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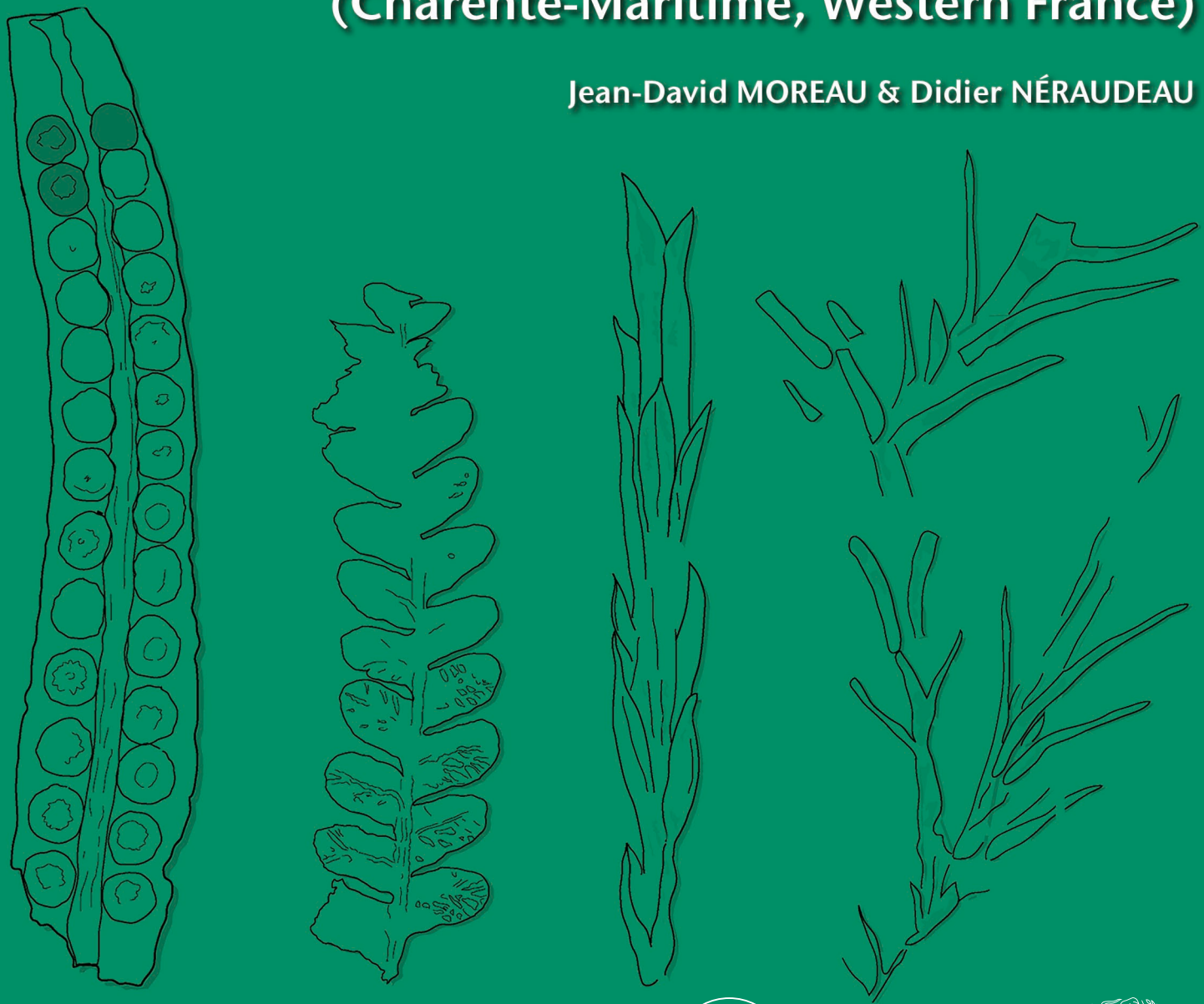
Jean-David MOREAU & Didier NÉRAUDEAU



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Amber and plants from the Upper Cretaceous of La Gripperie-Saint-Symphorien (Charente-Maritime, Western France)

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ABSTRACT
Amber and plant remains were discovered in the lower Cenomanian lignitic clay from La Gripperie-Saint-Symphorien (Charente-Maritime, western France). The amber mainly consists of scarce and infracentimetric pieces showing a wide range of sizes and colours. The shape of the amber grains greatly varies, including more or less cylindrical fragments of flows and spherical drops. Plants consist of foliar remains corresponding to isolated pinnae and pinnules of ferns (*Matonia* sp., *Weichselia reticulata* (Stokes & Webb, 1824) Fontaine emend. Alvin, 1971), leafy axes of conifers (*Geinitzia reichenbachii* (Geinitz, 1842) Hollick & Jeffrey, 1909, *Pagiophyllum* sp.) and leaves of angiosperms (including cf. *Eucalyptolaurus depreii* Coiffard, B.Gomez, Thiébaut & J.Kvaček and three morphotypes of undeterminable leaves). They are preserved as isolated cuticles, charcoalified compressions without cuticle, and external casts. Angiosperms are clearly the most abundant and diverse remains of the plant assemblage. This latter contrasts with most of Albian-Cenomanian coastal floras from the Aquitaine Basin, which are dominated by gymnosperms characterised by xeromorphic adaptations and tolerating halophytic conditions. Similar to the coeval sites of Puy-Puy (Charente-Maritime) and Jaunay-Clan (Vienne), the plant-rich clay from La Gripperie-Saint-Symphorien was probably deposited in innermost coastal environments heavily influenced by inland/continental freshwater.

KEY WORDS
Fossil resin,
angiosperms,
conifers,
Matoniaceae,
Cenomanian,
Aquitaine Basin.

RÉSUMÉ
Ambre et plantes du Crétacé supérieur de La Gripperie-Saint-Symphorien (Charente-Maritime, Ouest de la France).
De l'ambre et des plantes ont été découverts dans les argiles ligniteuses du Cénomanien inférieur de La Gripperie-Saint-Symphorien (Charente-Maritime, Ouest de la France). L'ambre correspond principalement à de rares pièces infracentimétriques qui montrent une large gamme de tailles et de couleurs. La forme des grains varie beaucoup, incluant des fragments de coulées plus ou moins cylindriques, ainsi que des gouttes sphériques. Les plantes correspondent à des pennes et pinnules isolées de fougères (*Matonia* sp., *Weichselia reticulata* (Stokes & Webb, 1824) Fontaine emend. Alvin, 1971), des axes feuillés de conifères (*Geinitzia reichenbachii* (Geinitz, 1842) Hollick & Jeffrey, 1909, *Pagiophyllum* sp.), ainsi que des feuilles d'angiospermes (incluant cf. *Eucalyptolaurus depreii* Coiffard, B.Gomez, Thiébaut & J.Kvaček et trois morphotypes de feuilles indéterminées). Ces restes sont préservés sous forme de cuticules isolées, compressions charbonneuses sans cuticule et moulages externes. Les angiospermes constituent les restes les plus abondants et les plus diversifiés de l'assemblage paléobotanique. Ceci contraste avec la plupart des flores littorales de l'Albien-Cénomanien du Bassin Aquitain, dominées par des gymnospermes montrant des adaptations xéromorphiques ainsi qu'une tolérance aux conditions halophytiques. Similairement aux sites contemporains de Puy-Puy (Charente-Maritime) et Jaunay-Clan (Vienne), les argiles à plantes de La Gripperie-Saint-Symphorien ont probablement été déposées dans des environnements côtiers plutôt internes et fortement influencés par de l'eau douce.

MOTS CLÉS
Résine fossile, angiospermes, conifères, Matoniaceae, Cénomanien, Bassin Aquitain.

INTRODUCTION

During the last decades, field prospecting and excavations organised in the Cretaceous formations from western France (in northern part of the Aquitaine Basin and southern part of the Paris Basin) led to the discovery of many palaeontological sites yielding amber and plant remains (e.g. Schlüter 1978; Néraudeau *et al.* 2002, 2008, 2009, 2013a; Perrichot 2005). The majority of these sites are located in the Albian-Cenomanian paralic and lignitic deposits from the Charentes region (departments of Charente and Charente-Maritime; Fig. 1A). Amber from these localities yielded various fossil inclusions such as arthropods (Néraudeau *et al.* 2002, 2008; Nel *et al.* 2004; Perrichot 2005, 2015; Perrichot *et al.* 2008a, 2010), microorganisms (Breton & Tostain 2005; Girard *et al.* 2009), plants (Moreau *et al.* 2017a, 2020) as well as vertebrate integuments (Perrichot *et al.* 2008b; Vullo *et al.* 2010). In the lignitic clay, floras are abundant and diverse, including palynomorphs (Dejax & Masure 2005; Peyrot *et al.* 2005, 2019; Batten *et al.* 2010; Polette 2019) as well as wood, foliar remains and reproductive structures (Néraudeau *et al.* 2002, 2005, 2020a; Gomez *et al.* 2004, 2008; Perrichot 2005; Coiffard *et al.* 2009; Kvaček *et al.* 2012; Moreau *et al.* 2017b). They are mainly ascribed to angiosperms, bennettitaleans, conifers, cycads, ginkgophytes and pteridosperms. Based on this extremely rich and exquisitely preserved biota, the fossiliferous lignitic beds from Charentes became a key for the reconstruction of mid-Cretaceous and coastal forest ecosystems from Laurasia.

Although Albian-Cenomanian plant meso- and macroremains are commonly dominated by conifers in most of the amber-bearing deposits from western France, angiosperm-dominated assemblages (or angiosperm-rich assemblages) remain extremely rare (Valentin *et al.* 2014; Néraudeau *et al.* 2020a). A new palaeontological site was recently discovered in the Upper Cretaceous lignitic clay from La Gripperie-Saint-Symphorien (Charente-Maritime, western France). These clayey deposits show the co-occurrence of amber and plant remains that are dominated by angiosperms. The purpose of this paper is to describe the flora from these layers and to discuss the palaeoenvironmental implications.

GEOGRAPHICAL AND GEOLOGICAL SETTING

The study area is located in the northern part of the Aquitaine Basin at La Gripperie-Saint-Symphorien, 15 km south of Rochefort (Charente-Maritime department, southwestern France; Fig. 1A). From the Middle Ages to the 20th century, several small quarries were dug in the uppermost Abian-lower Cenomanian sand and clay at La Gripperie-Saint-Symphorien (Platel 1979; Robert 2014). The sediments extracted from these quarries lie unconformably on Wealden multi-coloured clay and coarse white gravels (Platel 1976, 1979). The uppermost Albian-lower Cenomanian deposits are composed of alternating sand and clay that were mainly deposited in fluviatile and paralic contexts. They are regionally divided into two lithological units, A and B, the Albian/Cenomanian boundary lying within A. This latter includes two subunits, A1 and A2, historically distinguished according to the granulometry of the sand, more heterometric and coarser in A1 than in A2 (Moreau 1996), and separated in the Cadeuil area (close to La Gripperie-Saint-Symphorien) by a coarse fossiliferous conglomerate (Néraudeau *et al.* 2008; Fig. 1B). A1 is composed of sand and lignitic clay that has been dated as probable latest Albian, possibly lowermost Cenomanian, according to its palynological content (Néraudeau *et al.* 2002, 2008; Dejax & Masure 2005; Peyrot *et al.* 2019).

Regionally, the lignitic clay lens of A1 is commonly less than 1 m thick (Néraudeau *et al.* 2008, 2020a). Locally, these deposits are covered by a coarse to conglomeratic sandstone that has been referred to the lower Cenomanian according to its ostracod fauna (Néraudeau *et al.* 2008). The base of A2 is mainly composed of metric sand beds whereas the upper part of A2 is composed of clay beds or alternating lenticular sand and lignitic clay beds (Néraudeau *et al.* 2002, 2008, 2020a). The stratigraphic interval of A2 yielding clay is up to several metres thick (e.g. more than 8 m thick in the neighbour quarry of Cadeuil; Néraudeau *et al.* 2008). Both subunits A1 and A2 yielded amber and plant remains (e.g. Néraudeau *et al.* 2002, 2008, 2020a; Gomez *et al.* 2004; Perrichot 2005; Moreau *et al.* 2017b). Overlying Unit A, Unit B consists of shallow marine, carbonate shelly facies (B1), rich in sand, large benthic foraminifers (*Orbitolina plana* d'Archiac, 1837 and *O. conica* d'Archiac, 1837), as well as oysters (*Rhynchostreon suborbiculatum* Lamarck, 1801), echinoids (e.g. *Catopygus columbarius* Lamarck, 1816 and *Mecaster cenomanensis* Cotteau, 1856), and rudists (e.g. *Ichthyosarcolithes triangularis* Desmarest, 1812 and *Radiolites desmoulinsianus* d'Orbigny, 1842) (Vullo *et al.* 2003; Néraudeau *et al.* 2013b).

Amber and plant remains from La Gripperie-Saint-Symphorien were collected by the first author (J.-D.M.) in 2016. As all quarries from La Gripperie-Saint-Symphorien had already been partially filled in or covered by forests at the time of this study, it was not possible to describe a stratigraphic section. However, based on observations made previously during the 1990's by the second author (D.N.), the quarries exposed deposits showing strong similarities with the stratigraphic section of the neighbour quarry of Cadeuil (Fig. 1B). The clay beds exposed in quarries from La Gripperie-Saint-Symphorien were stratigraphically located some metres under the first marine deposits of B1 (Fig. 1B). Thus, the amber- and plant-yielding deposits presented here correspond to the lithological subunit A2, lower Cenomanian in age (subunit A2; Fig. 1B).

MATERIAL AND METHODS

All material presented here was collected *ex-situ* in the heap from the quarry. In order to find fossil plants, we analysed a few dozens of kilograms of sediment. Blocks of clay were split into slabs with hammers and knifes to obtain hand specimens as complete as possible. Additionally, in order to extract plant remains and amber, the sediment was soaked in a solution of hydrogen peroxide (12%) and water for a few days. The disaggregated sediment was then washed with tap water through a column of sieves. The pieces of amber as well as fossil plants were picked out by naked eye. In total, 54 foliar plant remains were collected (including fragmented leaves of angiosperms, fragmented leafy axes of conifers, as well as fragmented pinnae and pinnules of ferns). Excluding the undeterminable specimens, angiosperms, conifers and ferns represent 50%, 26% and 24% respectively of the plant macroremains. Due to the high fragmentation of remains, only 14 specimens were identifiable to the genus level.

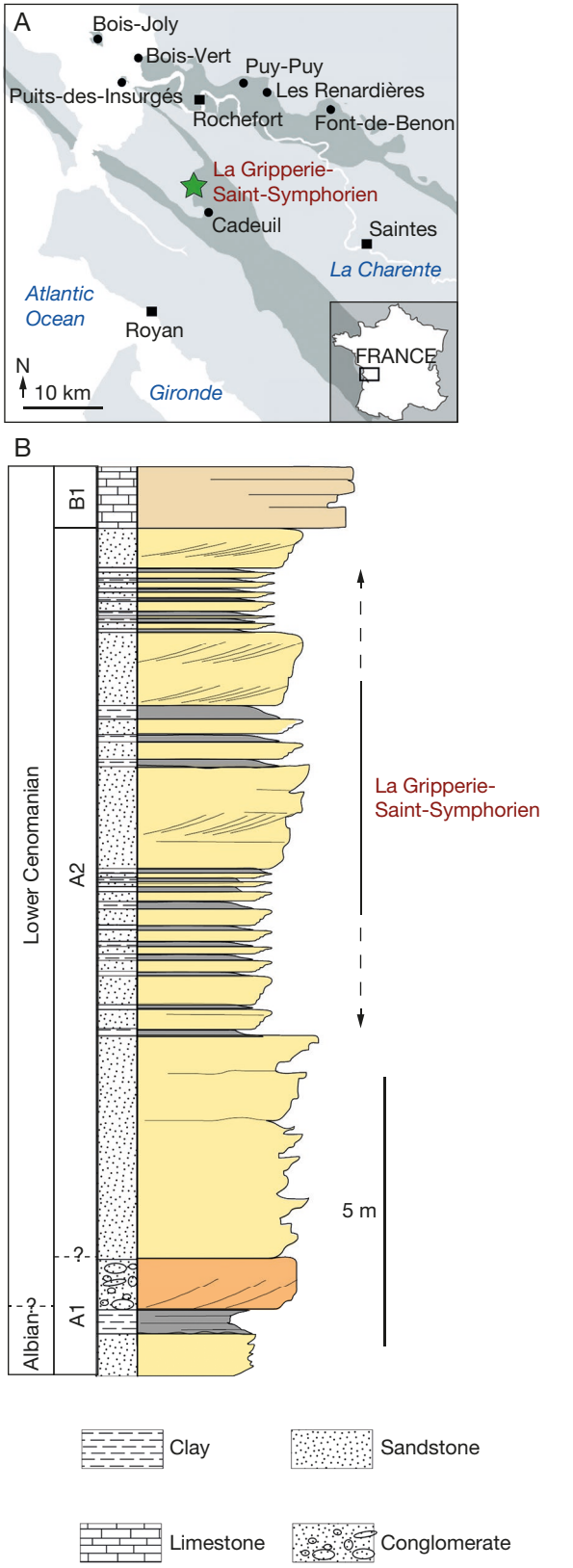

FIG. 1. — **A**, Simplified geological map of Charente-Maritime with uppermost Albian Cenomanian outcrops (**dark grey**) and location of La Gripperie-Saint-Symphorien, **black dots** indicate other Albian-Cenomanian sites yielding amber and plant remains; **B**, stratigraphic section of Cadeuil (modified after Néraudeau *et al.* 2008) and location of the lower Cenomanian clay from La Gripperie-Saint-Symphorien.

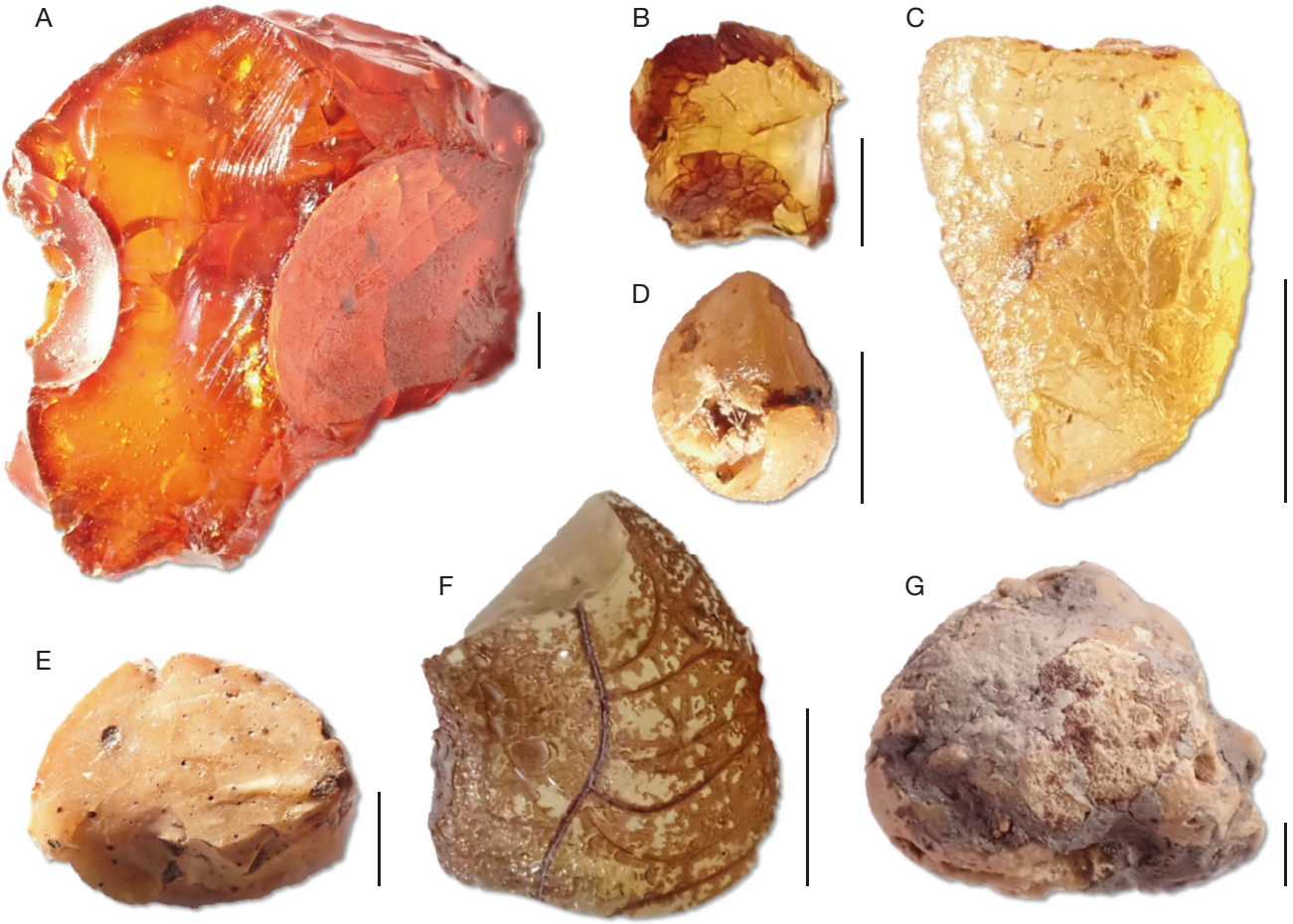

Fig. 2. — Amber from the Cenomanian deposits of La Gripperie-Saint-Symphorien: **A**-**G**, small pieces of fossil resin showing a wide range of sizes and colours. Scale bars: 1 mm.

Plant remains are greatly disarticulated and vary in size from millimetric to pluricentimetric remains. Foliar remains are mainly preserved as cuticles (mainly angiosperm leaves). However, they also include charcoalified compressions without cuticle and impressions (i.e., external casts). All specimens are housed in the palaeontological collection of Géosciences Rennes, CNRS UMR 6118, Université Rennes I (Rennes, France), with the numbers IGR-23244 to IGR-23259.

RESULTS

Amber

Amber consists of scarce and small pieces of fossil resin showing a wide range of sizes and colours (Fig. 2). They include yellow and orange translucent pieces (Fig. 2A-C) and brown opaque pieces (Fig. 2D-G) with a resinous brilliance. Their size varies from 1 mm to 10 mm in diameter. The shape of grains greatly varies, including more or less cylindrical fragments of flows (Fig. 2C) and spherical drops (Fig. 2D). Some of the grains include tiny bubbles (Fig. 2E). Surface of some grains bears cracks (Fig. 2B, F). Some opaque grains show a clear beige crust (Fig. 2G).

Systematic palaeontology

Ferns

Order GLEICHENIALES Link, 1833
Family Matoniaceae Presl, 1847
Genus *Matonia* R.Br. *in* Wallich, 1830

Matonia sp.
(Fig. 3A-D)

Material. — Three specimens: IGR-23244; IGR-23245_A; IGR-23246.

Description

The material consists of fragments of fertile pinnules (Fig. 3A-D). The largest specimen is 22 mm long and 4 mm wide. Pinnules are elongated, narrow and their margins are entire with parallel sides. Bases and apices of pinnules are not preserved. The mid-vein is strongly marked, forming a groove and is up 1 mm wide. Abaxial surface of pinnules displays secondary veins which are arranged opposite to alternate, forming an angle varying from 68 to 81° with the mid vein (Fig. 3C, D). Abaxial surface of pinnules bears sunken, indusiate and circular to slightly oval

FIG. 3. — Ferns and conifers from the Cenomanian deposits of La Gripperie-Saint-Symphorien: **A**-**D**, *Matonia* sp., fragment of elongated and narrow pinnule bearing sunken, indusiate and circular sori; specimen (**A**, **B**) and its counterpart (**C**, **D**); photograph (**A**, **C**) and interpretative sketches (**B**, **D**); IGR-23246; **E**, sketch of a pinnule of *Matonia* sp. in transverse section, showing the persistence of indusia on both, the specimen and its counterpart; **F**, **G**, *Weichselia reticulata* (Stokes & Webb, 1824) Fontaine emend. Alvin, 1971, pinna fragment bearing alternate, entire, oblong and leathery pinnules; photograph (**F**) and interpretative sketch (G); IGR-23247; **H**-**J**, *Geinitzia reichenbachii* (Geinitz, 1842) Hollick & Jeffrey, 1909, photograph (**H**) and interpretative sketches (**I**) of a leafy shoot bearing helically arranged, elongated and falcate leaves; sketches of several transverse sections in a leave showing a rhomboidal to triangular shape, drew from broken surfaces of leaves (**J**); IGR-23248; **K**, **L**, *Pagiophyllum* sp., leafy axis bearing helically arranged, highly adpressed and imbricated scale-like leaves; photograph (**K**) and interpretative sketches (**L**); IGR-23250. Abbreviations: **I.In.**, imprint of the indusium; **I.St.**, insertion of the stalk; **Mi.**, midvein; **P.In.**, persisting indusium; **So.**, sorus; **St.**, stalk. Scale bars: A-I, K, L, 1 cm; J, 1 mm.

sori (Fig. 3A, B). Sori are 1.0-1.3 mm in diameter and arranged in two rows close to the midvein. The distance between two neighbouring sori varies from 50 to 250 µm. Each indusium completely covers the sorus. Some indusia were detached and are preserved on the counter part of the specimen (Fig. 3E). They display a coalified and highly fractured aspect. When the indusium is detached, the sorus shows a central mark which is 360-640 µm in diameter and that corresponds to the insertion of the stalk. Sporangia were not observed.

Remarks

Gross morphology of fertile pinnules from La Gripperie-Saint-Symphorien is close to those of *Phlebopteris* Brongn., 1837. However, the presence of indusia excludes this genus. As pointed by Nagalingum & Cantrill (2006), *Matonidium* Schenk, 1871 and *Matonia* are very similar. They mainly differ in the size of the indusium relative to the sorus. In *Matonidium*, the indusium partially covers the sorus, whereas in *Matonia* the indusium completely covers the sorus. *Matonia* is for the first time reported in the Cretaceous deposits from the Aquitaine Basin.

Genus *Weichselia* Stiehler, 1857

Weichselia reticulata (Stokes & Webb, 1824)
Fontaine emend. Alvin, 1971
(Fig. 3F, G)

Weichselia reticulata Stokes & Webb, 1824: 423. – Alvin 1971: 27 [cum syn.].

Material. — Two specimens: IGR-23245_B; IGR-23247.

Description

The material consists of fragmented secondary pinnae (Fig. 3F, G). The largest pinna fragment (IGR-23247) is 20 mm long and 5 mm wide. The pinnae bear up to 230 µm long and up to 165 µm wide alternate, entire, oblong and leathery pinnules. They are attached by a broad base to the rachis and display a rounded apex and an entire margin. The pinnules are slightly inclined forward, forming an angle of 60-70° with the rachis. Adjacent pinnules are not in contact between them, being inserted at 160-190 mm from each other. The main vein of pinnules is straight and ends before the apex. The secondary veins display anastomosing lateral venation forming a polygonal mesh.

Remarks

The gross morphology of pinnules as well as the reticulate venation allow to ascribe these specimens to *Weichselia reticulata* which is a common fern in the Cretaceous floras from Europe (Blanco-Moreno *et al.* 2018). In Northern France, *W. reticulata* was previously reported from the Barremian-Aptian of the Paris Basin (Carpentier 1927, 1929; Deconinck *et al.* 2021). In Charente-Maritime, this fern was reported from the Cenomanian clay of the Puy-Puy Lagerstätte (Le Diouron 2005).

Conifers

Order CONIFERALES Engler, 1897
Family Geinitziaceae Kunzmann, 1999
Genus *Geinitzia* Endlicher, 1847

Geinitzia reichenbachii (Geinitz, 1842)
Hollick & Jeffrey, 1909
(Fig. 3H-J)

Geinitzia reichenbachii Geinitz, 1842: 98. – Kunzmann 2010: 125-126 [cum syn.].

Material. — Two specimens: IGR-23248; IGR-23249.

Description

The largest specimen (IGR-23248) is 50 mm long and 25 mm wide (Fig. 3H, I). Shoot is up to twice branched. Branches arise at up to 40°. Leafy shoots are up to 13 mm in diameter and straight. Leaves are helically arranged (Fig. 3H, I). They are elongated, falcate and show a long free part that forms an angle of up to 50° with the main axis of the shoot (Fig. 3H, I). Leaves are up to 14 mm long and up to 1.5 mm wide. The leaf margin is entire. The apex of leaves is acute and slightly curved inward to slightly recurved outwards (Fig. 3H, I). Leaves are rhomboidal to triangular in transverse section (rhomboidal at the base, triangular at the apex; Fig. 3J).

Remarks

Specimens are preserved as charcoalified compressions, the cuticle is not preserved.

The gross morphology of *Geinitzia* shows some similarities with several Cretaceous conifers such as *Cunninghamites* C.Presl *in* Sternberg, 1838 and *Elatocladus* T.Halle, 1913 (elongated, lanceolate, helically arranged leaves forming an acute angle with the main axis of the twig). *Geinitzia* differs from *Elatocladus* by the absence of contraction at the leaf base (Kvaček 1999). Leaves of *Geinitzia* differ from *Cunninghamites* in having a triangular to quadrangular form in cross section, not flattened needles (Kvaček 1999; Herman & Kvaček 2010).

Although the gross morphology of leaves of *Geinitzia formosa* Heer, 1871 from the Cretaceous of Germany (Heer 1871) and those of *G. reichenbachii* are quite similar (Kunzmann 1999), they differ in size, *G. formosa* showing smaller leaves (Kunzmann 1999; Herman & Kvaček 2010). *Geinitzia rigida* (J.Phillips) T.M.Harris from the Middle Jurassic of Yorkshire (Harris 1979) differs from *G. reichenbachii* in having smaller and shorter leaves, with rounded adaxial and abaxial surfaces, and a slightly incurved apex. *Geinitzia divaricata* (Bunbury) T.M.Harris from the Middle Jurassic of Yorkshire differs from *G. reichenbachii* in showing well-spaced and never crowded leaves arising perpendicularly (Harris 1979). *Geinitzia reichenbachii* is a common member of Cretaceous floras from western France. This species was reported from numerous Albian (Lower Cretaceous) to Senonian (Coniacian-Maastrichtian; Upper Cretaceous) palaeobotanical sites, particularly in the Charente, Charente-Maritime, Dordogne, Maine-et-Loire and Vienne departments (e.g. Néraudeau *et al.* 2005, 2020a; Saint-Martin *et al.* 2013; Moreau *et al.* 2021).

Family Cheirolepidiaceae Tahktajan, 1963
Genus *Pagiophyllum* Heer, 1881,
emend. T.M.Harris, 1979

Pagiophyllum sp.
(Fig. 3K, L)

Material. — Two specimens: IGR-23250; IGR-23251.

Description
Leafy axes are straight, narrow, up to 15 mm long and up to 3 mm in diameter. Leaves are persistent, helically arranged, highly adpressed and imbricated (Fig. 3K, L). Leaves are scale-like, rhomboidal, longer than wide, and keeled on abaxial side. They are up to 3.8 mm long and up to 0.6 mm wide. Apically, leaves display a short free part which is up to 2 mm long. The leaf margin is entire and the shape of the leaf apex is quite pointed.

Remarks
Specimens are preserved as charcoalified compressions, the cuticle is not preserved. The gross morphology of *Pagiophyllum* is close to those of *Brachyphyllum* Brongn., 1828 (e.g. straight twigs having needles helically arranged and small leaves). This latter differs from *Pagiophyllum* by its leaves that are as long as wide, with a shorter free part strongly adpressed to the stem (Harris 1979). In western France, the conifer *Pagiophyllum* was rarely reported in the Cenomanian amber of Charente-Maritime (Moreau *et al.* 2020) and the Cenomanian clay from Vienne (Valentin *et al.* 2014).

Angiosperms

Order LAURALES Perleb, 1826
Famille Lauraceae Juss., 1789
Genus cf. *Eucalyptolaurus* Coiffard, B.Gomez,
Thiébaut & J.Kvaček, 2009

cf. ***Eucalyptolaurus depreii*** Coiffard, B.Gomez,
Thiébaut & J.Kvaček, 2009
(Fig. 4A-D)

Eucalyptolaurus depreii Coiffard, B.Gomez, Thiébaut & J.Kvaček, 2009: 326 [cum syn.].

Material. — Four specimens: IGR-23252-IGR-23255.

Description
The specimens consist of fragmented leaves (Fig. 4A-D). They are simple, narrow and lanceolate. The fragments are up to 24 mm long and up to 10 mm wide. The lamina has entire margins. The apex is acute (Fig. 4A). The primary venation is pinnate (Fig. 4 A-D). The primary vein is straight.

Remarks
The gross morphology of leaves (simple, narrow and lanceolate) shares some similarities with *Eucalyptolaurus depreii* which is common in Cretaceous floras from western France (Coiffard *et al.* 2009; Valentin *et al.* 2014; Fleury *et al.* 2017; Moreau *et al.* 2017b; Néraudeau *et al.* 2020a). However, the fragmentation of specimens as well as the lack of some characters (e.g. veins, stomatal apparatuses) do not allow to clearly ascribe these specimens to *E. depreii*. This species was described based on Albian-Cenomanian specimens from Charente-Maritime (Coiffard *et al.* 2009).

Angiosperm indet.

Morphotype A
(Fig. 4E-I)

Material. — One specimen: IGR-23256.

Description
The specimen consists of a single fragment of a simple and quite narrow leave (Fig. 4E, F). Only the base of the leave is preserved. The specimen is 3.7 mm long and 2.5 mm wide. The lamina has entire margins. The primary venation is pinnate (Fig. 4E, F). The primary vein is straight. The secondary venation is brochidodromous, merging into intramarginal veins (Fig. 4E, F). They have an opposite arrangement, forming an angle of 30 to 40° angle with the primary vein. The tertiary venation is percurrent and composed of straight to sinuous veins forming a nearly right angle with the secondary veins (Fig. 4E, F). Ordinary epidermal cells are mainly tetragonal, hexagonal and square (Fig. 4G, H). They measure up to 49 µm long and up to 31 µm wide. They form lines of cells on the marginal band. The anticlinal walls of ordinary epidermal cells are straight to slightly curved. Leave is hypostomatic (Fig. 4G, H). Stomata are randomly oriented, scattered and paracytic (mainly brachyparacytic; Fig. 4H, I). The stomatal apparatuses are up to 56 µm long and up to 49 µm wide. The stomatal pits show an elliptic shape.

Remarks
The specimen is preserved as cuticle. Many characters of this leave being unknown, we cannot reasonably propose a determination.

Morphotype B
(Fig. 5A, B)

Material. — One specimen: IGR-23259.

Description
The specimen consists of a strongly fragmented, simple and quite narrow leave (Fig. 5A, B). The apex and the base are not preserved. The specimen is 25 mm long and 15 mm wide. The lamina has entire margins. The primary venation is pinnate and straight. The secondary venation is eucamptodromous, merging into intramarginal veins (Fig. 5B). They are oppositely to alternately arranged, forming an angle of 35 to 50° angle with the primary vein. The tertiary venation is reticulate (Fig. 5B).

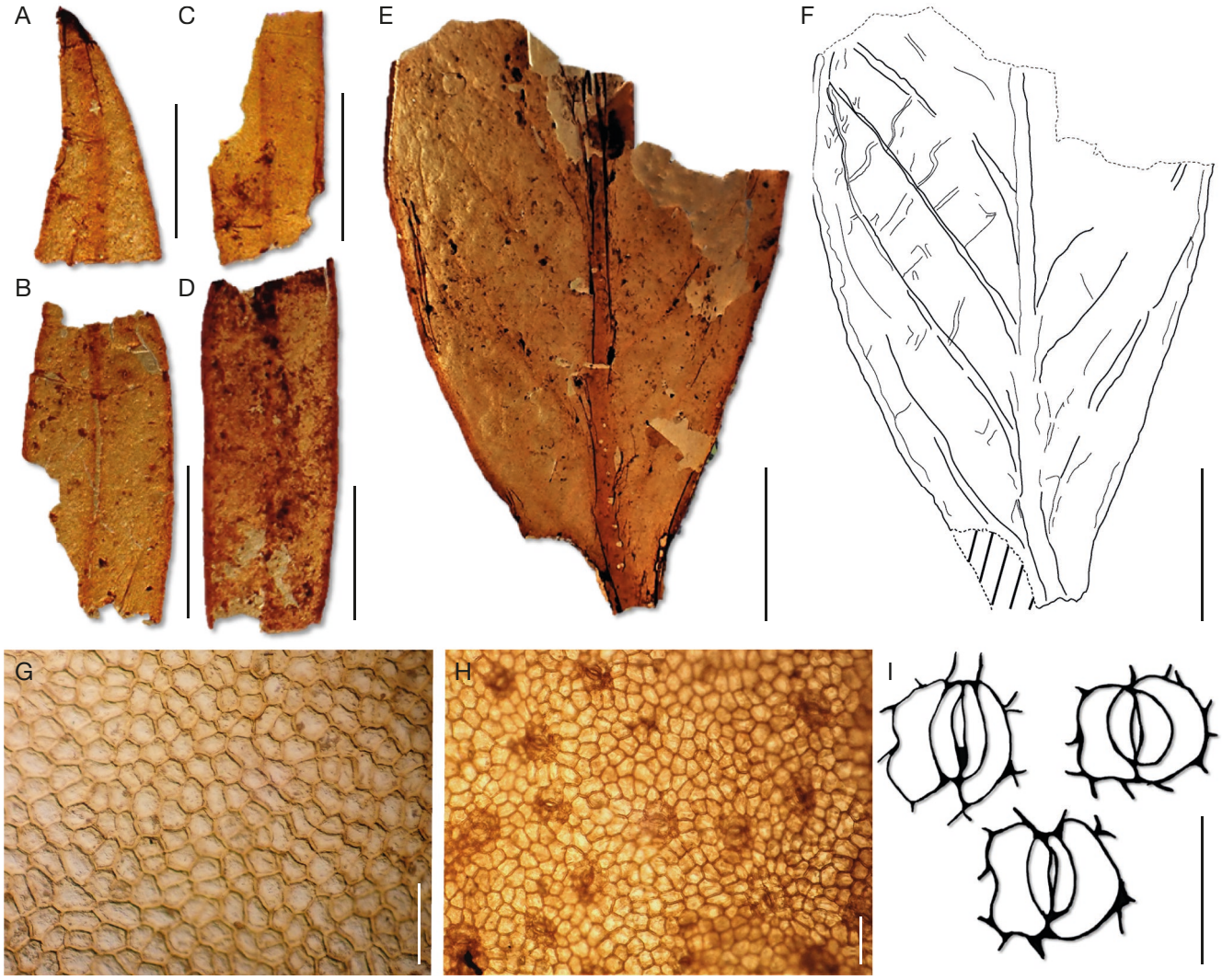

Fig. 4. — cf. *Eucalyptolaurus depreii* Coiffard, B.Gomez, Thiébaut & J.Kvaček as well as fragmented and undetermined leave of angiosperm (Morphotype A) from the Cenomanian deposits of La Gripperie-Saint-Symphorien: **A**-**D**, cf. *Eucalyptolaurus depreii*, apex (**A**) and median part (**B**-**D**) of simple, narrow and lanceolate fragmented leaves; IGR-23252–IGR-23255; **E**-**I**, Morphotype A, base of a leaf (**E**, **F**) with a straight primary vein, brochidodromous secondary venation and percurrent tertiary venation composed of straight to sinuous veins forming a nearly right angle with the secondary veins; photograph (**E**) and interpretative sketch (**F**); **G**, ordinary epidermal cells from the adaxial cuticle without stomata; **H**, ordinary epidermal cells from the abaxial cuticle bearing randomly oriented and scattered stomatal apparatuses; **I**, paracytic stomatal apparatuses; IGR-23256. Scale bars: A-F, 1 cm; G, H, 100 µm; I, 50 µm.

Remarks

The specimen is preserved as impression. IGR-23259 differs from the Morphotype A by the absence of brochidodromous secondary venation and percurrent tertiary venation.

Morphotype C
(Fig. 5C, D)

Material. — Two specimens: IGR-23257; IGR-23258.

Description

The morphotype C includes two small fragments of leaves showing serrate margins (Fig. 5C, D). Although leaves are very fragmented, it seems that they were lobed (see IGR-23258 in Figure 5D). Specimens are up to 3 mm long and up to 1.8 mm wide. The apex and the base are not preserved. Specimens are too fragmented to clearly identify the kind of venation.

Remarks

These specimens are poorly preserved as adpressions. The Morphotype C differs from all other angiosperm morphotypes in showing serrate margins.

DISCUSSION

Sedimentological and palaeontological data demonstrated that the Albian-Cenomanian lignitic layers from western France were deposited in a range of coastal environments, some of which were open to the sea, while others were brackish to freshwater environments (e.g. Néraudeau *et al.* 2002, 2005,

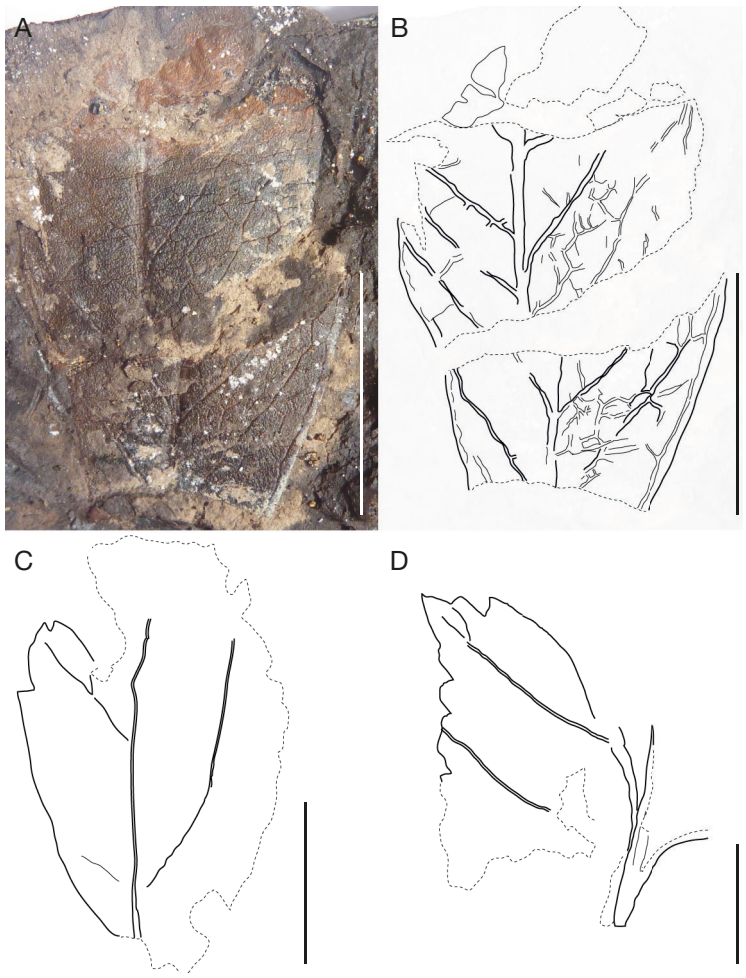

FIG. 5. — Fragmented and undetermined leaves of angiosperms (Morphotypes B and C) from the Cenomanian deposits of La Gripperie-Saint-Symphorien: **A**, **B**, Morphotype B; photograph (**A**) and interpretative sketches (**B**): IGR-23259; **C**, **D**, Morphotype C: IGR-23257 (**C**); IGR-23258 (**D**). Scale bars: 1 cm.

2020a). As observed in most of Albian-Cenomanian plant-rich sites from the Aquitaine Basin (e.g. Bois Joly, Bois Vert, Cadeuil, Font-de-Benon, Les Renardières and Puits-des-Insurgés in Charente-Maritime; Fig. 1A), palaeobotanical assemblages from paralic environments with strong marine inputs are dominated by conifers and ferns whereas angiosperms are poorly represented or lacking (Gomez *et al.* 2004, 2008; Néraudeau *et al.* 2005, 2008, 2009; Moreau *et al.* 2017b). Coastal floras from mangrove-type habitats were characterised by conifer-dominated assemblages commonly including taxa (e.g. *Brachyphyllum*; *Frenelopsis* Schenk, 1869 emend. J.Watson, 1977; *Glenrosa* J.Watson & H.L.Fisher, 1984) showing xeromorphic adaptations (e.g. presence of fleshy shoots, small leaves pressed against the axis, thick cuticle, stomatal crypts or sunken stomata apparatuses, hypodermis) and tolerating halophytic conditions (Gomez *et al.* 2008; Moreau *et al.* 2015). Plants from these environments were likely adapted to withstand intense sunlight and coastal environments exposed to desiccant conditions coupled with saline sea water. By contrast, Cenomanian floras from innermost environments were characterised by the poorness of xerophytic conifers and the abundance of angiosperm remains (Coiffard *et al.* 2007).

Eucalyptolaurus depreii, *Geinitzia reichenbachii* and *Weichselia reticulata* have been reported in a wide range of depositional settings including marginal marine and continental environments (Coiffard *et al.* 2009; Blanco-Moreno *et al.* 2018; Moreau *et al.* 2021). The fragmentation of foliar remains indicates that debris were transported from the living environment to the depositional area. It suggests the para-autochthony or the allochthony of the remains composing the taphocoenosis. However, at La Gripperie-Saint-Symphorien, several arguments suggest to exclude environments open to the sea with strong marine inputs: 1) the absence of marine organisms; 2) the conifers *Brachyphyllum*, *Frenelopsis* and *Glenrosa* are absent from the plant assemblage; 3) flowering plants are the main component of the palaeobotanical assemblage showing at least four morphologies of leaves (Figs 4; 5); and 4) *Matonia* preferentially grew in wet and warm habitats from freshwater environments (e.g. Nagalingum & Cantrill 2006; Barbacka *et al.* 2016). Similarly to the coeval sites of Puy-Puy (Charente-Maritime; Néraudeau *et al.* 2020a; Fig. 1A) and Jaunay-Clan (Vienne, Valentin *et al.* 2014), the plant-rich clay from La Gripperie-Saint-Symphorien was probably deposited in protected coastal environments heavily influenced by inland/

continental freshwater. During the Cenomanian, a transition in the dominant flora in coastal environments from conifers and ferns to angiosperms has been recognised (Coiffard *et al.* 2007). The mechanism of replacement are tentatively explained by climate changes and shorter life cycles (linked to faster seedling growth) of angiosperms (Coiffard *et al.* 2012).

The general aspect of the amber from La Gripperie-Saint-Symphorien is close to those of the Cretaceous amber from many French localities. Small grains are abundant in Cretaceous sites from the Aquitaine Basin (e.g. in Ariège, Aude and Dordogne; Breton *et al.* 2013, 2018; Saint Martin *et al.* 2013; Néraudeau *et al.* 2016), the Armorican Basin (e.g. in Mayenne, Néraudeau *et al.* 2020b), the Paris Basin (e.g. in Sarthe and Vienne; Girard *et al.* 2013, Valentin *et al.* 2020) and the Sud-Est Basin (in Alpes de Haute Provence, Bouches-du-Rhône, Var and Vaucluse; Saint Martin *et al.* 2021). Amber from several localities of Charentes differs with amber from La Gripperie-Saint-Symphorien by including larger nodules containing meso- and macroinclusions such as arthropods, conifers and vertebrate integuments (e.g. Néraudeau *et al.* 2002, 2008; Nel *et al.* 2004; Perrichot 2005, 2015; Perrichot *et al.* 2008a, 2008b, 2010; Vullo *et al.* 2010; Moreau *et al.* 2017a, 2020). In the Albian-Cenomanian formations from Charentes, the plant beds deposited in paralic environments (with strong marine inputs) yield the greatest number and the biggest nodules of amber (e.g. sites from Archingeay, Cadeuil; Perrichot 2005; Néraudeau *et al.* 2008). Since the chemical signature of the "Charentese amber" indicates a conifer source (possible Araucariaceae or Cheirolepidiaceae; Nohra *et al.* 2015) it could explain why these deposits yield conifer-dominated assemblages (including wood, foliar remains and reproductive structures). By contrast, Cenomanian fossiliferous beds deposited in innermost environments and showing a lower abundance of conifers also yield scarce and small grains of amber.

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