Albian flora from Archingeay-Les Nouillers (Charente-Maritime): comparison and synthesis of Cretaceous meso- and macro-remains from the Aquitaine Basin (southwestern France)

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ABSTRACT
Over recent decades, diverse structures ascribed to angiosperms, bennettitaleans, conifers, cycads, ginkgophytes and pteridosperms have been reported from the Cretaceous deposits of the Aquitaine Basin (southwestern France). However, Albian macrofloras remain uncommon in Aquitania as well as in France. The clay from the Archingeay-Les Nouillers quarries is one of the rare deposits of the Aquitaine Basin to yield Albian plant meso- and macro-remains. Although Albian plant-bearing beds are not accessible any more in these quarries, samples collected from excavations conducted at the end of the XXth century were deposited in the collections of the University of Rennes 1. This paper provides a synthesis of the meso- and macro-remains contained in these collections, including angiosperm leaves and leafy conifer axes, dated as Late Albian. Providing here an inventory of the Cretaceous meso- and macro-remains from the Aquitaine Basin, we compare the Albian flora from Archingeay-Les Nouillers with pre-Albian, Albian, Cenomanian, and Turono-Coniacian floras from other localities in southwestern France.

KEY WORDS
Angiosperms,
Bennettitaleans,
Conifers,
Berriasian,
Hauterivian,
Albo-Cenomanian,
Turonian,
Charentes,
Dordogne,
Vienne.

RÉSUMÉ
Flore albienne d'Archingeay-Les Nouillers (Charente-Maritime) : comparaison et synthèse des méso- et macrorestes crétacés du Bassin Aquitain (Sud-Ouest de la France).
Ces dernières décennies, diverses structures attribuées à des angiospermes, des bennettitales, des conifères, des cycadales, des ginkgophytes et des ptéridospermes ont été signalées dans les dépôts crétacés du Bassin Aquitain (Sud-Ouest de la France). Cependant les macroflores albiennes restent peu communes, en Aquitaine comme en France. Les argiles des carrières d'Archingeay-Les Nouillers font partie des rares dépôts du Bassin Aquitain ayant livré des méso- et macrorestes végétaux d'âge Albien. Bien que ces niveaux à plantes ne soient plus accessibles aujourd'hui, les campagnes de fouilles menées à la fin du XX^{e} siècle avaient permis de collecter puis déposer quelques spécimens dans les collections paléontologiques de l'Université de Rennes 1. Cet article fait la synthèse des méso- et macrorestes végétaux contenus dans ces collections, incluant des feuilles d'angiospermes ainsi que des axes feuillés de conifères, d'âge Albien terminal. À partir d'un inventaire des méso- et macrorestes crétacés du Bassin Aquitain, nous comparons la flore albienne d'Archingeay-Les Nouillers avec celles anté-albiennes, albiennes, cénomaniennes, et turono-coniaciennes issues des autres localités du Sud-Ouest de la France.

MOTS CLÉS
Angiospermes,
Bennettitales,
Conifères,
Berriasien,
Hauterivien,
Albo-Cénomanien,
Turonien,
Charentes,
Dordogne,
Vienne.

INTRODUCTION

Over recent decades, palaeontological prospecting undertaken in the Aquitaine Basin of southwestern France, demonstrated the importance of Cretaceous deposits for the reconstruction of Laurasian floras at that time. Several localities yielded clays bearing abundant and diverse macro-foliar remains, preserved as impressions and compressions with and without cuticles as well as fossil wood (Néraudeau *et al.* 2002, 2005, 2009, 2012, 2016; Gomez *et al.* 2004, 2008; Coiffard *et al.* 2009; Valentin *et al.* 2014; see Fig. 1 and Table 1). Most of the localities containing Cretaceous plants are located in Charente, Charente-Maritime, Dordogne and Vienne. The fossils recovered were assigned to angiosperms, bennettitaleans, conifers, cycads, ginkgophytes and pteridosperms. Recently, Upper Cretaceous permineralized plants inside flint nodules have been found in Charente and Charente-Maritime (Moreau *et al.* 2014a, 2015, 2016; Néraudeau 2014; see Fig. 1 and Table 1). Cretaceous plant beds in southwestern France are mainly Hauterivian to Turonian in age (Fig. 1; Table 1). Albian macrofloras are uncommon there, as in most of France. In the Aquitaine Basin, only four localities have yielded upper Albian plant beds (Néraudeau *et al.* 2002, 2005, 2008). The Font-de-Benon quarries, between the villages of Archingeay and Les Nouillers are one of these four. The first palaeobotanical study undertaken on Albian clays (sub-unit A1sl1 *sensu* Néraudeau *et al.* 2002) at Font-de-Benon focused on wood (Néraudeau *et al.* 2002). Based on bulk macerations of cuticles in hydrogen peroxide, a preliminary list of the flora from these Albian deposits was presented in Gomez *et al.* (2004). Based on angiosperm remains from this locality Coiffard *et al.* (2009) described a new Lauraceae leaf. Although the Cenomanian flora from Archingeay-Les Nouillers was later listed by Gomez *et al.* (2008), the Albian flora of this locality is still only partially described and illustrated.

The first objective of this paper is to provide a synopsis of the Albian meso- and macro-remains from Archingeay-Les Nouillers area housed in the collections of the University of Rennes 1. The second objective is to produce an inventory of Cretaceous meso- and macro-remains from the Aquitaine Basin (Fig. 1; Table 1). Here, the Albian flora from Archingeay-Les Nouillers is compared to the pre-Albian, Albian, Cenomanian, and Turono-Coniacian floras from other localities in southwestern France.

GEOLOGICAL SETTING

The Archingeay-Les Nouillers quarries, also called the Font-de-Benon quarries, are located 20 km east of Rochefort, in Charente-Maritime (Fig. 1). Historically, Cenomanian sands from the villages of Archingeay and Les Nouillers were exploited by two successive and contiguous quarries, "Archingeay 1" (Néraudeau *et al.* 2002) then "Archingeay 2" (Gomez *et al.* 2008), both being nearly completely backfilled today. Néraudeau *et al.* (2002) defined exposed levels from subunit A1 to subunit B1 (Fig. 2). The first Cretaceous deposits (A1) overlie upper Jurassic limestone (J). Based on palynology, A1 is latest Albian in age (Néraudeau *et al.* 2002; Dejax & Masure 2005). It consists of sandy beds with cross-bedded stratification and clay lenses. A1 mainly yielded cuticles, wood and amber containing a rich arthropod fauna (Néraudeau *et al.* 2002; Nel *et al.* 2004; Perrichot 2005), micro-organisms (Girard *et al.* 2009), dinosaur feathers (Perrichot *et al.* 2008), and mammalian hairs (Vullo *et al.* 2010). Palynological analysis has revealed abundant and diverse material from mixed origins, both marine and terrestrial (Dejax & Masure 2005). The lowermost Cenomanian (A2) shows alternations of sand and clay beds, and yielded abundant and diverse plant meso-and macrofossils with cuticles (Gomez *et al.* 2008). B1 consists of shelly sand yielding abundant marine fauna including molluscs, echinoderms, foraminifera (*Orbitolina conica* d'Archiac, 1837) and vertebrates (Vullo *et al.* 2003). Locally, at the top of quarry Archingeay 2, the deposits are overlain by 1 to 2-m thick horizontal beds of diachronous flint (Moreau *et al.* 2014a).

MATERIAL AND METHODS

All illustrated specimens are housed in the collections of the Université of Rennes 1 (coll. Néraudeau; Figs 3, 4). They

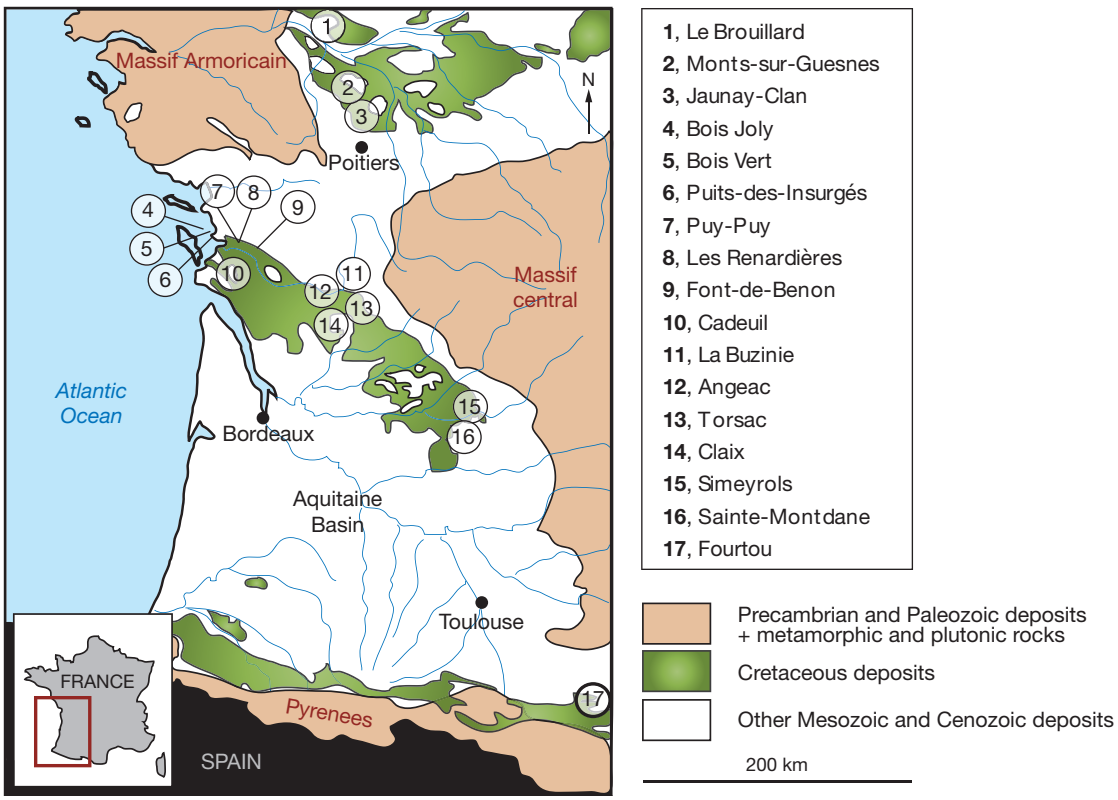


FIG. 1. — Synthetic geological map of the Aquitaine Basin (southwestern France) providing an inventory of the main localities yielding plant macro-foliar remains, reproductive structures and isolated cuticles (excluding woods and pollen). The map includes some localities of the southwestern- part of the Paris Basin, in Maine-et-Loire (**1**, Le Brouillard), of the Seuil du Poitou, in Vienne (**2**, Monts-sur-Guesnes and **3**, Jaunay-Clan), of Charente-Maritime (**4**, Bois Joly; **5**, Bois Vert; **6**, Puits-des-Insurgés; **7**, Puy-Puy; **8**, Les Renardières; **9**, Font-de-Benon; **10**, Cadeuil), of Charente (**11**, La Buzinie; **12**, Angeac; **13**,Torsac; **14**, Claix), of Dordogne (**15**, Simeyrols; **16**, Sainte-Mondane) and from the Pyrénées, in Aude (**17**, Fourtou).

were all collected from the sub-unit A1sl1 (*sensu* Néraudeau *et al.* 2002), in 1999, before the plant-bearing bed was totally backfilled. All specimens discussed in this paper were collected from "Archingeay 2". Claystone was split into slabs using hammers and knives to obtain hand specimens as complete as possible. Specimens consist of macro-foliar remains of angiosperms, conifers and indeterminate terrestrial plants. All are preserved on surfaces of clay slabs. Preservation consists of impressions, adpressions, and compressions with cuticles. The preservation of details is quite variable. The fossils were examined under a Leica MZ9.5 stereomicroscope. Photographs were taken using a Nikon D5200 camera. Fossil wood is rather uncommon in the A1 unit, however two pieces were collected, close to the contact with underlying upper Jurassic limestone (Fig. 2). One (MP1158) was found associated with pyritized oysters (*Striostrea* sp.), in a sandy level, in contrast to the clay-rich levels which yielded most other plant remains (A1g in Néraudeau *et al.* 2002). Another (MP1059) was collected just above, within A1sl1. Wood pieces were split along their radial direction, mounted on aluminum stubs, gold-palladium spur coated, and observed in a GEOL 35-CF scanning microscope under a 5 keV acceleration voltage. Corresponding material and stubs are kept in the Laboratoire de Paléobotanique collections, Université Lyon-1.

SYSTEMATIC PALAEONTOLOGY

CONIFERS

Family CHEIROLEPIDIACEAE Takht. ex Doludenko, 1978
Genus *Frenelopsis* Schenk, 1869
emend. J.Watson (1977)

Frenelopsis sp.
(Fig. 3C)

MATERIAL. — 1 specimen: IGR 2769a.

DESCRIPTION

Specimen consists of isolated, narrow internodes, 35 mm long, and up to 4 mm wide. Each internode is composed by one whorl of three proximally fused leaves. Distally, internodes show three small, triangular free tips up to 1.5 mm long.

REMARKS

The gross morphology of the specimen is close to that of *Frenelopsis alata* (K. Feistmantel, 1881) E. Knobloch, 1971. Based on isolated cuticles, this taxon was first recorded from the sub-unit A1sl1 by Gomez *et al.* (2004).

Family *Incertae sedis*
Genus *Geinitzia* Endl., 1847

Geinitzia sp.
(Fig. 3A, B)

Material. — 1 specimen: IGR 2769b.

Description
Leafy axes straight, up to 85 mm long, and up to 14 mm wide. Branches arise at up to 45°. Leaves are helically arranged, elongated, triangular in sagittal view, and show a long free part. The angle between the leaves and the main axis of the shoot is up to 60°. The leaves are up to 9 mm long, and up to 3 mm thick. The leaf margin is entire. The apex is acute and slightly curved adaxially.

Remarks
This is the first record of *Geinitzia* from the Albian clay of Archingeay-les Nouillers. *Geinitzia* sp. is only known from a single specimen (two opposite slabs of the same specimen, i.e. part and counterpart) preserved as an adpression. The leaves and stems are broken into small pieces displaying a charcoalified aspect. Cuticle is not clearly distinguishable. Spirally arranged, elongated, lanceolate leaves forming an acute angle with the main axis are known among several Cretaceous conifers such as *Elatocladus* (T.Halle, 1913), *Geinitzia* and *Pagiophyllum* (Heer, 1881 *emend.* T.M.Harris [1979]). The leaf base of *Geinitzia* differs from the constricted leaf base of *Elatocladus* (Kvaček 1999). The leaves of *Geinitzia* from Archingeay-Les Nouillers differ from the more elongated leaves of *Pagiophyllum* from the Cenomanian of Jaunay-Clan (Vienne; Valentin *et al.* 2014).

Genus Glenrosa J.Watson & H.L.Fisher, 1984
emend. Srinivasan (1992)

Glenrosa carentonensis
Moreau, Néraudeau, Tafforeau & Dépré, 2015
(Fig. 3D, E)

Material. — 1 specimen: IGR 2769c.

Description
The specimen consists of a single shoot 10 mm long and 3.5 mm in diameter. Leaves are helically arranged. They are small, claw shaped and up to 3 mm long and 1.5 mm wide. They show a short free part. The leaf margin is entire and the apex is rounded.

Remarks
The gross morphology and dimensions of the specimen are close to that of *Glenrosa carentonensis* described by Moreau *et al.* (2015) from the Cenomanian flints from Charentes. This conifer is characterized by an unusual stomatal arrangement inside deep crypts. These crypts consist of ampulla-shaped pits that are sunken in the mesophyll and contain stomatal apparatuses.

Genus Agathoxylon Hartig, 1848

Agathoxylon gardoniense (Crié, 1890)
Néraudeau *et al.,* 2002

Material. — 1 specimen: MP1158.

Description
Homoxylous wood, with axial tracheids and radial ray parenchyma. Growth-rings present, with a limited amount of late wood. Radial tracheid pitting of araucarian type. Cross-fields with numerous contiguous alternating cupressoid oculipores.

Agathoxylon sp.

Material. — 1 specimen: MP1059.

Description
Poorly preserved homoxylous wood, with axial tracheids and radial ray parenchyma. Growth-rings not clearly observed. Radial tracheid pitting of araucarian type, similar to that of *Agathoxylon gardoniense*. The few preserved cross-fields we managed to observe were also of araucarian type, with poorly preserved oculipores.

Remarks
Both specimens of fossil wood fit well within the variability of *Agathoxylon gardoniense*, as observed in numerous samples collected from the Charentes ranging in age from the Albian to the late Cenomanian.

Angiosperms

Family Lauraceae Juss., 1789
Genus Eucalyptolaurus
Coiffard, Gomez, Thiébaut & J.Kvaček, 2009

Eucalyptolaurus depreii
Coiffard, Gomez, Thiébaut & J.Kvaček, 2009
(Fig. 4A-C)

Material. — 3 specimens; IGR 2770-IGR 2772.

Description
The specimens consist of a single complete leaf and two lamina fragments. The leaf is falcate, narrow lanceolate, 87 mm long and up to 10 mm wide. The leaf apex is acute. The leaf base is cuneate and asymmetric. The petiole is 9 mm long and 1 mm wide. The lamina has entire margins. The primary venation is pinnate. The primary vein is straight except at the leaf base where it is slightly curved. The secondary venation is brochidodromous. Although the primary vein is well-marked, secondary veins are only weakly visible. These are arranged opposite to subopposite and quite regularly spaced, forming an angle of up to 60° angle with the primary vein.

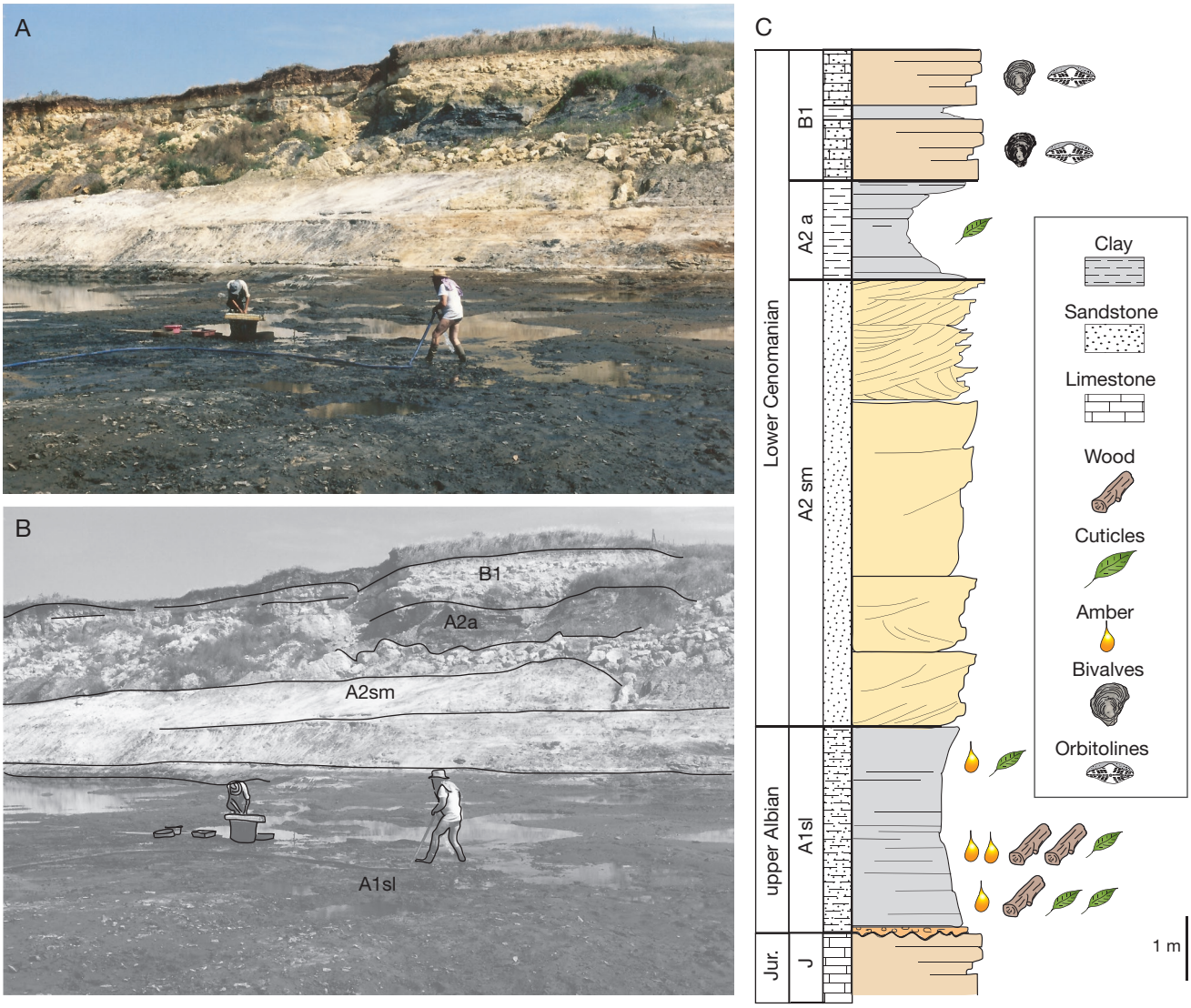


Fig. 2. — **A**, **B**, general view of the Font-de-Benon quarry section (Archingeay 1), showing the different units; the plant-bearing beds are located in the lignite at the bottom of the quarry; **C**, synthetic stratigraphical section of the Albian-Cenomanian deposits showing plant beds at the bottom of the column.

Remarks

The preservation of the leaves varies greatly from impressions to compressions with cuticle. When preserved, the cuticle breaks into small pieces that commonly curl up on themselves. Details of the stomatal apparatus and epidermal cells of the species were previously described and illustrated by Coiffard *et al.* (2009). *Eucalyptolaurus depreii* is documented from the uppermost Albian (unit A1) to the lowermost Cenomanian (unit A2; Coiffard *et al.* 2009).

Plant indet.

Family *Incertae sedis*
Genus *Incertae sedis*

Plant indet. 1
(Fig. 3D, E)

Material. — 1 specimen: IGR 2773.

Description

This single specimen consists of a fragment of leaf or pinnule showing numerous thin parallel veins. The fragment is 45 mm long and up to 15 mm wide.

Remarks

Cuticle is not preserved, only the imprint. The base and apex of the leaf or the pinnule being absent, determination of the specimen is not possible. In mid-Cretaceous floras from western France, quite broad and elongated leaves or pinnules with parallel veins are known among conifers such as *Dammarophyllum* Velen., 1889, ginkgophytes such as *Nehvizdya andegavense* (D.Pons, Boureau & Broutin, 1976) Gomez, 2000, and bennettitaleans such as *Zamites* Brongn., 1828. The specimen differs from the *Nehvizdya andegavense* leaves previously found at Archingeay (Gomez *et al.* 2004) by the absence of dichotomous veins and resin bodies between veins. Its shape seems to be similar to that of the conifer leaf *Dammarophyllum* which had not been reported previously from the uppermost Albian deposits of Archingeay-Les Nouillers.

DISCUSSION: COMPARISON WITH CRETACEOUS MESO- AND MACROFLORAS FROM THE AQUITAINE BASIN

Lower and Upper Cretaceous deposits (i.e. Aptian to Coniacian) yielding plant macro-foliar remains and cuticles have been reported from western France since the first half of the XIXth century (e.g. Fleuriau de Bellevue 1817; Coquand 1860; Crié 1884, 1890; Rioult 1966; Alvárez-Ramis *et al.* 1981; Samuel & Gaillard 1984). Although naturalists from the XIXth century listed or briefly mentioned some floras from the Cretaceous from several localities in northwestern France (i.e. Basse Normandie, Centre-Val de Loire, Haute-Normandie, and Pays de la Loire), these have not been revisited recently. By contrast, in the Aquitaine Basin Cretaceous meso- and macro-foliar have been intensively investigated during recent decades (Table 1). Table 1 lists the plant taxa (excluding wood and pollen) reported from Cretaceous localities in the Aquitaine Basin, including localities on the edge of this region, from the Seuil du Poitou and from the southwestern-most part of the Paris Basin (e.g. Le Brouillard; Jaunay-Clan; Monts-sur-Guesnes; see Fig. 1).

Pre-Albian floras

In the Aquitaine Basin, pre-Albian plant beds are rare. The only locality yielding abundant plant meso- and macro-remains is the Angeac quarry, in Charente, presumed to be Berriasian to Hauterivian in age (Fig. 1; Néraudeau *et al.* 2012; Benoît *et al.* 2017). In common with the Albian flora of Font-de-Benon, conifers seem to be one of the main components. However, these floras differ significantly. All conifers reported from the uppermost Albian deposits of Charente-Maritime are absent in the pre-Albian clay of Angeac (dominance of *Watsoniocladus* Srinivasan, 1995; Table 1; Néraudeau *et al.* 2012). The flora of Angeac also differs from the Albian flora from Font-de-Benon by the lack of angiosperms and the presence of ferns. These differences may be explained by different palaeoenvironments, the Angeac deposits being interpreted as a swamp, only very occasionally connected to the sea, whereas the Albian lignitic beds of Charente-Maritime where deposited in environments more influenced by marine input (Néraudeau *et al.* 2002).

The genus *Agathoxylon* might be present in Angeac (Néraudeau *et al.* 2012), but the material is too poorly preserved for a positive generic identification. *Agathoxylon* is reported from the Purbeckian facies (Berriasian) of Cherves-de-Cognac (Philippe *et al.* 2008). There, however, the fossil wood material is too limited for a specific attribution. The genus *Agathoxylon*, might represent several taxonomical groups, not only the Araucariaceae, so few palaeoecological inferences can be drawn from its occurrence.

Albian floras

In the Aquitaine Basin, apart from the clay level at Archingeay-Les Nouillers, only three other localities have yielded Albian plant macro-remains are the Cadeuil quarry (basal deposits), at Sainte-Gemme, and Puy-Puy and Renardières quarries, both at Tonnay-Charente (basal deposits, sub-unit A1 of the uppermost Albian *sensu* Néraudeau *et al.* 2005; Fig. 1). Today, these quarries are no longer accessible, being partially to totally backfilled. The uppermost Albian floras from the Cadeuil and Renardières quarries are very rich in conifers such as *Frenelopsis alata* and *Glenrosa* sp. but poor in angiosperm remains (Néraudeau *et al.* 2005, 2008). In common with Font-de-Benon, the conifer *Geinitzia reichenbachii* (Geinitz) Hollick *et* Jeffrey, 1909 and the ginkgoalean *Nehvizdya andegavense* have also been reported from Les Renardières (Table 1; Gomez *et al.* 2004; Néraudeau *et al.* 2005). Angiosperms are mainly represented by isolated stamens ascribed to *Pseudoasterophyllites cretaceous* (Feistm.) Velen., 1887 at Les Renardières (Kvaček *et al.* 2012) and cuticles of indeterminate leaves at Puy-Puy (Le Diouron 2005). The flora from Les Renardières also consists of cuticles of cycads, bennettitaleans such as *Zamites* sp., and ferns such as *Osmunda cretacea* (Gomez *et al.* 2004; Néraudeau *et al.* 2005). The fossil woods of the Albian flora in the Aquitaine Basin are more abundant and varied than the pre-Albian ones in comprising not only *Agathoxylon*, but also *Brachyoxylon*, *Podocarpoxylon*, and *Protopodocarpoxylon* (Philippe *et al.* 2008). As the source area and general palaeogeography were the same as for the pre-Albian period, the greater diversity of the Albian flora probably indicates an improvement in palaeoecological conditions that coincided with the warming period beginning in the early Albian (Price & Hart 2002; Leckie *et al.* 2002).

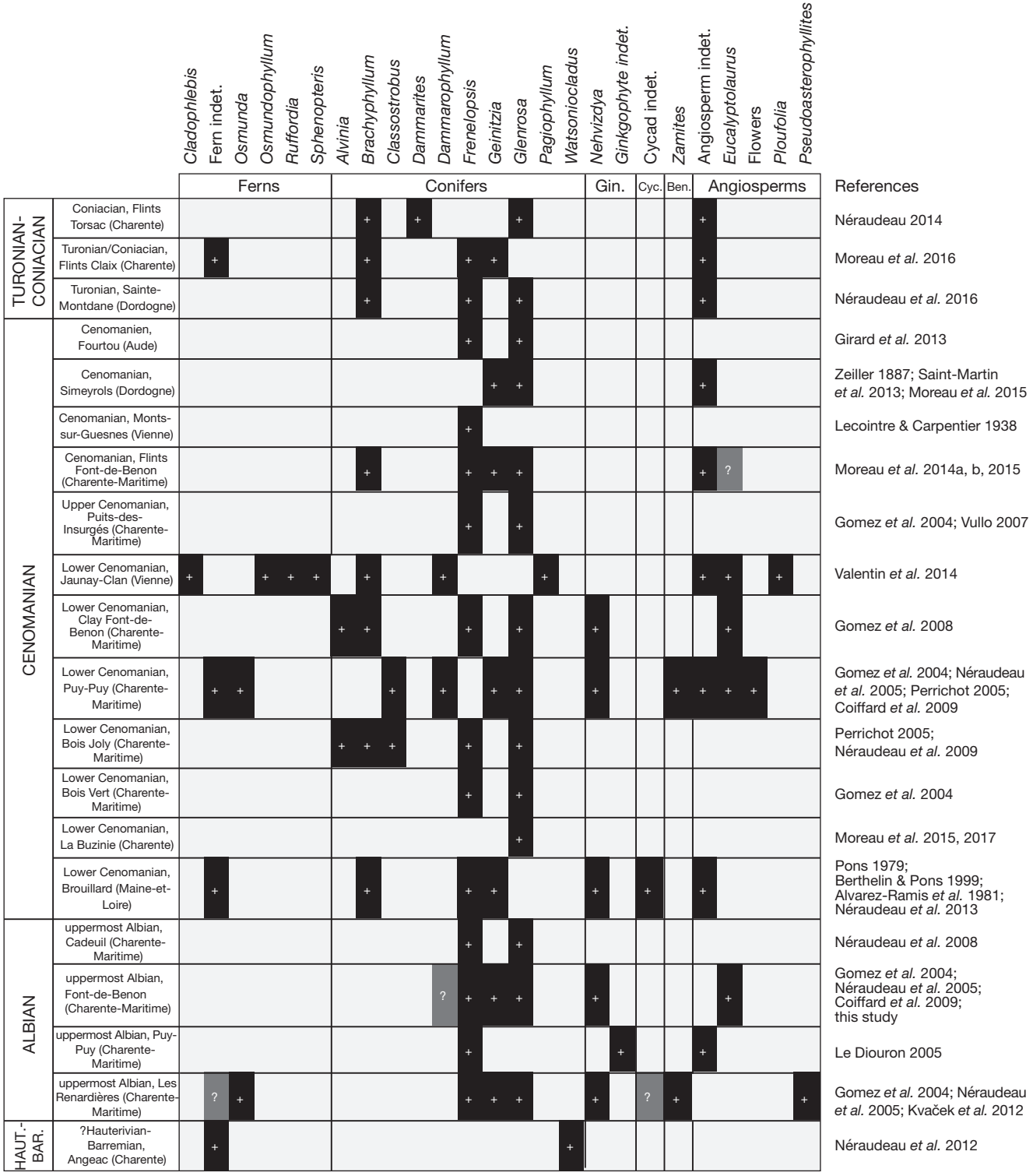
Cenomanian floras

Although Albian floras are uncommon in western France, Cenomanian floras are more numerous. The uppermost Albian flora of Font-de-Benon differs from some Cenomanian floras by the absence of ferns (e.g. Puy-Puy quarry at Tonnay-Charente in Charente-Maritime; Jaunay-Clan road works in Vienne; see Fig.1 and Table 1). This may be explained by palaeoenvironment differences, clays of Puy-Puy and Jaunay-Clan having been deposited in innermost littoral environments with strong brackish to freshwater influences, but only partially or occasionally connected to the sea. As demonstrated by Coiffard *et al.* (2012), during the Albian-Cenomanian, in littoral areas of Europe, ferns inhabited brackish environments, but they seem dominant in landward environments. Among conifers, cuticles ascribed to *Frenelopsis alata* were previously reported from Cenomanian lignites that crop out on the shore of Bois-Joly (Aix island), and at Bois-Vert (Fouras peninsula), Puits-des-Insurgés (Madame island), and the Font-de-Benon quarries in Charente-Maritime (Table 1; Gomez *et al.* 2004, 2008; Néraudeau *et al.* 2009) and from Le Brouillard quarry (at Ecouflant), in Maine-et-Loire (Berthelin & Pons 1999; Néraudeau *et al.* 2013). Leaves of *Dammarophyllum* were reported from the Cenomanian clay from the Puy-Puy Lagerstätte (Néraudeau *et al.* 2005), and from the road works of Jaunay-Clan (Vienne; Valentin *et al.* 2014). Shoots assigned to *Geinitzia* were previously described from the Cenomanian clays of Tonnay-Charente (Néraudeau *et al.* 2005), Ecouflant (Néraudeau *et al.* 2013), and Simeyrols (Dordogne, Saint-Martin *et al.* 2013). *Glenrosa* was reported from the Cenomanian clays of Charente (La Buzinie; Moreau

FIG. 3. — **A**, *Geinitzia* Endl., 1847, leafy axis showing pointed and spirally arranged leaves; Géosciences Rennes, IGR 2769b; **B**, detail of **A**; **C**, *Frenelopsis* Schenk, 1869, leafy axis showing three small tips (**arrows**) on the apex, Géosciences Rennes, IGR 2769a; **D**, **E**, *Glenrosa carentonensis* Moreau, Néraudeau, Tafforeau & Dépré, 2015, leafy axes showing short and spirally arranged leaves, Géosciences Rennes, IGR 2769c. Scale bars: 1 cm.

et al. 2015, 2017), Charente-Maritime (Bois-Vert, Bois-Joly, Cadeuil, Puits-des-Insurgés, and Puy-Puy; Gomez *et al.* 2004; Néraudeau *et al.* 2005, 2008), Dordogne (Simeyrol; Moreau *et al.* 2015), and Maine-et-Loire (Le Brouillard; Néraudeau *et al.* 2013). The conifers *Frenelopsis* and *Glenrosa* were probably the main components of the Albian-Cenomanian littoral floras of western France. In the Cenomanian clays of Archingeay-Les Nouillers, *Nehvizdya andegavense* is the more striking plant taxon from the assemblage (Gomez *et al.* 2008). Impressions and compressions of this ginkgoalean were also reported from

TABLE 1. — Inventory of the Cretaceous plant meso- and macro-remains from the Aquitaine Basin, including the border localities of the Seuil du Poitou, the southwestern-most part of the Paris Basin, the Seuil du Lauragais, and the Pyrénées. Abbreviations: **Ben.**, bennettitaleans; **Cyc.**, cycads; **Gyn.**, ginkgophytes; **Haut.**, Hauterivian; **Bar.**, Barremian. References: Alvarez-Ramis *et al.* 1981; Berthelin & Pons 1999; Coiffard *et al.* 2009; Girard *et al.* 2013; Gomez *et al.* 2004, 2008; Kvaček *et al.* 2012; Lecointre & Carpentier 1938; Le Diouron 2005; Moreau *et al.* 2014a, b, 2015, 2016, 2017; Néraudeau 2014; Néraudeau *et al.* 2005, 2008, 2009, 2012, 2016; Perrichot 2005; Pons 1979; Saint-Martin *et al.* 2013; Valentin *et al.* 2014; Vullo 2007; Zeiller 1887.



the Cenomanian Puy-Puy Lagerstätte (Néraudeau *et al.* 2005), and from the Cenomanian of Anjou (Néraudeau *et al.* 2013). It is noteworthy that bennettitales are reported from only one Cenomanian locality (Fig. 1, Table 1). As for angiosperms, although several Cenomanian outcrops in western France have yielded abundant and diverse leaf assemblages (Gomez *et al.*

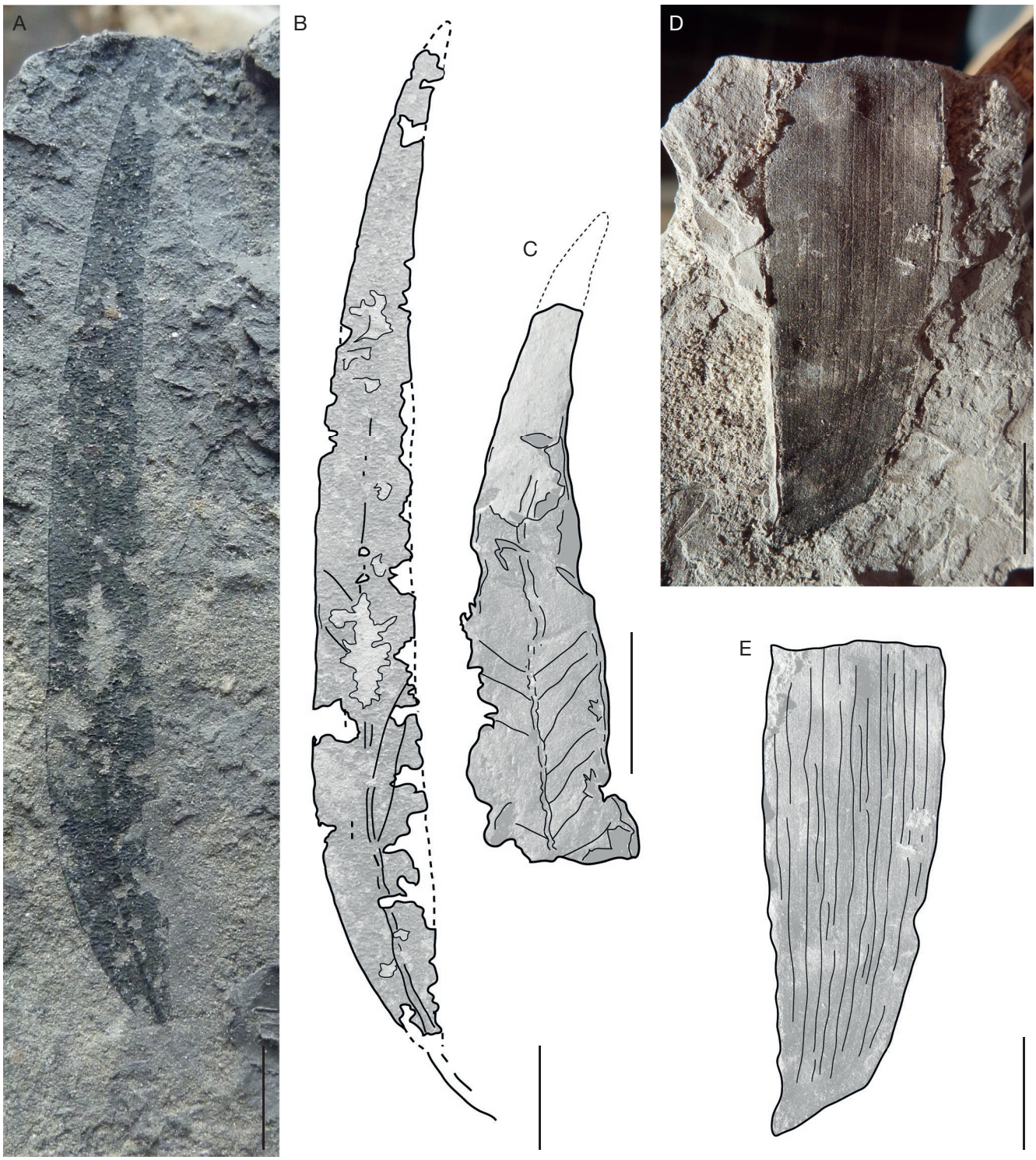


FIG. 4. — **A**-**C**, *Eucalyptolaurus depreii* Coiffard, Gomez, Thiébaut & J.Kvaček, 2009, falcate, narrow lanceolate leaf (**A** and **B**) showing pinnate primary venation and brochidodromous secondary venation (**C**), Géosciences Rennes, IGR 2770 and IGR 2771; **D**, Plant indet.1, fragment of leaf or pinnule showing numerous thin parallel veins, Géosciences Rennes, IGR 2773. Scale bars: 1 cm.

2004; Le Diouron 2005; Néraudeau *et al.* 2005; Valentin *et al.* 2014), only a few of them have been studied in details. Hitherto, *Eucalyptolaurus depreii* is based on a single well-described leaf from the Cretaceous of western France (Coiffard *et al.* 2009). Although most Cenomanian floras are restricted to impressions and compressions in clays, recently the Font-de-Benon quarry has yielded exceptionally preserved, silicified plant macro-remains (petrifications/permineralizations: Moreau *et al.* 2014a, b, 2015). In common with the Albian clays of Archingeay-Les Nouillers, the Cenomanian flints from the same locality also

yielded *Geinitzia* sp., *Glenrosa carentonensis*, and *Frenelopsis* sp. and a leaf similar to *Eucalyptolaurus depreii* (pers. obs.). The species *Glenrosa carentonensis* was described on the basis of material from this locality (Moreau *et al.* 2015).

Turonian-Coniacian floras

Frenelopsis sp. and *Glenrosa* sp. were reported recently from the Turonian lignitic clays of Dordogne which contain abundant cuticles of conifers and a few cuticles of eudicot angiosperms (Table 1; Sainte-Mondane; Néraudeau *et al.* 2016). Furthermore, in Charente, *Frenelopsis* sp. and *Geinitzia* sp. were also found preserved within the upper Turonian-lowermost Coniacian flints from Claix (Moreau *et al.* 2016), while *Glenrosa* sp. was reported from the upper Turonian-lowermost Coniacian flints of Torsac (Néraudeau 2014). Among conifers, the Turonian-Coniacian floras from Charente differ from that of the Dordogne in containing an abundance of the conifer *Brachyphyllum* Brong., 1828. Finally, although they remain unnamed, leaves and cuticles of angiosperms have been reported from all the Turonian-Coniacian localities yielding plant meso- and macro-remains (Néraudeau 2014; Moreau *et al.* 2016). Both angiosperm and gymnosperm woods have been reported from the Turonian lignitic clays of Garnache, in Vendée (Néraudeau *et al.* 2017).

CONCLUSION

Late Albian meso- and macro-remains from the Archingeay-Les Nouillers quarries include angiosperm leaves (*Eucalyptolaurus depreii*), conifer leafy axes (*Frenelopsis* sp., *Geinitzia* sp., and *Glenrosa carentonensis*) and wood (*Agathoxylon* sp., and *Agathoxylon gardoniense*), as well as ginkgophyte leaves (*Nehvizdya andegavense*). Pre-Albian floras from western France differ significantly with Albian flora from Archingeay-Les Nouillers quarries by a lower diversity, the lack of angiosperms and ginkgophytes, and the presence of ferns. The numerous Cenomanian plant beds from the Aquitaine Basin show diversified floras, including abundant meso- and macro-remains of angiosperms and conifers, whereas some localities also yield cycads, bennettitaleans and ferns. Turonian-Coniacian plant assemblages from western France are dominated by leafy axes and wood of conifers, whereas angiosperms and ferns are also documented. These variations in the composition of Lower and Upper Cretaceous palaeobotanical assemblages from western France were probably linked both to the portion of vegetation that has been preserved according to fossil localities and to the diversity of deposit environments and climate changes.

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