encore aujourd'hui, des guêpes Scelionidae (coll. Univ. Rennes 1 n° IGR.FOU-10.2). D. Larve d'un coléoptère ou neuroptéroïde indéterminé (Morel coll. n° IGR.FOU-106). E. Premier type d'inclusion rapportée à des protistes. F. Second type d'inclusion rapportée à des protistes.*

brachyceran remains. Other identified insect orders are each represented by a single or a couple of specimens. These include one thorny lacewing (Neuroptera: Rhachiberothidae), a neuropteroid or coleopteran larva (Fig. 4D), two barklice (Psocoptera), and remains of two cockroaches (Blattaria). Other arthropods found in this amber are two mites (Acari) and one spider (Araneae) of the arachnids, and one synxenid millipede (Diplopoda: Polyxenida). Finally five crustaceans were discovered, which belong to the aquatic Tanaidacea, an order whose most living representatives are marine, while some others are found in freshwater coastal habitat or estuaries. The fossil record

of tanaids is excessively meagre, with no more than 15 species known between the Carboniferous and the Cretaceous. Within amber, they were mentioned previously only from the Cretaceous of Spain (Vonk and Schram, 2007) and southwestern France (Perrichot et al., 2010). Their presence in amber is indicative of a coastal habitat for the resin-producing forest.

Finally arthropods are also recorded in Fourtou amber through their traces, in the form of coprolites (Breton, 2012). Unfortunately no plant or fungal remains compose these coprolites and they do not exhibit any characteristic shape, thus it is not possible to assign them to any group of arthropods as for some other coprolites in Cretaceous amber (Schmidt et al., 2010; Colin et al., 2011).

*4.2.2.2. Plants remains.* Plants remains are rather abundant inclusions in amber, present in many pieces. Most of them correspond to wood fibres or to stellate hairs. Other remains are scant and too poorly preserved for a precise determination.

### *4.3. Protist-like inclusions*

Fourtou amber contains many protist-like inclusions (*sensu* Girard et al., 2011) that are mostly of two kinds. One form represents dark red spherical inclusions sometimes with a distinct orientation in the resin flow (Fig. 4E). Their shape recalls those of some unicellular organisms such as the Arcellinida. However, no surface ornamentation was observed and the variation of size (from a few μm to more than 100 μm in diameter) is too important to reliably attribute these inclusions to microorganisms. The second kind of protist-like inclusions are elongated inclusions of reddish to brown colour (Fig. 4F). They are always oriented in the resin flow and many of them are characterised by two more or less long and pointed endings. As for the first kind of protist-like inclusions, their size varies a lot, being comprised of between a dozens of micrometers in length to several hundreds micrometers.

It is possible that the protist-like inclusions are artefacts that resemble protists. It could be a substance produced at the same time than the resin or a product of its polymerisation.

## 5. The Cenomanian amber forest of Aude

### *5.1. Botanical origin of the amber*

The botanical origin of Fourtou amber is unclear yet, as only few data are available. FTIR analyses have yet not been performed on Fourtou amber. Plant remains associated to the amber allow hypothesising that Fourtou amber was produced by conifers. Cenomanian amber in France (such as this of Archingeay-les Nouillers, Fouras, etc.) is always found associated to the fossil wood *Agathoxylon* (Néraudeau et al., 2002, 2003, 2005, 2008, 2009), an araucaria-like wood, and often exclusively to this wood genus. It is often assumed that, at least by the Late Cretaceous, in Europe, *Agathoxylon* can be safely assigned to the Araucariaceae, an extant conifer family. This family is reported from the Cretaceous, e.g. in northern Spain (Barale, 1992) and south-eastern France (Onoratini et al., 2009). Leafy plant remains reported here from Fourtou Cenomanian levels, belong to the Cheirolepidiaceae (*Frenelopsis* and *Glenrosa* also). Although the wood of Cheirolepidiaceae is often supposed to fit within the morphogenus *Protocupressinoxylon* Eckhold, a taxonomically poorly circumscribed genus, or *Brachyoxylon* Hollick et Jeffrey, the wood of *Glenrosa* is not yet known, whereas that of *Frenelopsis* was reported in one unique case (Doludenko et al., 1992). In this Late Albian Ukrainian specimen of *Frenelopsis kaneviensis*

Barale & Doludenko, partially preserved wood anatomy was observed in twigs and branchlets and is compatible with *Agathoxylon*. Several *Frenelopsis*-rich or exclusive levels in the Cretaceous of France yielded only *Agathoxylon* as associated wood (Barale and Bréhéret, 1995; Philippe et al., 2008; D. Néraudeau and M. Philippe, unpublished results). As a conclusion the associated plant remains suggest that amber was produced by a conifer, possibly of the Cheirolepidiaceae family. The co-occurrence of *Agathoxylon* does not demonstrate an araucariacean origin for the resin, an unfortunately too frequent statement.

### 5.2. The amber-producing vegetation

As compared to the Mid-Cretaceous (Aptian to Cenomanian) amber forest yet documented from Western Europe, the amber forest of Aude has a relatively low floral diversity (one wood and two foliage types). At the same epoch, amber forest developed a few hundreds kilometres to the north-east and north-west of Aude, respectively in Gard (Dumas, 1876; Philippe et al., 2008; Girard et al., 2012) and Charentes (Perrichot, 2005; Philippe et al., 2008; Girard, 2010), and in northern Spain as well (Arbizu et al., 1999). In most of these cases, diversity of plant remains is higher than in the Aude. Conifers from Charentes and Gard include several conifer wood taxa (*Agathoxylon*, *Brachyoxylon*, *Podocarpoxylon*) and various conifer foliages (*Frenelopsis*, *Glenrosa*, *Mirovia*, etc.) (Perrichot, 2005; Philippe et al., 2008). In these two regions, Ginkgoales are represented by the wood *Ginkgoxylon* (Perrichot, 2005; Philippe et al., 2008) and angiosperms have been clearly identified by heteroxylous charcoals (Philippe et al., 2008; Girard et al., 2012) or *Myrtophyllum*-like foliages. The low diversity in Aude could be explained by limited prospections. Only two localities (Fourtou and Cubières-sur-Cinobes) were studied whilst 7 localities were observed in Gard and much more in the Charentes (Perrichot, 2005; Philippe et al., 2008; Perrichot et al., 2010; Girard et al., 2012). A second hypothesis could be that of a taphonomical bias. It might also be that the flora had originally a low diversity as similar floristic assemblages (limited to *Agathoxylon* with *Frenelopsis* and *Glenrosa*) were reported to be associated to amber in the Charentes and in northern Spain (Peñalver and Delclòs, 2010). *Glenrosa*, with its strongly marked xerophytic adaptations, probably inhabited vegetations under strong ecological pressure, with limited diversity; it is absent from localities with the most diverse Cenomanian fossil flora, like Puy-Puy (Néraudeau et al., 2005).

### 5.3. Zoological record

The low number of arthropod inclusions is obviously related to the rather small quantity of amber collected to date, however the actual frequency in arthropods seems good in comparison to the major world deposits. Grimaldi et al. (2002) mentioned 3100 inclusions in 75 kg of Burmese amber, which is 41 per kg, while Fourtou amber revealed 35 inclusions in about 2 kg. Additional material will be necessary for a more accurate estimation of the arthropod richness.

### 5.4. Microfossil record

Only prokaryotes have been found. Unicellular eukaryotes are surprisingly absent of the assemblage. Contrary to the arthropods, a bias due to the low number of samples studied has to be excluded. More than one hundred fragments of amber were studied by two of us (VG and GB) and no unicellular eukaryotes were observed. A taphonomical bias can be possible for the absence of unicellular eukaryotes. Indeed Fourtou amber has probably been produced by a Coniferales

(as explained above). Foissner et al. (1999) demonstrated that a resin has specific properties for soft-tissues preservation depending on its botanical origin. Conifer resins are not the best ones, as unicellular such as ciliates died and are destroyed within few minutes when they are enclosed in such resins. Thus botanical origin of Fourtou amber could explain the absence of unicellular eukaryotes, at least those without tests. Absence of testate amoebae is more problematic as remains of their shell should have been preserved. Another hypothesis for such absence could be the fact that Fourtou amber could have been mostly "aerial" amber. Most arthropods observed here correspond to flying insects such as wasps, flies, mosquitoes, beetles... Others like cockroaches, arachnids and millipedes typically live in litter but are frequently encountered on tree barks where they forage and can be engulfed in resin. The prokaryotes could have been trapped on the tree bark, explaining the absence of unicellular eukaryotes that are mostly soil inhabitants. The scarcity of fungi is more enigmatic as many fungal filaments develop on the tree barks also.

Another specificity of the prokaryotic assemblage of Fourtou amber is that most of the bacteria found seem to have been resin colonisers. The rod-shaped bacteria and the perpendicular branched actinobacteria form spherical colonies as if they grew in the resin from its solidification. Also the two sheathed bacteria (cf. *Sphaerotilus* and cf. *Leptotrichites*) are always found at the periphery of the samples and their filaments are always centripetally orientated. Girard et al. (2009a) interpreted such a fossilisation as the evidence of a colonisation of the resin by the sheathed bacteria before the complete resin solidification. Schmidt and Schäfer (2005) cultivated *Leptothrix* filaments on fresh resins and demonstrated that the bacterial filaments were able to grow of 200–300 μm into the resin within 2–3 days. The comparison of Schmidt and Schäfer's results to the length of our fossil filaments (500–600 μm) indicates that sheathed bacteria of Fourtou probably grew during a week before the resin solidification. Such a long period of solidification maybe due to the effect of a retarder on the resin solidification. Schmidt and Dilcher (2007) indicated that water could slow the resin solidification. Observing resin flows at the surface of water in a *Taxodium* swamp in Florida (USA), these authors found that the solidification of resin flows requires a week. In the case of Fourtou, water immersion cannot be involved to explain the long solidification as most of the fossils are "aerial" organisms (flying insects or tree bark bacteria). However the discovery of several specimens of tanaid crustaceans shows that the resin was produced in a humid environment (coastal or estuarine). Humidity of such environments could be the cause of the delay before the Fourtou amber get solidified. Presence of freshwater organisms such as *Sphaerotilus* is consistent with a resin produced on the banks of an estuary (probably where the water had a lower salinity).

The perpendicular-branched filaments were probably another kind of amber coloniser. Indeed, the previous discussed microorganisms colonised in depth Fourtou amber. The perpendicular-branched actinomycete only colonised amber surface and it does not penetrate deep into the fossil resin. It indicates that this actinomycete probably used the resin as a growth medium.

The last kind of actinobacteria found in Fourtou amber (twisted filaments) is the evidence, contrary to the previous bacteria, of a real trapping. Indeed, its filaments are longer than those of the other kinds of bacteria (having sometimes a length of more than several millimetres). This kind of filaments is mostly oriented into the resin flows or developed on plants debris, mostly wood fibres. It is difficult to precise the real place of trapping (soil? tree bark?), but the presence of tiny plant debris associated with the filaments privileges a trapping on the soil. Also the association of oriented filaments and non-oriented filaments demonstrated that, after the initial trapping, the twisted actinobacteria were able to grow in the resin.

## 6. Conclusion

The revival of studies on Cretaceous French amber in the last decade has allowed for insights into the biodiversity and complexity of these amber forest ecosystems (Perrichot and Girard, 2009; Adl et al., 2011). Studies had primarily focused on the outcrops of Charentes until now, but they are now developed on other contemporaneous localities. The department of Aude, and especially the locality of Fourtou, appears one of the most interesting areas since both microinclusions and macroinclusions have been found (Breton, 2012). Despite the small quantity of amber collected to date, a well diversified entomofauna and an interesting microassemblage have been found. Yet the temporal and geographical position of Fourtou amber makes it interesting for comparison with the rich entomofauna from the Albian-Cenomanian amber of Charentes and the Albian amber of Spain. So far the arthropod assemblage from Fourtou amber shows more similarities with that of Spanish amber than with that Charentes amber (Perrichot, pers. obs.). New collecting field trips will soon be conducted, that should provide more material from Fourtou and possibly other contemporaneous localities with fossiliferous amber.

## Disclosure of interest

The authors declare that they have no conflicts of interest concerning this article.

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