Amber, plant and vertebrate fossils from the Lower Cenomanian paralic facies of Aix Island (Charente-Maritime, SW France)

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ABSTRACT
Lower Cenomanian paralic facies outcrop widely on Aix Island (Charente-Maritime, France). Since the beginning of the 19th century, there has been repeated

mentions of abundant fossil wood and amber from this locality, with particular focus on the wood when amber remained poorly studied. New investigations beginning 8 years ago have led to the discovery of additional fossil material, including vertebrate remains and the first fossil amber inclusions. This paper provides a sedimentological, stratigraphical and palaeontological description of the local Lower Cenomanian section, and the fossil assemblages are discussed in a wider palaeoenvironmental context.

KEY WORDS
Amber,
lignite,
conifers,
Selachians,
Reptiles,
Cenomanian,
Charente-Maritime,
SW France.

RÉSUMÉ

Ambre, plantes et vertébrés des faciès paraliques du Cénomanien inférieur de l'île d'Aix (Charente-Maritime, Sud-Ouest de la France).

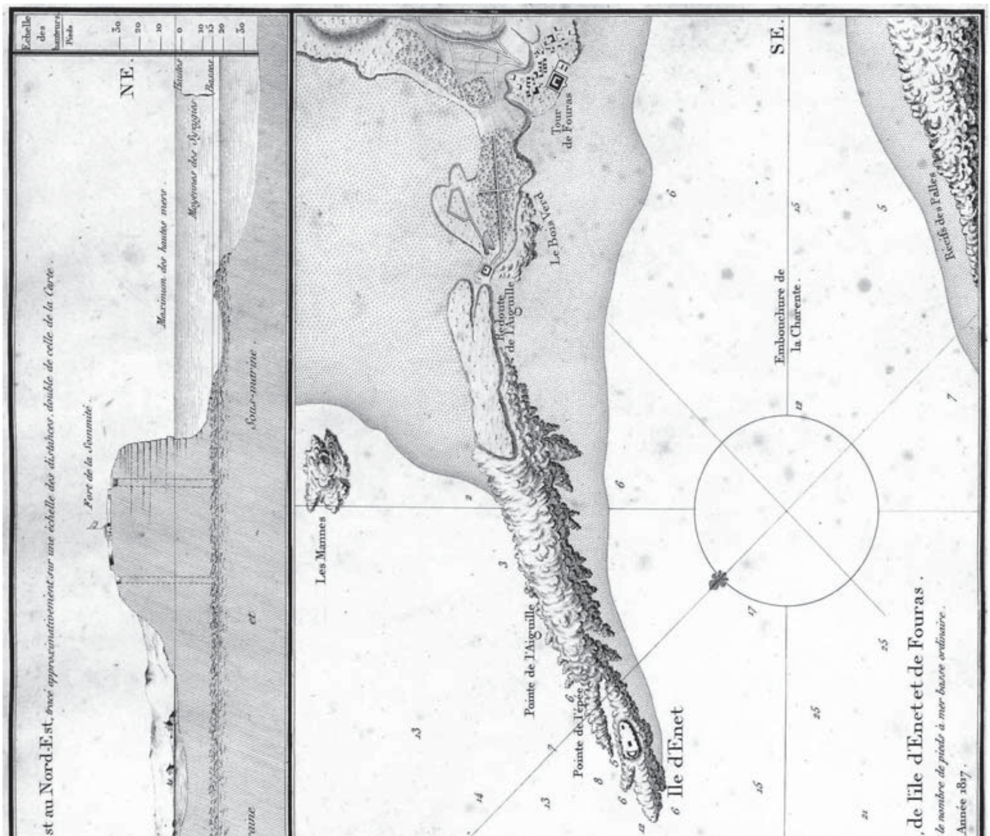
Des faciès paraliques d'âge Cénomanien inférieur affleurent sur une large partie de l'île d'Aix (Charente-Maritime, France). Des restes abondants de bois fossiles et de l'ambre y ont été mentionnés depuis le début du XIXe siècle, focalisant sur les bois tandis que l'ambre demeurait peu étudié. De nouvelles investigations menées sur l'île depuis huit ans ont permis la découverte d'une quantité importante de matériel fossile inédit, incluant des restes de vertébrés et les premières inclusions fossiles répertoriées dans cet ambre. Cet article donne une description sédimentologique, stratigraphique et paléontologique de la coupe cénomanienne de l'île, et les assemblages fossiles sont discutés dans un contexte paléoenvironnemental.

MOTS CLÉS
Ambre,
lignite,
conifères,
Sélaciens,
Reptiles,
Cénomanien,
Charente-Maritime,
SW France.

INTRODUCTION

Aix Island (Charente-Maritime, SW France) houses one of the main historical Cretaceous lignite deposits in France and was first studied in the early 19th century. Fleuriau de Bellevue (1817, 1820, 1823) was likely the first to mention the lignite, with several handwritten works that attracted the attention of his friends such as Brongniart or von Humboldt (cf. Collectif 1862). His stratigraphic section of Aix Island (1817) was the first to illustrate what he named the "subterraneous and submarine forest" ("forêt souterraine et sous-marine") or "fossil forest" ("forêt fossile") of Aix (Fig. 1). Another short paper written in 1823 by Fleuriau de Bellevue was included in Brongniart's (1823) *Dictionnaire des Sciences naturelles* under the chapter *Lignite*. In fact, Brongniart recognized this same "lignite of Aix Island" ("lignite de l'île d'Aix") formation in other parts of the Charentes region, such as in the Fouras peninsula (cf. Néraudeau *et al.* 2003). Throughout the 19th century, others described the lignite, including Lacurie (1836), Manes (1853), Coquand (1856, 1860), Hébert (1864), Arnaud (1865, 1869, 1877), Boisselier (1881, 1891), and Crié (1890). Coquand (1860) thought the lignite of Aix Island was the oldest Cretaceous stratum known in the Charentes, a facies he named "*Gardonian*". During the 20th century, the rare works dealing with the lignite were those by Koeniguer (1977, 1980, 1981) and Moreau (1976, 1993a), while Garnier (1909) only reworded the in-depth description by Lacurie (1836). Lacroix (1910) and Corlieux (1972) mainly referred to previous papers,

FIG. 1. — Map and section of Aix Island made by Fleuriau de Bellevue in 1817, with the location of the lignitic bank in the substratum of the island, designated by the name "Forêt souterraine et sous-marine" (subterraneous and submarine forest).


Profil de l'île d'Aix sur la ligne AB, du Sud-Ouest au Nord-Est, tracé approximativement sur une échelle des distances, double de celle de la Carte.
SO.
NE.
Rade des Vaisseaux de ligne.
Fort de la Rade.
la Ville.
Fort de la Sommité.
Maximum des hautes mers.
Moyennes des Syzygies
Forêt
Souterraine
et
Sous-marine
Carte de l'île d'Aix, de l'île d'Enet et de Fouras.
Nota: Les numéros indiquent le nombre de pieds à mer basse ordinaire.
Année 1817.
Ile d'Enet
Pointe de l'Aiguille
Les Mannes
Le Bois Vert
Tour de Fouras
Redoute de l'Aiguille
Embouchure de la Charente.
Recifs des Palles
Pointe de Rechignard
Pointes de Coudepont
Fauchon
Pointe de St Hilaire
L'Epine
Anse de Fougères
Rocher des Jamblets
Anse des quatrelure
Rocher de Tridou
Anse de la Croix
Pointe des Cailloux
Le Port ou Anse des Anglais
Fort de la Rade
Pointe de l'Epée
NO.
SE.
1000 Toises.

and Corlieux (1977) synthesized the geography and geology of Aix Island.

While describing the lignitic deposits of the island, the naturalists of the 19th century discovered amber, which they named "*succin*". Fleuriau de Bellevue (1817), in a handwritten description of a "35-feet exposure of a cliff of Aix Island, at the Ance de Fougère" ("coupe d'une falaise de l'île d'Aix, à l'Ance de Fougère, sur une hauteur de 35 pieds") mentioned "a 7-inch large nodule of friable *succin*" ("un rognon de *succin* friable de 7 pouces de longueur") and "numerous fragments of bituminous lignite embedded in sandstones as well as friable *succin* nuclei" ("beaucoup de fragments de lignite bitumineux empâtés dans le grès ainsi que de noyaux de *succin* friable"). Brongniart (1823) described "*succinic* resin nodules, in some cases as large as the head, mostly smaller, brown, yellow-brown, yellow-orange, soft and very friable (…) scattered in lignite masses, mainly in peaty lignite, and in accompanying and overlying sandy and marly layers" ("résines *succiniques* en nodules, quelquefois de la grosseur de la tête, souvent plus petits, bruns, jaune-brun, jaune-orangé, tendres et très friables […] disséminées dans l'amas de lignite, principalement dans le lignite tourbeux, et dans les couches sableuses et marneuses qui l'accompagnent et le recouvrent"). Lacurie (1836) also wrote that "lignite often perforated by *Teredo* passed to the chalcedonian state, accompanied by sulfurated and hydrated iron, by siliceous products, by peat in which some marine plants are still recognizable, and *retinasphalt*" ("des lignites souvent perforées par des tarets passés à l'état calcédonien, accompagnés de fer sulfuré et hydraté, de produits siliceux, de tourbe dans laquelle quelques plantes marines sont encore reconnaissables, et de *rétinasphalte*") was collected on Aix and Enet islands. Coquand (1860) described the *Gardonian* facies as consisting of "glauconitic sandstones alternating with clays bearing lignite, silicified wood and *succin*" ("grès glauconieux alternant avec des argiles à lignite, à bois silicifiés et à *succin*"). Thus, Aix Island amber was referred to as "*succin*", "*résine succinique*" and "*rétinasphalte*" in most 19th century works, as was followed by Corlieux (1972) who used the term "*succin* fragments" ("morceaux de *succin*"). During the 20th century, only two papers dealt with the study of Aix Island amber: the works of Galippe (1920) on the preservation of microorganisms in fossil resins and that of Schlüter (1978) who unsuccessfully looked for animal and plant inclusions. More recently, Videt (2004), Perrichot (2005), Vullo (2007) and Girard (2008) have studied the palaeontology and stratigraphy of the Charentes region for their Ph.D. theses, which have provided detailed descriptions of fossil oysters, amber inclusions and vertebrates of the Aix Island lignitic facies.

The sedimentary and palaeoenvironmental context of the Cenomanian lignitic deposits of Aix Island is reviewed herein, providing details on the vertebrates and plants fossil assemblages in the lignite and the arthropod and microorganism inclusions in amber.

MATERIAL

The outcrops of Aix Island are primarily composed of sandstone, clay and limestone of Early Cenomanian age. In addition to coastal marine facies that contain orbitolines (Moreau 1993b), echinoids (Néraudeau & Moreau 1989; Néraudeau 1990), oysters (Videt 2004; Videt & Néraudeau 2007) and rudists (Macé-Bordy 2007a, b), there are deposits with intercalations of paralic lignite-rich facies that locally contain amber (Perrichot 2005) and vertebrate remains (Vullo 2007) (Fig. 2). Although these facies are exposed at the base of a few cliffs (Pointe Saint-Eulard, Pointe de Coudepont) (Fig. 3), they more often occur on the tidal flats, when they are not covered by sand or mud brought by tides. Regular collecting during the last decade has distinguished three lignitic levels that range from the lowermost Cenomanian (lithological subunit A2 *sensu* Néraudeau *et al.* 1997) to the middle part of the Lower Cenomanian (subunits B1 and B2 *sensu* Néraudeau *et al.* 1997).

Lignitic facies

The oldest lignitic facies (Aix-A2s) is a clay layer poor in fossil plants and devoid of amber in the exposed part, formerly considered by Brongniart (1821) as Wealden. Brongniart's (1821) description of the fossil plants was referred to several times, especially by d'Archiac (1837) and Coquand (1859), but was revised by Crié (1890). Moreau (1993b) dated the clay of A2 as lowermost Cenomanian based on sporomorphs from various localities of Charentes (see Peyrot *et al.* 2005).

The middle lignitic facies (Aix-B1b) is a dark grey limestone rich in centimetric to pluricentimetric lignite fragments with diverse vertebrate remains (selachians, turtles, snakes) and occasional small amber pieces. The Aix-B1b layer on Aix Island is unusual in the Cenomanian series of Charentes. Indeed, the first stratum of the lithological unit B, namely subunit B1, which is the first marine carbonate formation with rudists in the Cenomanian, generally contains abundant shells with orbitolinas and oysters (= *faluns*, see Vullo *et al.* 2003). Stratigraphically, the closest lignitic facies is the one found at the boundary A2/B1 at La Buzinie near Angoulême (Perrichot *et al.* 2007a).

The youngest lignitic level in the lithological subunit B2 (middle part of the Lower Cenomanian) is the thickest and the richest in amber. Elsewhere in the Charentes, the subunit B2 outcrops on the tidal flat of Bois-Vert in the Fouras Peninsula (Néraudeau *et al.* 2003), the tidal flat of Chaucres in the southwestern coast of Oleron Island (Koeniguer 1981; Néraudeau 2009), a little bit more eastward in the locality La Varenne at Tonnay-Charente (Néraudeau *et al.* 2005), and much more south-eastward in the locality La Buzinie at Angoulême (Perrichot *et al.* 2007a). On Aix Island, this lignitic level can be subdivided into four successive sub-facies: 1) a clay with few fossil plants and devoid of amber at the base (Aix-B2a); 2) a clay with lenticular lignite accumulations, sometimes very rich in cuticles and amber, or containing metric to plurimetric fossil trunks (Aix-B2l); 3) a carbonated and glauconitic sandstone rich in oysters (*Rhynchostreon suborbiculatum* (Lamarck, 1801)) and lignite, containing large pieces of amber (Aix-B2g); and 4) locally, small lenses of glauconitic sand and gravels, rich in lignite debris (Aix-B2s) and containing vertebrate remains (selachians, turtles) (Vullo 2007), interbedded between lignitic clay levels (Aix-B2l) and glauconitic limestone (Aix-B2g).

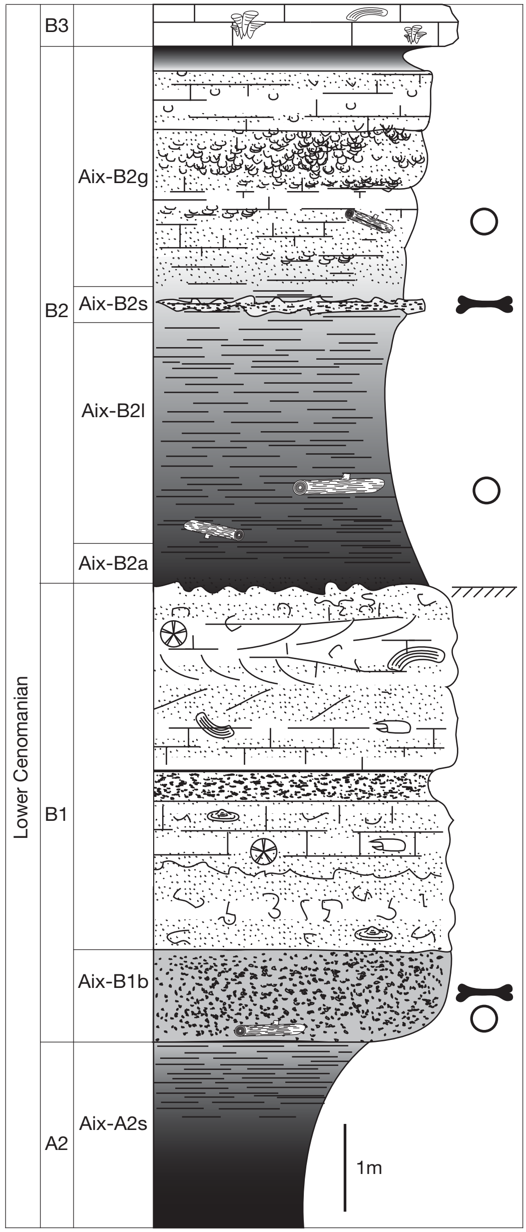


FIG. 2. — Stratigraphic section of Aix Island with the location of the six main lignitic facies: Aix-A2s with rare plant remains only; Aix-B1b with fossil wood, vertebrate remains (bone symbol) and small pieces of amber (O); Aix-B2a with rare plant microremains only; Aix-B2l with fossil trunks, plant cuticles and amber; Aix-B2s with fossil wood and vertebrate remains; Aix-B2g with fossil wood and large pieces of amber.

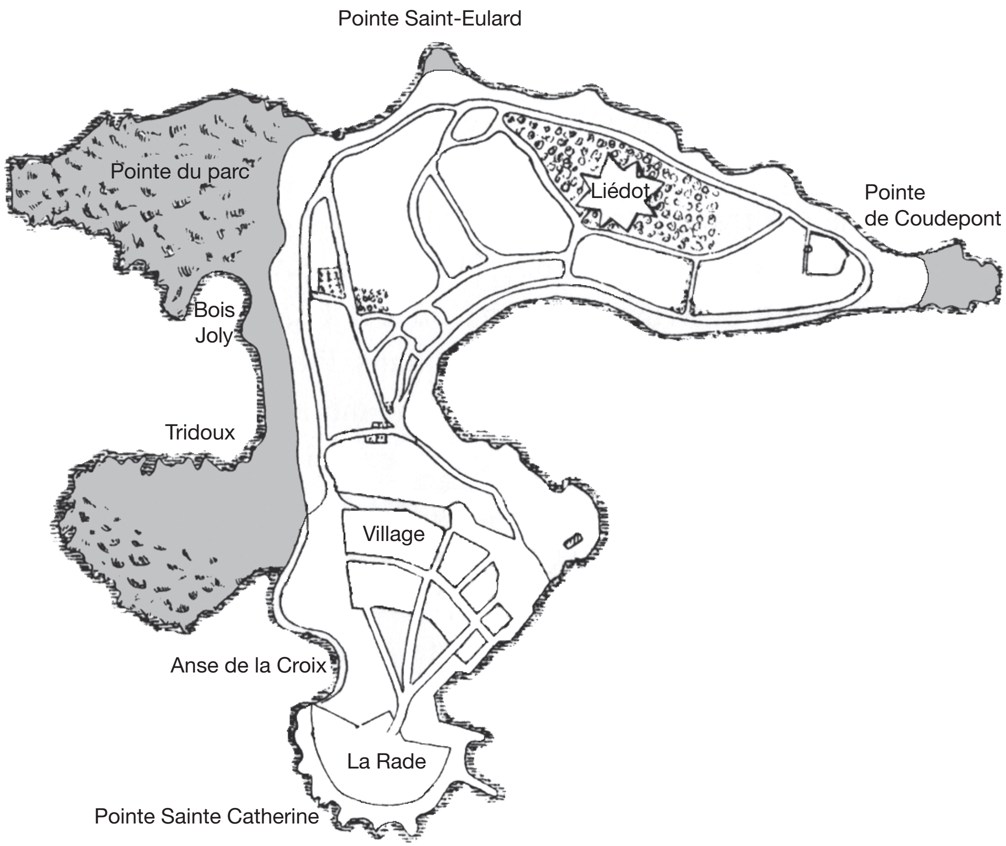


FIG. 3. — Map of Aix Island after Garnier (1909). The main lignite outcrops are located at Bois Joly and Tridoux (B2 subunit of the Lower Cenomanian) and at the Pointe Saint-Eulard and the Pointe de Coudepont (A2 and B1 subunits of the Lower Cenomanian).

The four lignitic levels from Aix Island are quite distinct and can be distinguished by their stratigraphic location and their palaeontological contents.

UPPERMOST CLAY OF A2 (AIX-A2S)

The clay at the top of subunit A2 primarily outcrops at Pointe Saint-Eulard, with a thickness of 1 to 2 m when the base of the cliffs and the tidal flats are exposed at low tides. Pyrite nodules are abundant, but fossil plant remains are rare, being limited to a few fine lignitic fragments (Perrichot 2005) and sporomorphs. No amber, vertebrate or marine macrofossils have been encountered in this facies. The grey clay is almost azoic and corresponds to a quiet and confined depositional environment, unfavourable to benthic organisms and containing only fine plant debris transported and accumulated by water or wind.

BASALMOST GREY LIMESTONE OF B1 (AIX-B1B)

The grey limestone is about 50 cm thick and composes the base of the carbonated lowermost Cenomanian. It is widely exposed on Aix Island, especially on the tidal flat between Pointe du Parc and Pointe Saint-Eulard, and extends toward the tidal flat of the Pointe de Coudepont (Fig. 3). The layer is also exposed at the base of several cliffs in the northern part of the island.

The fossil content is rich and diversified, with a combination of marine, paralic and terrestrial organisms. The most common marine organisms are oysters such as *Ceratostreon flabellatum* (Goldfuss, 1833) and *Rastellum carinatum* (Lamarck, 1806) (Videt & Néraudeau 2003, 2007; Videt 2004), pectinid bivalves (e.g., *Neithea quinquecostata* (Sowerby, 1895)), and echinoids, mainly *Anorthopygus orbicularis* (Grateloup, 1836) (Néraudeau & Moreau 1989). The coastal marine to paralic vertebrates consist mainly of selachians, pycnodont fishes, turtles and snakes (Vullo 2007). The first primitive snake vertebra of *Simoliophis rochebrunei* Sauvage, 1880, was found in this facies, and was described in a handwritten letter addressed to Cuvier by Fleuriau de Bellevue in 1820. Gervais (1848-1852) figured and mentioned it under the name "Ophidian of Aix Island" ("Ophidien de l'île d'Aix") but the species was formally described by Sauvage (1880). The vertebra previously published by Gervais (1848-1852) was studied and illustrated again by Rochebrune (1880) who placed it in the "Upper Green Sand" ("Grès vert supérieur") (i.e. Cenomanian) of Aix Island. The rest of the bulk fossil assemblage is strictly terrestrial and consists primarily of lignitic wood fragments of *Agathoxylon gardoniense* (Crié) Philippe and a few millimetric to centimetric amber pieces.

Glauconitic limestones of B2

On Aix Island, as in Fouras Peninsula and Oleron Island, the Cenomanian subunit B2 is a glauconitic-rich, sandy, carbonated series containing large lenticular accumulations of fossil plant remains (Néraudeau *et al.* 2003; Videt 2004; Vullo *et al.* 2005). This B2 subunit mainly outcrops on the western coast of Aix Island and is particularly well exposed at low tides on the Tridoux and Bois Joly flats (Fig. 3). The deposit is a lignitic and glauconitic, amber-rich formation that has attracted the attention of naturalists since the beginning of 19th century. The geological section of Fleuriau de Bellevue (1820) was erroneously ascribed to the Ance de Fougères area, but he clearly described the subunit B2 that only occurs at Bois Joly and Tridoux. Thus, Fleuriau de Bellevue (1820) described the facies Aix-B2l as "a blue clay in which are lain down horizontally bituminous and pyritized trees" ("argile bleue dans laquelle sont couchés horizontalement et pêle-mêle des arbres bitumineux et couverts de pyrite") and with "bituminous laminated peat composed of agglutinated twigs, leaf debris and (…) numerous fragments of (…) friable *succin* of diverse colours" ("terreau bitumineux feuilleté composé de brindilles agglutinés de débris de feuille et […] beaucoup de fragmens de […] succin friable de diverses couleurs"). The above Aix-B2g facies is also clearly defined by the same author as "a bluish-green soft sandstone that becomes grey and hard when drying" ("grès tendre d'un vert bleuâtre qui devient gris et dur en séchant") with "many bituminous lignite fragments embedded in the sandstone as well as friable *succin* nuclei" ("beaucoup de fragmens de lignite bitumineux empâtés dans le grès ainsi que de noyaux de *succin* friable"). Overlying subunit B2, the author described a "limestone bar (…) covered by madrepores and containing (…) *Ichthyosarcolithes*" ("banc de calcaire […] couvert de madrépores et contenant […] l'Ichtyosarcolite") above "a very similar but more sandy rock (…) bearing quartz geodes" ("une roche à peu près semblable […] mais plus sablonneuse contenant des géodes de quartz"). This description corresponds to the carbonate subunit B3 that outcrops only at Tridoux, and contains rudists, corals, and quartz geodes.

RESULTS

Vertebrate assemblage

The vertebrates from the Lower Cenomanian of Aix Island are not abundant and were mainly collected from the grey limestones at the base of the subunit B1 (facies Aix-B1b). The most notable remains are centimetric vertebrae of the ophidian *S. rochebrunei* (Fig. 4D). Additionally, pluricentimetric to decimetric fragments of chelonian carapaces are found, sometimes in abundance, which probably represent two different species. Plates with a granulated-vermiculated decoration are attributed to solemydids, while smooth plates belong to an undetermined chelonian (Vullo 2007). Crushing teeth of pycnodont fishes (Fig. 4B), teeth of selachians (e.g., *Squalicorax* Whitley, 1939) (Fig. 4A), and rare teeth of undetermined crocodilians (Fig. 4C) are also present in the vertebrate assemblage.

A few chelonian shell fragments (1, Fig. 5) and teeth of osteichthyan (*Enchodus*, 3, Fig. 5) and

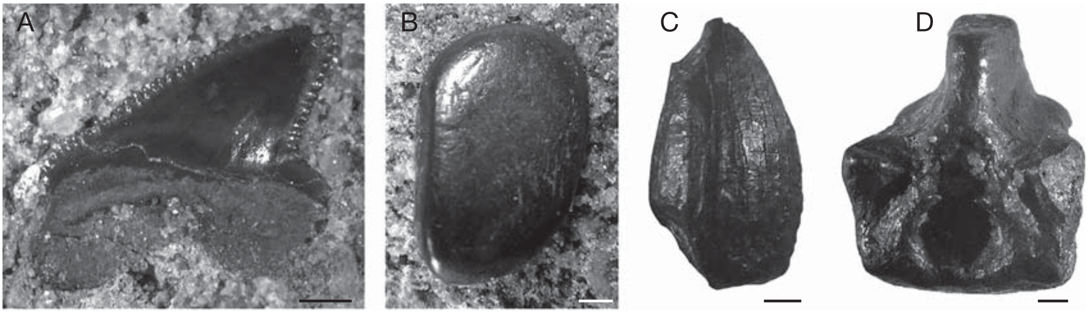


FIG. 4. — Main vertebrate remains of the facies Aix-B1b: **A**, tooth of the shark *Squalicorax* Whitley, 1939; **B**, crushing tooth of a pycnodontiform fish; **C**, tooth of an undetermined crocodilian; **D**, vertebra of the marine snake *Simoliophis rochebrunei* Sauvage, 1880. Scale bars: 1 mm.

chondrichthyan ("*C.*" *amonensis* Capetta & Case, 1975, 2, Fig. 5) fishes occur in the green lignitic sandstones of the subunit B2 (facies Aix-B2s) (Fig. 4). This facies is widely distributed in the Charentes region and extends from the Fouras Peninsula (Néraudeau *et al.* 2003; Vullo *et al.* 2005 in press) till Angoulême, more than 100 km south-eastward (Perrichot *et al.* 2007a; Vullo 2007).

PLANT ASSEMBLAGE

The type material of the fossil wood *Araucarioxylon gardoniense* described by Crié (1890) came from Aix Island. However *Araucarioxylon* Kraus being illegitimate according to Philippe (1993), and its characteristics being similar to those of *Agathoxylon* Hartig, Philippe *in* Néraudeau *et al.* (2002) proposed the new combination *Agathoxylon gardoniense* (Crié) Philippe. Perrichot (2005) illustrated *A. gardoniense* based on new preparations and a comparison with the lectotype housed in the Geological Department of the University of Rennes I. Subunits B1 and B2 contain abundant remains of *A. gardoniense* in the form of centimetric to pluridecimetric fragments (B1) or metric to plurimetric logs (B2). Large logs partly embedded in the Cenomanian clay are still preserved as lignite, while those freed and released by sea erosion have been progressively silicified. The most outstanding piece of *A. gardoniense* on Aix Island is a 10-m-long and 30-cm-wide trunk exposed during lowest tides between rocks of the Tridoux tidal flat near the semaphore. Crié (1890) described *Cedroxylon gardoniense* Crié, of which the lectotype is also housed at the University of Rennes I. Perrichot (2005: 123) noted that *C. gardoniense* has a microstructure close to that of the Recent *Abies* (Pinaceae). Perrichot (2005: fig. 55) also identified *Brachyoxylon* sp. from the subunit B2 (Philippe *et al.* 2008).

Apart from the fossil wood, the most abundant plant remains are cuticle compressions of more or less complete vegetative and reproductive organs (Fig. 6). Preliminary analysis based on small quantities of lignite from subunit B2 yielded small fragments of leafy axes of the conifers *Frenelopsis alata* (Feistm.) Knobloch (Fig. 6B) and *Glenrosa* sp. (Fig. 6C-H') and a few female scales (Gomez *et al*. 2004). These leaf-rich accumulations are likely those that Fleuriau de Bellevue (1820) described as bituminous compost ("terreau bitumineux feuilleté composé de brindilles agglutinées de débris de feuilles"). Two types of small leafy axes of *Brachyphyllum* Brongn. (Fig. 6I-O) and several types of cones (Fig. 6P-γ) have been identified as well. The *Brachyphyllum* are characterized by leaves arranged helically along the axis and with free parts shorter than the height of the leaf cushions (i.e. leaf part fixed onto the axis). The cuticles are extremely thin in the two *Brachyphyllum* types, which can be identified based on the axis diameter and the leaf length (one type is about 0.5 mm compared to 2-3 mm in the other type). Without a detailed study of the cuticles, it is not possible to determine if the types belong to different taxa. One type of cone is 5-6 mm long when complete, which can be assuredly assigned

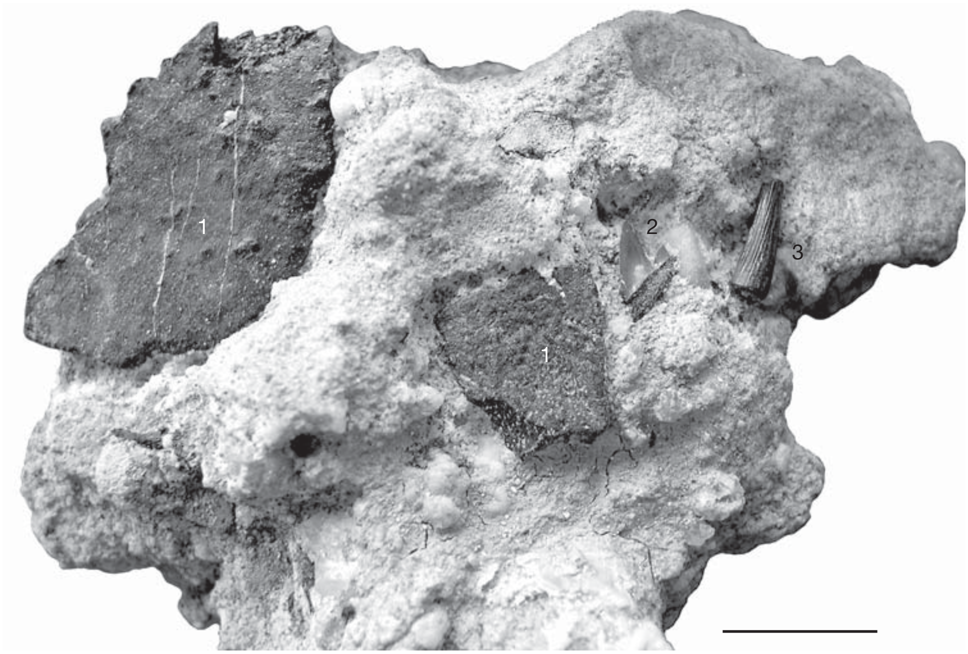


FIG. 5. — Sandstone with lignite and vertebrate accumulations of the facies Aix-B2s. The sample shows two fragments of chelonian carapaces (**1**), one tooth of the selachian "*Carcharias*" *amonensis* (Cappetta & Case, 1975) (**2**), and one tooth of the osteichthyan fish *Enchodus* Agassiz, 1835 (**3**). Scale bar: 1 cm.

to the genus *Classostrobus* Alvin, Spicer & Watson (Fig. 6Q-W) and likely correspond to the male cone of *Frenelopsis* Schenk (study in progress).

THE AMBER AND ITS INCLUSIONS

Only the youngest lignitic facies from Aix Island, located in the lithological subunits B1 and B2, have yielded amber. Galippe (1920) was the first to examine amber for biological inclusions, studying material from Enet Islet (between Aix and the Fouras Peninsula). He discovered a few microbes but the amber was likely polluted by Recent microorganisms. More recently, Schlüter (1978) unsuccessfully searched for fossils in amber pieces from Aix Island and Fouras.

Amber is uncommon on Aix Island. Only small pieces (from a few millimetres to one centimetre in diameter and often translucent) have been found in the subunit B1, between the Pointe du Parc and Pointe Saint-Eulard tidal flat (Fig. 3). The only fossil inclusions that have been found to date are a fragment of insect too incomplete to determine and the cyanobacterium *Paleocolteronema cenomanensis* Breton & Tostain, 2005 (Breton & Tostain 2005).

In the subunit B2, amber is more abundant, with large pluricentimetric to decimetric pieces. Those in the Aix-B2g are milky opaque. In the facies Aix-B2l, amber is represented by numerous millimetric to centimetric pieces (Fig. 6A) and more rarely by large nodules. Numerous pieces possess a clear beige crust. A few insects, including a primitive ant of the extinct subfamily Sphecomyrminae Wilson & Brown, 1967 (Perrichot *et al.* 2007b, c) (Fig. 7C), a brachyceran Diptera, an undetermined Hymenoptera and a spider (Fig. 7D), have been found in translucent amber collected on the tidal flat of the Bois Joly bay. The historical collections of Lacroix (1910), however, which are housed at the Muséum national d'Histoire naturelle, Paris, contain another species of ant (Lacau *et al.* unpublished data) and a Trichoptera. Other small collections of

Aix Island amber exist in the "Musée Vert" of Le Mans and the natural history museums of Nantes and La Rochelle but contain no arthropod inclusions. In a study of this amber from subunit B2, Tostain (2004) found diverse microorganisms such as nostocale and stigonematale cyanobacteria, non-flagellate unicellular algae of zygnematale-type, dinoflagellate cysts, and rhizopod protozoans. A reinvestigation of the same samples, however, has revealed that some of these microorganisms were actually modern organisms that had contaminated the crust and micro-cracks of amber nodules. A new method of sample decontamination using chemical attacks, developed by Girard *et al.* (2009), has been applied, and observations after decontamination confirmed that various fossil microorganisms are indeed included in the resin. These organisms divide into two different kinds of prokaryotic filaments. The first filament is a trichoma of 1-1.5 µm in diameter surrounded by a sheath of 6-10 µm in diameter. Based on macroscopic and microscopic features, as well as measurements of the pigment concentration, these filaments have been identified as the cyanobacterium *P. cenomanensis* (Fig. 7B). The second type of filaments is non-sheathed and 1 to 1.5 µm in diameter, and their anatomical structure place them close to actinomycete filaments. Amber from the subunit B2 also contains green algae, both of Chlorococcale (with the new species *Enallax napoleoni* Girard, 2009) (Girard 2009 [this volume]) and Siphonoclade affinities, testate amoebae (genus *Arcella* Ehrenberg, 1832), fungi (Fig. 7A) and possibly Euglenophycea.

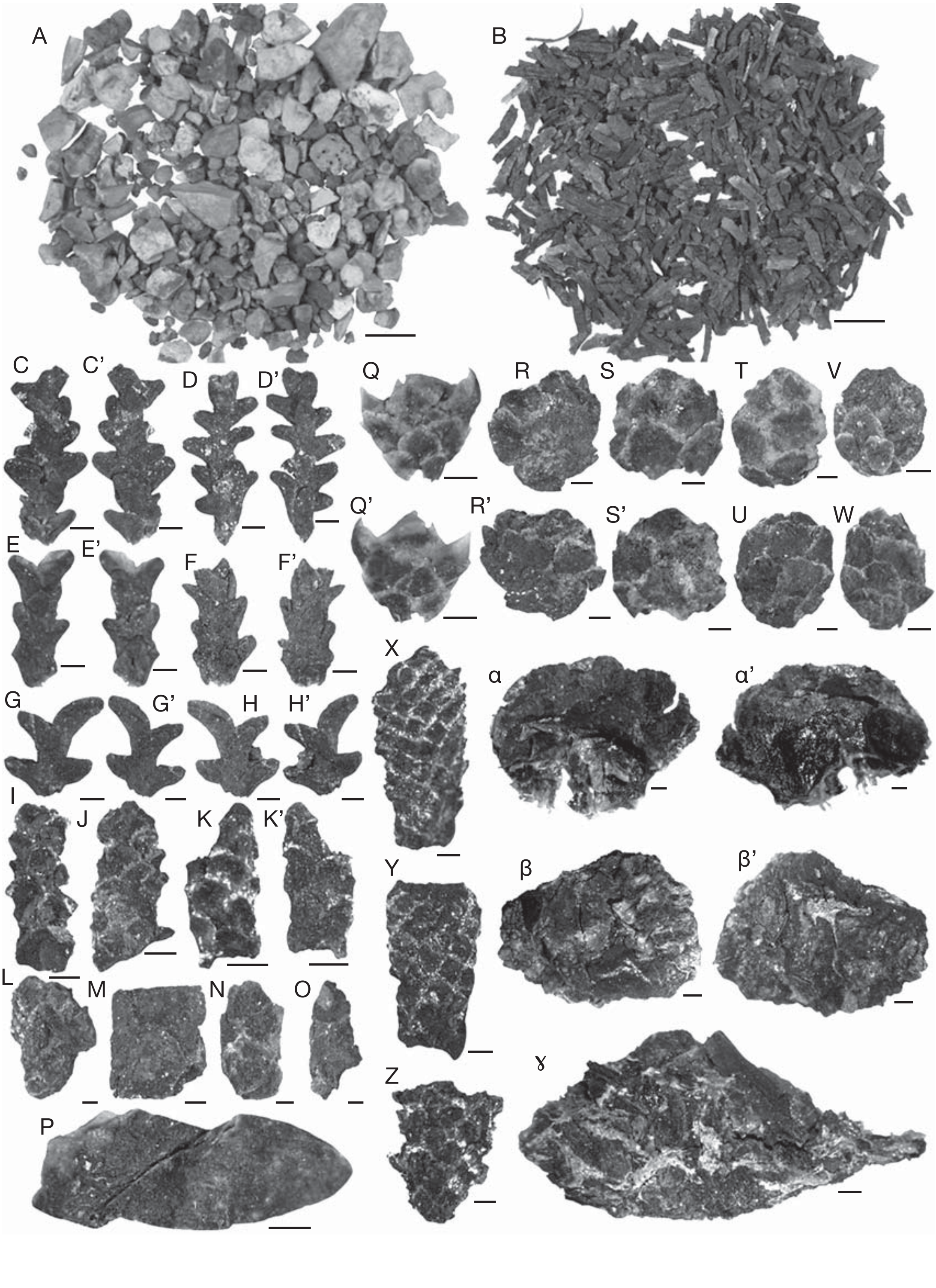
PALAEOENVIRONMENTAL DISCUSSION

Palaeontological and sedimentological analyses of the lignitic deposits from Aix Island suggest they were deposited at the boundary between marine and brackish estuarine conditions. Both the scarcity and small size of the plant remains and the absence of amber or reptiles in the uppermost clay of the subunit A2 (Aix-A2s) indicate that the depositional environment was relatively far or isolated from terrestrial influences. The clay laminations and abundance of pyrite nodules denote a calm and confined depositional environment unfavourable to benthic organisms. Overall, the lignitic beds were probably formed in the outer part of an estuary or on a shallow and muddy marine shore.

The fossiliferous grey limestone of the B1 subunit (Aix-B1b), rich in echinoids, corals, oysters, marine snakes and turtles, is the most marine lignitic facies from Aix Island. The small wood fragments of *Agathoxylon*, which are associated with the marine organisms, suggest some terrestrial influences but exclude a true terrestrial or even brackish depositional environment.

The four lignitic facies of the B2 subunit were deposited in differing hydrodynamic and hydrologic conditions. The laminated clay from the base (Aix-B2a), which is poor in fossil plants and devoid of amber, marine macro-invertebrates and terrestrial vertebrates, corresponds to a calm and confined environment similar to that mentioned above in subunit A2. The clay from the mid-part (Aix-B2l), with lenticular accumulations of lignitic trunks, plant cuticles and amber, is probably closest to the estuary mouth and the bordering forests. This layer may have been deposited in calm and shallow brackish or marine water. The carbonated and glauconitic sandstones rich in oysters, lignite and amber (Aix-B2g) were deposited in a coastal, shallow marine environment subject to moderate to high energy. The lentils of glauconitic sand and gravels rich in lignitic debris (Aix-B2s) and containing vertebrate remains (selachians, turtles) were likely deposited in a higher energy environment, close to a beach or estuarine bank.

FIG. 6. — Main plant meso-remains from the Aix-B2l facies: **A**, pieces of caramel, yellow and orange coloured amber; **B**, *Frenelopsis alata* (Feistm.) Knobloch internodes, some of them showing typical three-leafed whorls; **C**-**H'**, leafy axes of *Glenrosa* sp., showing helically arranged leaves; **I**-**K'**, leafy axes of *Brachyphyllum* type 1, showing tiny, adpressed and helically arranged leaves; **L**-**O**, leafy axes of *Brachyphyllum* type 2, showing large, adpressed and helically arranged leaves; **P**, lanceolate leaf apex of *Nehvizdya andegavense* Knobloch; **Q**-**W**, male cones of *Classostrobus* sp., showing a few helically arranged scales; **X**-**Z**, probable cones, showing tiny helically arranged scales; **α**-**γ**, female cone scales of *Alvinia*, showing multilayered cuticles. Scale bars: A, B, 1 cm; C-γ, 1 mm.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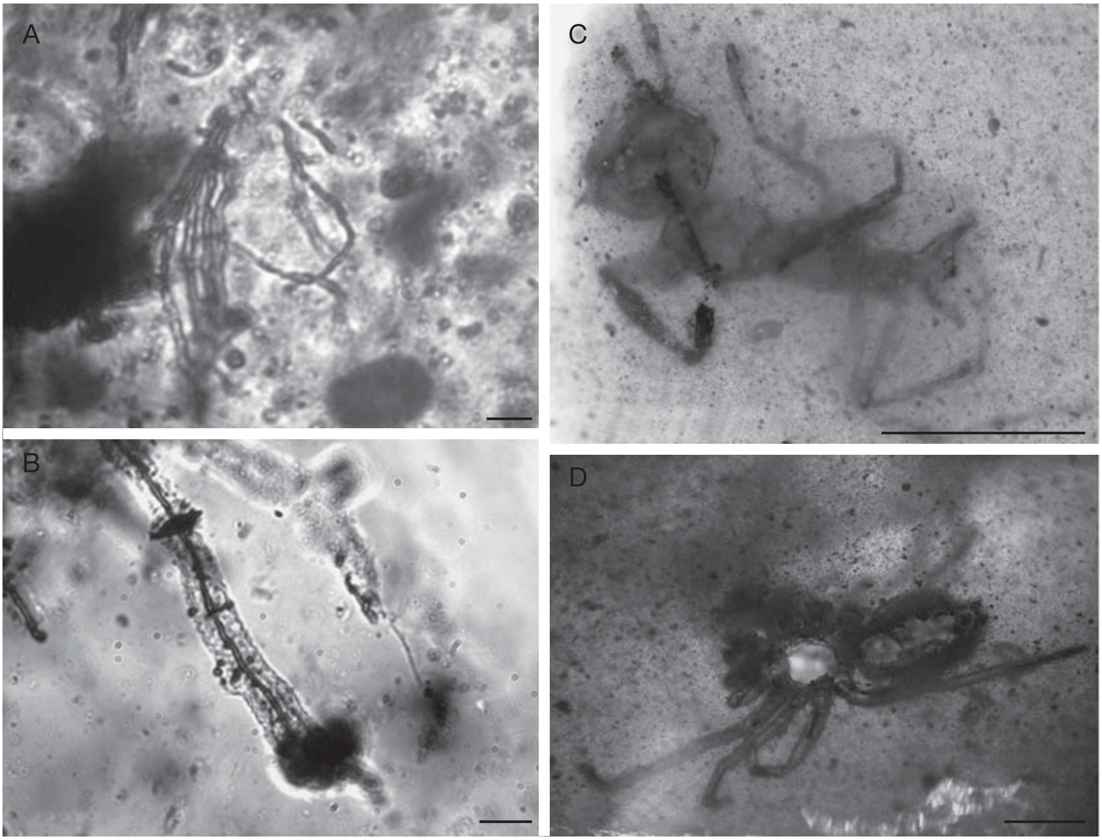

FIG. 7. — Arthropod and microorganism inclusions from amber of the Aix-B2g facies: **A**, Mycelium; **B**, Cyanobacteria; **C**, ant of the extinct subfamily Sphecomyrminae; **D**, undetermined spider. Scale bars: A, B, 10 µm; C, D, 1mm.

Compared to other ambers from the Albian-Cenomanian of the Charentes region, the fossil resin from the B2 subunit of Aix Island is similar to the coeval subunit B2 from the Fouras peninsula, located about 5 km away (Néraudeau *et al.* 2003). These ambers share common microorganism assemblages dominated by freshwater species (amoebae, cyanobacteria, actinomycetes), as is the case for the Late Albian amber (subunit A1) from Cadeuil (Néraudeau *et al.* 2008). However, the Aix Island biotic assemblage is very different from amber of the subunit B2 from Angoulême (La Buzinie district), located more than 100 km southeast (Perrichot *et al.* 2007a). Indeed, this Early Cenomanian fossil resin contains numerous marine microorganisms, such as diatoms and sponge spicules, as is the case for the Late Albian amber (subunit A1) from Archingeay-Les Nouillers (Girard *et al.* 2008).

Aix Island amber from subunit B1 (Aix-B1b) is known from only a few very small pieces and the material is not abundant enough to make significant interpretations. The arthropod inclusions are very scarce in Early Cenomanian ambers of Aix Island, which prevents any valuable comparison with the rich entomological assemblages of Archingeay-Les Nouillers and Cadeuil (Late Albian) and of La Buzinie and Fouras (Early Cenomanian). It is noteworthy, however, that like other mid-Cretaceous ambers from the Charentes region, Aix Island amber contains ant fossils, when these are still absent from other rich, coeval ambers of Spain (Delclòs *et al.* 2007) and Lebanon (Azar 2007).

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