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Conifers from the Cenomanian amber of Fouras (Charente-Maritime, western France)

Jean-David Moreau^{1,*}, Didier Néraudeau² and Vincent Perrichot²

¹ UMR CNRS 6282 Biogéosciences, Université de Bourgogne Franche-Comté, 6, boulevard Gabriel, 21000 Dijon, France

² Univ. Rennes, CNRS, Géosciences Rennes – UMR 6118, 35000 Rennes, France

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Abstract – Fossil inclusions of arthropods and microorganisms are abundant in the Cretaceous amber from western France, but plant meso- or macroremains are scarce. Preserved remains are mostly tiny, very fragmented, and indeterminable. Only one amber locality in the Charente department has already provided conifer remains. Here, we report the first plant mesoremain ensnared in Cenomanian amber from Fouras–Bois Vert, in the Charente-Maritime department. They consist of three well-preserved leafy axes and one cone of Cheirolepidiacean conifers. Based on the helical arrangement of rhomboidal, longer than wide, and highly adpressed leaves, leafy axes are ascribed to the genus *Pagiophyllum*. The ovoid cone bears more than 15 imbricate, helically arranged, scale-like leaves and is ascribed to *Classostrobus* sp. Although Cretaceous flora is abundant in lignitic clay from the Charentes region, *Pagiophyllum* is reported for the first time in Albian–Cenomanian deposits from this area. Xerophytic features of *Pagiophyllum* further support a harsh and instable coastal environment seasonally exposed to hot, dry conditions during the mid-Cretaceous in the Charentes region.

Keywords: fossil plants / amber / Cretaceous / *Pagiophyllum* / xerophytic / France

Résumé – **Conifères de l’ambre cénoomanien de Fouras (Charente-Maritime, Ouest de la France).** Les inclusions fossiles d’arthropodes et de microorganismes sont abondantes dans l’ambre crétacé de l’Ouest de la France, mais les méso- et macrorestes végétaux sont quant à eux rares. Les restes préservés sont essentiellement minuscules, très fragmentés et indéterminables. Jusqu’ici, seule une localité du département de la Charente a livré de l’ambre contenant des conifères. Ici, nous présentons les premiers mésorestes végétaux connus dans l’ambre cénoomanien de Fouras–Bois Vert, dans le département de la Charente-Maritime. Il s’agit de trois axes feuillés et d’un cône de conifère Cheirolepidiaceae bien préservés. Les axes feuillés sont attribués au genre *Pagiophyllum* sur la base de l’arrangement hélicoïdal de feuilles qui sont rhomboïdales, plus longues que larges et très plaquées sur les axes. Le cône est ovoïde, constitué de plus de 15 écailles arrangées de manière spiralée et est attribué à *Classostrobus* sp. Bien que les flores crétacées soient abondantes dans les argiles ligniteuses de la région des Charentes, *Pagiophyllum* est pour la première fois signalé dans les dépôts albo-cénomaniens de ce secteur. Les caractéristiques xérophytiques de *Pagiophyllum* sont des arguments pour soutenir que les flores du Crétacé moyen de Charente-Maritime étaient adaptées à des milieux côtiers saisonnièrement exposés à de fortes températures.

Mots clés : plantes fossiles / ambre / Crétacé / *Pagiophyllum* / xérophytique / France

1 Introduction

Plant remains such as bryophytes, conifer leafy axes, ferns, and flowers have been reported in Cretaceous amber from many localities worldwide (Chambers *et al.*, 2010; Crepet *et al.*, 2016; Ignatov *et al.*, 2016; Schneider *et al.*, 2016; Moreau *et al.*, 2017a; Kvaček *et al.*, 2018). However, such fossil inclusions remain

extremely rare in the French Cretaceous amber which has otherwise yielded abundant and diverse fossils of arthropods (Néraudeau *et al.*, 2002, 2008; Nel *et al.*, 2004; Perrichot, 2005, 2015; Perrichot *et al.*, 2008a, 2008b, 2010), microorganisms (Breton and Tostain, 2005; Girard *et al.*, 2009), as well as rare vertebrate integuments (Perrichot *et al.*, 2008c; Vullo *et al.*, 2010a). Plant meso- or macroremains found in this amber are commonly indeterminable, altered, and limited to stellate hairs (Girard, 2010), or tiny fragments of cuticle or wood sometimes

*Corresponding author: jean.david.moreau@gmail.com

preserved as partially empty casts (Perrichot, 2005; Girard *et al.*, 2013). Until now, a single foliar plant remain was described in amber from La Buzinié in the Charente department (Moreau *et al.*, 2017a). It consists of an exquisitely preserved conifer leafy axis ascribed to *Glenrosa carentonensis* Moreau, Néraudeau, Tafforeau & Dépré, an extinct Cretaceous taxon characterized by an unusual stomatal arrangement inside crypts (Moreau *et al.*, 2015). Recently, several leafy axes and a cone were discovered in the Cenomanian amber from the palaeontological site of Fouras which has hitherto provided various insect and vertebrate fossils (Néraudeau *et al.*, 2003; Vullo *et al.*, 2005). Here, we describe these specimens and discuss palaeoecophysiological implications.

2 Geological setting

The pieces of amber containing the plant remains described herein were discovered in Cretaceous deposits from the “Plage de la Vierge” at Fouras–Bois Vert in the Charente-Maritime department (western France). Regionally, the upper Albian–Cenomanian series are divided into seven units, A to G (Néraudeau and Moreau, 1989; Moreau, 1996; Néraudeau *et al.*, 1997). At Fouras–Bois Vert, the deposits are exposed from subunit B1 to subunit B3 which are early Cenomanian in age based on the presence of the foraminifera *Orbitolina* (*Conicorbitulina*) *conica* d’Archiac in the three subunits (Néraudeau *et al.*, 2003). Subunit B1 consists of up to 5 m of fossiliferous silty to sandy limestone yielding rudists (*Ichthyosarcobites triangularis* Desmarest), oysters (*Rhynchostreon suborbiculatum* Lamarck) and the foraminifera *Orbitolina plana concava* Lamarck. Subunit B2 corresponds to up to 5 m of marl and glauconitic sand. Basally, this subunit (B2ms) consists of laminated grey to lignitic clay yielding abundant wood fragments (sometimes large trunks of up to 3 m long), amber and vertebrate remains (Néraudeau *et al.*, 2003; Perrichot, 2005; Vullo *et al.*, 2005). The wood was mainly ascribed to coniferous taxa such as *Agathoxylon gardoniense* Crié, *Brachyoxylon* Hollick & E. Jeffrey and *Podocarpoxylon* Gothan whereas a single specimen was ascribed to the Ginkgoalean wood *Ginkgoxylon* Saporta. The surface of trunks often bears marine oysters (*Acutostrea lingularis* Lamarck, *Gyrostrea cf. delettrei* Coquand) and xylophagous bivalve borings (*Teredolites* Leymerie). Amber from B2ms yielded various insect inclusions (Perrichot *et al.*, 2010), among which occur some of the oldest known ants and trogossitid beetles (Perrichot *et al.*, 2008b; Peris *et al.*, 2014). The vertebrate remains were ascribed to terrestrial groups, such as dinosaurs (Iguanodontids; Néraudeau *et al.*, 2003), pterosaurs (Vullo and Néraudeau, 2009) and turtles (*Solemys* de Lapparent de Broin & Murelaga; Vullo *et al.*, 2010b), as well as marine ones such as the snake *Simoliophis rochebrunei* Sauvage and the shark *Cretodus semiplicatus* Agassiz (Vullo *et al.*, 2005, 2011).

Upper part of the subunit B2 corresponds to sandstone with accumulation of oysters (*Rhynchostreon suborbiculatum*, *Ceratostreon flabellatum* Goldfuss). The subunit B3 consists of 6–8 m of limestone alternating with silty to sandy marl.

3 Material and methods

The pieces of amber were all collected in the subunit B2 (layer B2ms). The fossiliferous amber from Fouras–Bois Vert

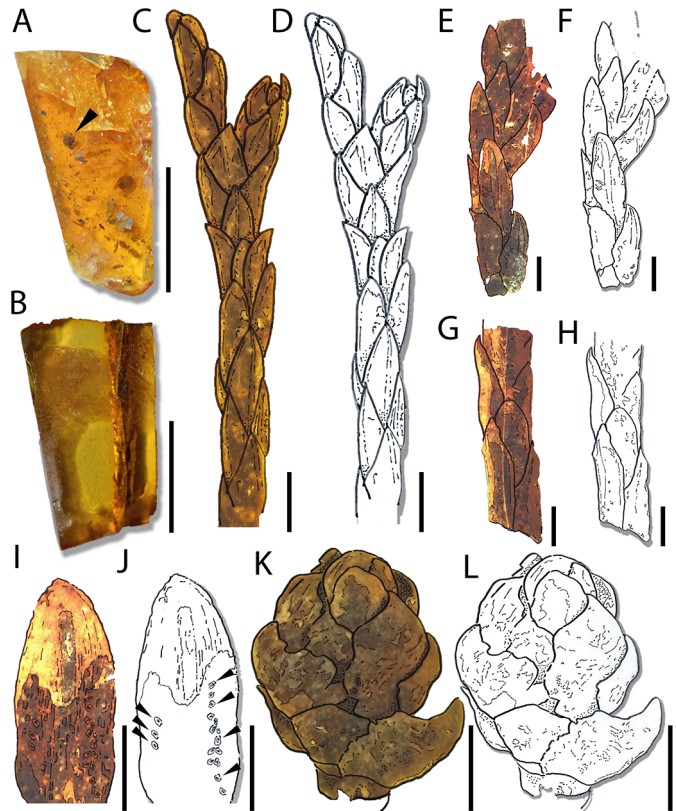


Fig. 1. Plant inclusions in Cenomanian amber from Fouras–Bois Vert. A–B. Fragment of amber bearing a conifer cone (A) and leafy axis (B); black arrow indicates location of the cone. C–H. Helically arranged leafy axis, *Pagiophyllum* sp. I–J. Abaxial surface of a leaf showing alignment of stomatal apparatuses; black arrows indicate location of stomatal apparatuses. K–L. Cone of conifer, *Classostrobus*. A, K–L. IGR.FRS-7.18; B, G–H, IGR.FRS-1.14; C–D. IGR.FRS-7.25; E–F. IGR.FRS-7.10. Scale bars: A = 10 mm; B = 5 mm; C–H = 1 mm; I–L = 0.5 mm.

is mostly translucent and yellow to orange (Figs. 1A and 1B). Plant remains consist of three leafy axes and one conifer cone, that were originally preserved in two amber pieces with numerous arthropod inclusions: the piece IGR.FRS-1 contained 13 hexapods; and the piece IGR.FRS-7 contained 57 arthropods (see detailed list in Cockx *et al.*, 2016: Tab. 1). For an optimal study of each fossil inclusion, these pieces were then cut in smaller fragments using scalpel blades, and each fragment was polished using silicon carbide papers on a Buehler Metaserv 3000 polisher. The conifer remains are preserved in three dimensions and show an exquisite preservation of the cuticle including stomatal apparatuses. Photographs were taken with a BMS digital USB camera (5 megapixels) mounted on a stereomicroscope Leica 125. The specimens presented in this paper are housed at the Geological Department and Museum of the University of Rennes 1.

4 Systematic palaeobotany

Order – Coniferales
Family – Cheirolepidiaceae

4.1 Leafy axes

Genus – *Pagiophyllum* Heer, emend. Harris, 1979

Pagiophyllum sp.

Figs. 1C–1J

Material. 3 specimens; IGR.FRS-7.10, IGR.FRS-1.14, IGR.FRS-7.25.

Description. Leafy axes are straight (Figs. 1C, 1D, 1G, 1H) to slightly curved (Figs. 1E and 1F). The largest specimen is 10 mm long. Shoots are narrow and up to 1.5 mm in diameter. Leaves are persistent, helically arranged (phyllotaxy 3/8), highly adpressed and imbricated (Figs. 1C–1H). Leaves are scale-like, rhomboidal, longer than wide, and keeled on abaxial side (Figs. 1C–1J). They are 1.7–2.5 mm long and 0.6–0.8 mm wide. Apically, leaves display a free part which is up to 0.8 mm long. The abaxial surface of leaves is convex whereas adaxial surface is concave. The leaf margin is entire and the shape of the leaf apex is quite pointed. Surface of leaves locally shows the outlines of epidermal cells. On the abaxial surface, stomatal apparatuses are arranged in longitudinal rows that converge toward the leaf apex (Figs. 1I and 1J). Stomatal apparatuses on the abaxial surface are 50–70 μm long and 35–45 μm wide. Stomatal rows are not sunken but guard cells of individual stomata are sunken in a pit. Pit apertures are mainly oval, and sometimes circular. Their orientation is quite stable, mainly oriented transversally to the leaf margin. However, they are sometimes oriented obliquely to leaf margin. Subsidiary cells form a thick and well-marked rim around the pit apertures. Abaxial surface of leaves partially shows the shape of ordinary epidermal cells which are rectangular and form longitudinal rows, that are oriented parallel to the leaf axis.

Remarks. The gross morphology of *Pagiophyllum* is close to those of the leafy axis *Brachyphyllum* Brongn. (*e.g.* straight twigs having needles helically arranged and small leaves). Harris (1979) highlighted the difficulty to distinguish both genera and proposed that the “sole distinction of *Pagiophyllum* from *Brachyphyllum* is its longer free leaf”. He specified in the emended diagnoses of *Brachyphyllum* and *Pagiophyllum* “leaf composed of a basal cushion tapering into a small free part, length of free part (upper surface beyond leaf cushion) or total height of leaf and cushion (outward from shoot) less than width of leaf cushion” for the first, whereas “leaf about as broad as its basal cushion, length exceeding width of cushion” for the second. *Brachyphyllum* was reported from many Cretaceous palaeobotanical sites of western France (*e.g.* Coquand, 1860; Gomez *et al.*, 2008; Néraudeau *et al.*, 2009; Moreau *et al.*, 2014a). It differs from *Pagiophyllum* by its leaves that are as long as wide, with a shorter free part strongly appressed to the stem. Following Harris (1979), the specimens from Fouras can be confidently ascribed to *Pagiophyllum*.

4.2 Cone

Genus – *Classostrobus* Alvin, Spicer & J. Watson 1978

Classostrobus sp.

Figs. 1K and 1L

Material. 1 specimen; IGR.FRS-7.18

Description. Cone is ovoid, 1.7 mm long, 1.3 mm wide and bears more than 15 imbricate, helically arranged, scale-like leaves. The scale-like leaves are convex, rhomboidal in shape,

and show acuminate or acute apices (Figs. 1K and 1L). They are up to 0.8 mm long and up to 0.7 mm wide.

Remarks. Inner structures of the cone are not visible. We may notice that tiny male cones ascribed to *Classostrobus* sp. and showing a gross morphology close to the specimen from Fouras–Bois Vert were discovered in Cenomanian lignitic clay from several areas of Charente-Maritime (*e.g.* Aix Island, Néraudeau *et al.*, 2009; Puy-Puy, Perrichot, 2005). *Pagiophyllum* and *Classostrobus* often co-occur in Mesozoic plant beds (Thévenard, 1993; Van Konijnenburg-Van Cittert, 1987). However, stomatal apparatuses being not visible, the cone from Fouras–Bois Vert cannot be confidently linked with the leafy axis *Pagiophyllum* described below.

5 Discussion and conclusions

Albian–Cenomanian plant remains have been reported from many localities in western France (*e.g.* Coquand, 1860; Zeiller, 1887; Lecointre and Carpentier, 1938; Pons *et al.*, 1976; Pons, 1979; Koeniguer, 1981; Berthelin and Pons, 1999; Néraudeau *et al.*, 2002, 2005, 2013, 2020; Gomez *et al.*, 2004, 2008; Coiffard *et al.*, 2009; Saint-Martin *et al.*, 2013; Moreau *et al.*, 2014a, 2014b, 2015, 2017b, 2017c; Valentin *et al.*, 2014; Fleury *et al.*, 2017). These reports included angiosperms, conifers, bennettitaleans, ferns, cycads and ginkgophytes. Conifers are represented by leafy axes, male cones, as well as isolated ovuliferous scales. Leafy axes of *Brachyphyllum*, *Frenelopsis* (Schenk) emend. J. Watson, *Geinitzia* Endl., and *Glenrosa* J. Watson & H.L. Fisher are abundant in most of conifer-dominated assemblages from the Cretaceous deposits of Charente-Maritime (*e.g.* Gomez *et al.*, 2008; Néraudeau *et al.*, 2009; Moreau *et al.*, 2014a, 2015, 2017c). However, the conifer *Pagiophyllum* is reported for the first time from this area, as it was hitherto known only from the Cenomanian deposits of the Vienne department (Valentin *et al.*, 2014).

Conifers with xerophytic characters have already been found among the Cretaceous coastal flora of western France (*e.g.* *Brachyphyllum*, *Frenelopsis*, and *Glenrosa*; Gomez *et al.*, 2008; Moreau *et al.*, 2015). According to these studies, these plants were adapted to withstand intense sunlight and coastal environments exposed to desiccant conditions coupled with saline sea water, and dry conditions. *Pagiophyllum* clearly shows fleshy shoots, small leaves pressed against the axis, thick cuticle, and sunken stomata apparatuses with subsidiary cells forming a thick rim. These features are those of a flora in a tropical climate with contrasted seasons cyclically dry (Thévenard *et al.*, 2003). In accordance with this hypothesis, Néraudeau *et al.* (2003) interpreted the amber-bearing bed from Fouras as a paralic deposit showing both marine and terrestrial inputs. Complementing previous palaeobotanical analyses (*e.g.*, Gomez *et al.*, 2008; Moreau *et al.*, 2015), the xerophytic features of *Pagiophyllum* are new arguments to support that Albian–Cenomanian coastal floras of Charente-Maritime were well-adapted to paralic environments seasonally exposed to hot, dry conditions.

The Cretaceous flora from western France is mostly preserved as impressions and compressions with or without cuticle in clayey and lignitic deposits. By contrast with these highly compressed fossil plants, the *Pagiophyllum* leafy axes and the cone from the Fouras amber are preserved in three

dimensions. Moreau *et al.* (2017a, 2017b, 2017c) demonstrated that some specimens can exquisitely preserved most of the tissues, including epidermis, palisade parenchyma, spongy parenchyma, transfusion tracheids and vascular bundles. However, the inner structures of the specimens from Fouras cannot be explored using classic light microscopy. Although we cannot ensure such preservation, future investigations using 3D imaging technique such as synchrotron tomography should be appropriate to explore the histology of these specimens from Fouras.

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