The paralic Albian–Cenomanian Puy-Puy Lagerstätte (Aquitaine Basin, France): an overview and new data

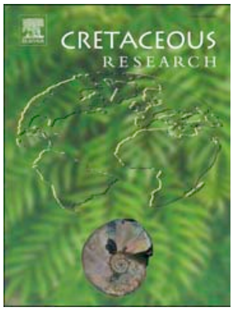
Didier Neraudeau, Romain Vullo, Pierre Bénéfice, Gérard Breton, Éric Dépré, Danièle Gaspard, Vincent Girard, Matthieu Le Couls, Jean-David Moreau, André Nel, et al.

To cite this version:

Didier Neraudeau, Romain Vullo, Pierre Bénéfice, Gérard Breton, Éric Dépré, et al.. The paralic Albian–Cenomanian Puy-Puy Lagerstätte (Aquitaine Basin, France): an overview and new data. Cretaceous Research, 2020, 111, pp.Art. n°104124. 10.1016/j.cretres.2019.03.022 . insu-02088578

HAL Id: insu-02088578
https://insu.hal.science/insu-02088578

Submitted on 3 Apr 2019



The paralic Albian–Cenomanian Puy-Puy Lagerstätte (Aquitaine Basin, France): An overview and new data

Didier Néraudeau, Romain Vullo, Pierre Bénéfice, Gérard Breton, Éric Dépré, Danièle Gaspard, Vincent Girard, Matthieu Le Couls, Jean-David Moreau, André Nel, Vincent Perrichot, Mónica M. Solórzano-Kraemer, Torsten Wappler

PII: S0195-6671(18)30403-8

DOI: https://doi.org/10.1016/j.cretres.2019.03.022

Reference: YCRES 4124

To appear in: *Cretaceous Research*

Received Date: 3 October 2018

Revised Date: 8 March 2019

Accepted Date: 24 March 2019

Please cite this article as: Néraudeau, D., Vullo, R., Bénéfice, P., Breton, G., Dépré, É., Gaspard, D., Girard, V., Le Couls, M., Moreau, J.-D., Nel, A., Perrichot, V., Solórzano-Kraemer, M.M., Wappler, T., The paralic Albian–Cenomanian Puy-Puy Lagerstätte (Aquitaine Basin, France): An overview and new data, *Cretaceous Research*, https://doi.org/10.1016/j.cretres.2019.03.022.

The paralic Albian–Cenomanian Puy-Puy Lagerstätte (Aquitaine Basin, France): An overview and new data

Didier Néraudeau[a], Romain Vullo[a,*], Pierre Bénéfice[b], Gérard Breton[a], Éric Dépré[c], Danièle Gaspard[d], Vincent Girard[e], Matthieu Le Couls[a], Jean-David Moreau[f, g], André Nel[h], Vincent Perrichot[a], Mónica M. Solórzano-Kraemer[i, j], Torsten Wappler[k]

[a]*Univ Rennes, CNRS, Géosciences Rennes, UMR 6118, 263 avenue du Général Leclerc, F-35000 Rennes, France*

[b]*23A rue des Barraudes, La Cotinière, F-17310 Saint-Pierre-d'Oléron, France*

[c]*GIP-GEVES (Groupement d'Étude et de Contrôle des Variétés et Semences), Le Magneraud, F-17700 Surgères, France*

[d]*CR2P, Centre de Recherche sur la Paléodiversité et les Paléoenvironnements, UMR CNRS 7207, Muséum National d'Histoire Naturelle, EPHE, UPMC, Sorbonne Université, CP 38, 8 Rue Buffon, F-75005 Paris, France*

[e]*Institut des Sciences de l'Evolution de Montpellier, Université Montpellier, UMR CNRS 5554, EPHE, IRD, Place Eugène Bataillon, F-34095 Montpellier, France*

[f]*Université Bretagne Sud, CNRS, Centre de Recherche Yves Coppens, Laboratoire Géoscienecs Océan,UMR 6538, rue André Lwoff, F-56017 Vannes, France*

[g]*European Synchrotron Radiation Facility, 71 avenue des Martyrs, F-39000 Grenoble, France*

[h]*ISYEB, Institut de Systématique, Evolution, Biodiversité, UMR CNRS 7205, Muséum National d'Histoire Naturelle, EPHE, UPMC, Sorbonne Université, CP 50, Entomologie, 45 rue Buffon, F-75005 Paris, France*

[i] *Senckenberg ForschungInstitut und Naturmuseum, Paläontologie und Historische Geologie-Berstein Sektion, Senckenberganlage 25, D-60325 Frankfurt am Main, Germany*

[j] *Steinmann Institut für Geologie, Mineralogie und Paläontologie, Universität Bonn, Nussallee 8, D-53115 Bonn, Germany*

[k] *Hessisches Landesmuseum Darmstadt, Friedensplatz 1, D-64283 Darmstadt, Germany*

[*] Corresponding author.

E-mail address: Romain.Vullo@univ-rennes1.fr

ABSTRACT

The Puy-Puy quarry at Tonnay-Charente (Charente-Maritime, SW France) is a sand quarry exposing a 9-m-thick series of latest Albian–earliest Cenomanian (mid-Cretaceous) age. The uppermost Albian deposits consist of lignitic clay containing fossiliferous amber. The lowermost Cenomanian sand deposits alternate with clay intercalations containing plant remains. One of these clay levels, named P1, shows an outstanding accumulation of conifer and angiosperm macrofossils including delicate reproductive structures such as flowers. Plant remains are associated with invertebrates such as insects (Odonata, Dictyoptera, Diptera), crustaceans (*Mecochirus* sp.), putative brachiopods (aff. *Lingula* sp.), and worms. A few vertebrate remains such as shark egg capsules (*Palaeoxyris* sp.) and a feather are present in the fossil assemblage, as well as an enigmatic specimen tentatively interpreted as a cephalochordate or a petromyzontiform. Various ichnofossils occur in abundance, such as crustacean coprolites and burrows (*Ophiomorpha* isp.), insect coprolites (*Microcarpolithes hexagonalis*), and leaves with grazing structures, galls and mines. The sediments have been deposited in a coastal, calm and brackish area.

Keywords:

Ichnofossils; Plants; Arthropods; Palaeoenvironment; Konservat-Lagerstätte; Cretaceous

1. Introduction

The uppermost Albian–lowermost Cenomanian series of the Puy-Puy quarry (Tonnay-Charente, Charente-Maritime, SW France) was first studied by Moreau (1993a, b), who examined the sedimentology, but the first palaeontological analyses were carried out by Coiffard (2003) for the palaeobotany, Perrichot (2003) for the amber and fossil wood, and Peyrot (2004) for the palynology, in unpublished university theses that were later formelly published in Perrichot (2005), Peyrot et al. (2005), and Coiffard et al. (2008). The plant assemblage of Puy-Puy has been studied in more detail by Gomez et al. (2004) and Le Diouron (2005). Then a first integrative treatment, giving the geological age (latest Albian to earliest Cenomanian), the sedimentological context (sand and clay alternation) and the main fossils (fern, angiosperm and gymnosperm leaves), was published by Néraudeau et al. (2005), who regarded the locality as a true Lagerstätte according to the outstanding accumulation and exquisite preservation of diverse plant remains (e.g., leaves, seeds, flowers). Palaeoecological studies have concluded to a depositional environment with brackish, freshwater and continental influences (Coiffard et al., 2008; Girard, 2010; Vullo et al., 2013). At Puy-Puy, basal lignites of the uppermost Albian beds contain numerous drops of oxidized red amber, poor in arthropod inclusions (only one complete insect), but very rich in prokaryotic filament accumulations (Girard, 2010; Girard et al., 2009, 2011). Above this, the lowermost Cenomanian clay beds are remarkably rich in plant macroremains, especially in leafy axes and cones of conifers, and leaves of angiosperms (Le Diouron, 2005; Coiffard et al., 2009).

Various additional, well-preserved fossils have been discovered since then, such as arthropod remains, including insects (Nel et al., 2008) and crustaceans (Breton et al., 2015), and uncommon shark egg capsules and feather (Vullo et al., 2013). Aquatic ichnofossils from Puy-Puy are very abundant but poorly diverse. They correspond mainly to crustacean coprolites (Breton et al., 2015) and burrows. The terrestrial ichnofossils are also numerous, more diverse, corresponding to insect coprolites (Colin et al., 2011) and to different kinds of traces made by insects on angiosperm and ginkgoale leaves. Several new fossil and ichnofossil specimens, representing a wide range of organisms, are described here for the first time, thus providing useful additional data for the palaeoecological reconstruction of this mid-Cretaceous Lagerstätte.

2. Geological setting

The Puy-Puy quarry is located near Tonnay-Charente town, about twenty kilometres from the Charente river estuary (Fig. 1). The uppermost Albian–lower Cenomanian deposits mainly consist of fluviatile and paralic sand, but contain several clay intercalations with local concentrations of plant fossils or lignite and amber (Néraudeau et al., 2005) (Figs. 2, 3). These alternations of sand and clay correspond to the lithological unit A, subdivided in two lithological subunits (Néraudeau et al., 1997): A1 for heterometric sand, with large-scale cross bedding and rich in lignite and amber (Girard, 2010), dated palynologically as latest Albian–earliest Cenomanian (Néraudeau et al., 2002; Batten et al., 2010); A2 for more homometric fine sand, mainly arranged in horizontal beds and poor in wood remains, dated as earliest Cenomanian (Néraudeau et al., 2002). The sand and clay of unit A are overlain by shelly sand (Vullo et al., 2003; level F in Fig. 3A), rich in orbitoline foraminifera and oysters, which marks the base of lithological unit B (subunit B1). In the Puy-Puy quarry, the outstanding fossiliferous facies (Lagerstätte) is located in the clay from the mid part of A2 (facies P1 and P2, level A2sm; Figs. 2, 3), exceptional preservation is also present in the basal uppermost Albian lignites and amber (level A1sl-A), but to a lesser extent.

The detailed description of the Puy-Puy section (Figs. 2, 3) shows at the base (uppermost Albian part of subunit A1) sand deposits (A1sl-S1) overlain by an approximately 1-m-thick clay bed (A1sl-A) with cuticle compressions (e.g., *Frenelopsis* and *Glenrosa*), lignites and amber. The lowermost Cenomanian bed consists a fine conglomerate (bed CO in Figs. 2, 3A), containing rare small examples of the oyster *Ceratostreon flabellatum* and reworked altered amber. This conglomerate is overlain by a 2–3-m-thick coarse sand layer with large-scale cross bedding (A1sl-S2). Within the basal sand of A1sl-S2, a few lenses of coarse sand contain juveniles of *C. flabellatum*, serpulids and small reptile bone pebbles. This sandy facies of subunit A1 is overlain by the sand and clay alternation of subunit A2; the laminated clay bed of A2sm contains abundant plant and invertebrate imprints, and ichnofossils. The thickest clay level (about 30 cm thick), bed P1, constitutes the Lagerstätte (Fig. 3C). Above P1, the facies A2sm continues with a 2.5-m-thick alternation of clay and fine sand. At its top, the alternation contains fewer and thinner clay layers when sand progressively becomes a more cemented sandstone with ripple marks and isopod tracks (level GB in Fig. 3A). The top of the sand and clay series is marked by a 2–3-m-thick bed of brackish lagoonal clay (A2a) very poor in plant remains, apart from millimetric fragments of cuticles. The top of the section corresponds to about 1 m thick of shallow marine carbonate facies (B1cs), enriched in the orbitoline *Orbitolina conica* and the small oyster *Rhynchostreon suborbiculatum* at the base (F), and overlain by a limestone with diverse marine invertebrates, especially large rudists such as *Ichthyosarcolites triangularis*.

3. Material and methods

The fossil plant accumulation from Puy-Puy was discovered in 1980 by one of us (P.B.), but was unstudied prior to 2000. During the last decade, thousands of plant impressions and ichnofossils, and about thirty invertebrate specimens and four vertebrate remains, have been collected from a few cubic metres of sediment, mainly by one of us (E.D.). The laminated clay was extracted by decimetric plates (diameter from 10 to 50 cm), using trowels and large knives, several laminae being then separated from each plate with a knife (Figs. 4, 5).

The preservation differs according to the kind of organism. Except amber, all plant remains (leaves, stems, flowers, cones, seeds) are compressions or brownish imprints, the former locally preserving cuticle with fine details (e.g., epidermal cells, stomata) and the latter only showing very thin residues of organic matter. Consequently, fossil plants are generally easy to observe on the grey–blue clay. Crustacean imprints are whitish, and are generally imprinted with a low relief in the clay, especially the legs that “incise” the clay laminae. Putative lingulid brachiopods have very few whitish shell remains, but present conspicuous relief with the shell curvature. Insect imprints, mainly isolated wings, are more difficult to see, due to the absence of colouration and their very low relief.

The only complete insect specimen preserved in amber was scanned on the BM5 beamline (European Synchrotron Radiation Facility, Grenoble, France; Tafforeau et al., 2006) using propagation phase contrast in 2009. The scans of the specimen were performed using a voxel size of 0.702 µm. The radiographs were acquired using a beam set at energy of 20 keV using a double Ru/B4C multilayer monochromator and a propagation distance of 7 cm between the specimen and the detector. We used a FReLoN CCD e2V camera mounted on lens-based optical system coupled with a 25-μm-thick YAG(Ce) scintillator. Scans were performed using 1500 projections and an exposure time of 2s per projection. The scans were reconstructed using a back-projection algorithm implemented in the PyHST2 software (High Speed Tomography in python version, ESRF, Mirone et al., 2014). Data were finally converted into a 16 bit tiff stack of slices using 0.001% saturation values on the whole 32 bits 3D histogram, corrected for residual ring artefacts and cropped. The three dimensional reconstructions of specimens were achieved with the software VG Studio Max 2.2 (Volume Graphics, Heidelberg, Germany).

The main part of the fossil material collected at Puy-Puy (Appendix 1) and the specimens illustrated here are housed in the Geology Department and Museum of the University of Rennes 1 (UMR CNRS 6118 Géosciences Rennes), under the collection numbers IGR.90-061 to IGR.90-098, plus IGR.PUY-4.1 and IGR-PUY-4.3. A few specimens, previously published, are housed in other institutions: the holotype (MNHN-LP-R 63889) of the odonatan *Enigmaeshna deprei*, housed at the National Museum of Natural History; the crustacean specimens, housed at the “Musée Vert” of Le Mans (Breton et al., 2015: LM2010.1.77; LM2010.1.79; LM2010.1.86; LM2010.1.783B); the vertebrate remains housed at the Museum of Natural History of La Rochelle (Vullo et al., 2013: MHNLR 2013.3.1, MNHLR 2313.3.2, MNHLR 2013.3.3); an inflorescence with two pedicellate flowers (Gomez et al., 2004, Le Diouron, 2005; Néraudeau et al., 2005: PUY-0065), a winged seed (Néraudeau et al., 2005; Le Diouron, 2005: PUY-0208) and the type specimens or previously figured specimens of the angiosperm *Eucalyptolaurus depreii* (Coiffard et al., 2009: PUY-0009/10, PUY-0039, PUY-0249, PUY-1244/45, PUY-1263/64/65), housed in the collections of palaeobotany of the University Claude Bernard-Lyon (UCBL); numerous other specimens of plants from Puy-Puy are housed in the UCBL collections, with curatory numbers beginning by the prefix “PUY-“ followed by the numbers mentioned in Appendix 1; an additional specimen of *Eucalyptolaurus depreii* is housed at the Musée of Angoulême (Coiffard et al., 2009: MA PUY 1243).

4. Plant assemblage

Conifers constitute the great majority of the Albian–Cenomanian plant remains from the Puy-Puy Lagerstätte (Gomez et al., 2004; Le Diouron, 2005; Néraudeau et al., 2005). The floristic assemblage of level P1 contains mainly leaf imprints of conifers, including *Dammarophyllum* sp., *Geinitzia reichenbachii* (Fig. 4A), and rare *Glenrosa carentonensis*. Conifers are also represented by some male cones (e.g., *Classostrobus*) and isolated ovuliferous scales. Rare winged seeds have also been found.

In the P1 clay lens, after conifers, angiosperms constitute the second most abundant plant macroremains. About twenty different leaf morphologies have been distinguished (Le Diouron, 2005; Delmail, 2007). They have been variously assigned to cf. *Grevillea dvorakii*, cf. *Debeya coriacea*, platanophyll leaves tentatively assigned to the Proteales (Néraudeau et al., 2005) and *Eucalyptolaurus depreii* considered close to the Lauraceae (Coiffard et al., 2009) (Fig. 4D). All indicate that the lower Cenomanian angiosperm assemblage (Fig. 4B–D) of the Puy-Puy Lagerstätte was dominated by magnoliids, mainly Lauraceae, and some possible basal eudicots (Proteales such as some Platanaceae).

The angiosperm remains from Puy-Puy also include exquisitely preserved reproductive structures. A simple inflorescence (cymose?) was illustrated, but not described, by Gomez et al. (2004) and Néraudeau et al. (2005). The inflorescence displays a peduncle bearing two pedicellate flowers in the distal part (Fig. 5A); a third flower, attached below the two flowers, is suggested by an oval scar. The specimen is 21 mm long. Flowers are 9 mm long and 7 mm wide. The peduncle measures 8 mm long and is 1.4 mm in diameter. The distal-most pedicellate flower terminates at the inflorescence axis; the second flower branches off slightly below at an angle of *c.* 50°. The two pedicels are 2.2 and 2.6 mm long and 0.9 and 1.2 mm in diameter respectively. The top of the pedicel is flared, with no distinction from the receptacle. Flowers are globular, cup-shaped, and seem to be actinomorphic. Perianth is well-developed. The sepals seem to be free, are 2.2–2.3 mm long and their apices are obtuse to acute. The petals seem to be free, account for the entire length of the flower. Insertion of floral organs seems to be hypogynous.

In addition, putative solitary flowers were reported from A2sm. They consist of actinomorphic isolated flowers, 3.5–5.0 mm in diameter (Fig. 5B). The receptacle is spherical, measuring 1.1–1.8 mm in diameter. The perianth is well-developed, tetramerous and consists of a distinct calyx and corolla. The four sepals are 1.5–1.8 mm long and 1.8–1.9 mm wide. Each sepal has a rounded apex. The number of petal whorls is uncertain. The petals seem to be slightly longer than the sepals.

Plant remains from Puy-Puy also include putative simple infructescences. They display up to 16 spirally arranged pedicels and a single fruit borne distally (Fig. 5C, D). Infructescence stems are up to 31 mm long and range between 0.35–0.60 mm in diameter. Pedicels are short, stocky, usually concaved, with either a pentagonal and keeled or cylindrical transversal section. They are regularly spaced, 1.6–2.3 mm long, and form angles of 42–90° with the infructescence stem measuring 0.9–1.1 mm long and 0.4–1.0 mm wide. Distally, the pedicels form an enlarged receptacle. Each pedicel bears a single fruit. The single fruit observed is 2.4 mm long and 1.3 mm wide. The pedicels remain attached to the stem after the fruits fall thereby leaving a star-shaped scar where they meet the pedicels. The perianth and the androecium are lacking. The carpels seem to number four or five per fruit but this cannot be confirmed (Fig. 5D). Carpels are elongate, oval and typically measure 2.1 mm long and 0.5 mm wide.

The Cenomanian flora from Puy-Puy also includes ferns represented by at least three morphologies of pinnules, including cf. *Osmunda cretacea*. Leaves of Ginkgoales (e.g., *Nehvizdya andegavense*), isolated leaflets of Bennettitales (e.g., *Zamites* sp.) as well as cuticles ascribed to putative Cycadales (Gomez et al., 2004; Le Diouron, 2005) were also reported but to a lesser extent.

In addition to these plant remains described or listed in previous works, a single fossil sphenophyte has been identified, with typical horsetail leaves. As in the modern species *Equisetum hyemale*, the leaves of this fossil species are joined to form a leaf sheath at each node. Here, only a fragment of a leaf sheath on which are three parts from bottom to top: the attachment of leaves to the node, the fused part of the lamina, and the free apexes of leaves. Therefore, we place this fossil in the genus *Equisetites* without specific assignment.

Fossil wood of conifers is relatively uncommon in the clay P1 and restricted generally to infracentimetric fragments ascribed to *Agathoxylon* and *Protopodocarpoxylon* (Perrichot, 2005; Philippe et al., 2008). A single type of underminable hetereoxylous wood (basal angiosperm or eudicot) has been found (Philippe et al., 2008).

5. Invertebrates

Compared to the myriad plant remains found at Puy-Puy in the Cenomanian clay, invertebrate fossils are much rarer, totaling no more than thirty specimens after more than fifteen years of sampling. Some specimens are poorly preserved and too incomplete for a systematic assignment, and even distinguishing between fragments of crustaceans and insects can be difficult. Identified specimens include three putative brachiopods, seven insects, and nine crustaceans. So far, no molluscs have yet been found.

5.1. Putative brachiopods

Imprints of possible brachiopod valves are identified as poorly preserved lingulids (Fig. 6A, B). Their shell is elongate, oval in outline, with conspicuous concentric growth lines. Only the largest specimen (28 mm long and 18 mm wide), preserved both as cast and imprint, seems complete at first sight, but the pedicle groove is crushed and not well preserved on the cast (Fig. 6A). The wide oval outline can be compared to the *Lingularia* species described in Lower Cretaceous deposits from Spitsbergen (Holmer and Nakrem 2012) and the Turonian of Sergipe, Brazil (Holmer and Bengtson, 2009). The outline is also similar to that of *Lingula subspatula* Hall and Meek, 1855, illustrated by Stephenson (1952) and Kirkland (1996) from the Cenomanian of Texas and Arizona, respectively. This kind of lingulid has been mentioned in several subsaline deposits from northern America. Finally, the imprints found at Puy-Puy show similarities with *Lingula truncata* Sowerby in Fitton, 1836 and *Lingula subovalis* Davidson, 1852 (both illustrated in Davidson, 1852: pl. 1), known from the Upper Greensand of Warminster, England.

The Puy-Puy specimens are larger and more rounded in outline than the *Lingula* sp. found in the upper Cenomanian clay of Roullet-Saint-Estèphe, in Charente (Néraudeau et al., 2013a) and a single specimen previously found (but unpublished) in the uppermost Albian–lowermost Cenomanian lignitic clay of Les Renardières, another quarry of Tonnay-Charente, located at 4 km from Puy-Puy (Néraudeau et al., 2005).

5.2. Crustaceans

Coprolites. Several clay laminae are covered with dense accumulations of white or yellow microstick imprints randomly arranged and regularly spaced (Fig. 6C) on several square centimetres. Each microstick is generally 1 to 1.5 mm long and 0.25 mm large, and are interpreted as crustacean coprolites. These are very abundant in some layers of the clay series and are rare or absent in some alternating beds. This shows a high frequency cyclicity in the deposit, parallel to the biological cycles of the coprolite producers, with probably daily periods of excretion linked to tide cycles or diurnal/nocturnal cycles. More uncommon clay laminae share accumulations of larger cigar-shaped, yellowish coprolites measuring about 1 cm in length and located in small lenses (Fig. 6D).

Burrows. Two fossils are interpreted as crustacean burrows. They correspond to a dense, subcylindrical arrangement of crushed pellets (Fig. 7A), each one being 4 to 5 mm in diameter. These traces clearly belong to the widespread ichnogenus *Ophiomorpha*, well known in Mesozoic and Cenozoic deposits, including Cretaceous rocks (Goldring and Pollard, 1995; Rogers et al., 2013). In Recent aquatic environments, the crustacean *Callianassa* produces similar structures (Frey et al., 1978) and this group of decapods is therefore considered as the trace maker of the ichnogenus *Ophiomorpha*.

Body fossils. The Puy-Puy crustaceans belong to the family Mecochiridae and more specifically to *Mecochirus* sp., a form close to *M. houdardi* Van Straelen, 1936, previously defined for the Albian Gault facies of the eastern Paris Basin and Pays de Bray. Previously unknown rostrum, hepatic furrow, endopleurites, posterior abdominal somites and urotelson have been found at Puy-Puy (Breton et al., 2015) (Fig. 7B). Both *Mecochirus* sp. and *M. houdardi* were seemingly burrowers, deposit and suspension feeders and lived in sheltered, quiet, clayey sedimentary bottoms, in a marine domain.

5.3. Indeterminate "worms"

A single elongate fossil can be provisionally identified as a worm (Fig. 7C). The specimen is 20 mm long and 1.6 mm wide, slightly decreasing in width at its ends. The median axis of the imprint is dark whilst the lateral margins of the body appear whitish on the clay. The specimen is slightly curved. The imprint does not show any mark of segmentation or ciliate ornamentation, excluding the specimen from annelid groups such as polychaetes (Parry et al., 2015; Wilson et al., 2016). The simple structure of the body, the dark median part likened to a pseudocoelom and the lack of features such as cilia and a well-defined head characterize more likely a nematode. Compared to other fossil worms, and especially Cretaceous ones, the Puy-Puy specimen is much larger than nematodes often preserved in various ambers (Poinar et al., 1994; Poinar and Buckley, 2006).

5.4. Insects

Insect coprolites. Termite coprolites of the ichnospecies *Microcarpolithes hexagonalis* are abundant in the amber-bearing lignitic clay (Colin et al., 2011). This ichnotaxon is also present as inclusions in the piece of amber that contains the two insect specimens.

Insect remains. Two insect inclusions (Hemiptera and Dictyoptera) have been found in a single piece of amber from the upper Albian lignitic clay, at the base of the Puy-Puy series, albeit investigation was limited by the small amount and poor quality of the amber. A cockroach is represented by a single leg; the single hemipteran (Fig. 8A) is represented by a lace bug (Cimicomorpha) assignable to *Ebboa areolata*, a species known from the coeval Charentese amber of Archingeay-Les Nouillers and the Cenomanian Alpine amber (Perrichot et al., 2006). *Ebboa areolata*, originally placed in its own extinct family (Ebboidae; Perrichot et al., 2006), was subsequently transferred to Microphysidae (Golub and Popov, 2008, 2012).

Insect fossils from the Cenomanian laminated clay are also rare, with one previously published specimen, i.e the odonatan *Enigmaeshna deprei* represented by a single fragmentary hind wing (Nel et al., 2008), and five new specimens. However, this insect assemblage is relatively diverse, including three wings of Dictyoptera (stem group Blattodea), one wings of Odonata, one pair of wings of a Neuroptera and one larval case of Trichoptera. Fragmentary cockroach wings have also been collected (Fig. 8B, C), but they lack diagnostic characters for assignment to any family. The neuropteran wings (Fig. 8D) are very large (50 mm long and 1.7 mm wide each) but cannot be identified more accurately. Finally, the presence of Trichoptera is attested by a typical larval case made of a sand sheath (Fig. 8E).

Insect damages on plants. Insect mediated damages were examined on 1605 specimens of plants. 357 leaves or leaf fragments, representing 22.1% of the material examined, exhibit some kind of damage (Fig. 9). Of these, 301 (84.3%) were damaged in one way, while the remaining 56 (15.7%) showed two or more forms of damage. Seventy-one damage types (DTs) attributable to insect herbivory and oviposition were identified and allocated to the seven functional feeding groups (FFGs) based on the widely used damage type system of Labandeira et al. (2007). In terms of abundance, herbivory on the Puy-Puy flora is dominated by external foliage feeding, particularly surface feeding (Fig. 9B–F), represented by several damage types (DTs), especially DT30 and DT31, comprising one-third of all recorded damage type occurrences. Galling is next highest at Puy-Puy, characterized mostly by featureless, small, hemispherical galls (DT80) (Fig. 9A). Hole feeding (DT2) and margin feeding (DT12) is found in approximately equal abundances at Puy-Puy (Fig. 9B–F). Nevertheless, the abundance data indicates a dominance of generalized damage (89.1%), when compared to specialized damage (10.9%). For the Puy-Puy Flora dicotylodonous angiosperms were the most herbivorized (33.1%), followed by conifers (17.8%), pteridophytes (6.2%), and cycadophytes (~1%). Particularly, the lauraceous taxon *Eucalyptolaurus depreii* exhibits the most diverse component community of herbivore activities (Fig. 9D, G–K), with a corresponding diversity of 40 DTs being the highest in the entire assemblage, including 23 specialized DTs. Second in rank order is the broad-leaved coniferous foliage *Dammarophyllum* sp. (Fig. 9L), representing a lower proportion of damaged leaves (23.4%) but also with an elevated level of consumption (34 DTs). Interestingly, there is one harboring specialized interaction (DT280), representing a leaf miner targeting the parenchyma. So far, this is only known from the broad-leaved conifer *Liaoningcladus boii* Sun, Zheng and Mai, 2000 from the mid Lower Cretaceous Yixian Formation (Ding et al., 2014, 2015).

6. Vertebrates and putative chordate

Vullo et al. (2013) described two relatively well-preserved hybodont shark egg capsules (*Palaeoxyris* sp.) from the plant-bearing beds of Puy-Puy. A third, incomplete specimen of *Palaeoxyris* sp. has been recovered and is described here (Fig. 10). It is similar in size and morphology to the other two specimens. The beak and the anterior half of the body are missing. The preserved portion of the body shows three parallel helicoidally-twisted bands. The slender pedicle is nearly complete (about 10 cm in preserved length) and shows a few parallel longitudinal ribs. This specimen provides new information on the pedicle length, thus supplementing the previous description of the Puy-Puy *Palaeoxyris*. The three shark egg capsules found at Puy-Puy are all almost identical, strongly indicating that they were produced by the same hybodont taxon (likely *Tribodus*; see discussion in Vullo et al., 2013).

They represent the first Cenomanian occurrence of the genus *Palaeoxyris*. It worth noting that no bony fish remains have been found so far at Puy-Puy.

The second vertebrate fossil is a well-preserved body contour feather, which is one of only a few very rare mid-Cretaceous feathers known from Europe (Vullo et al., 2013). Fossil feathers have been previously discovered in the mid-Cretaceous deposits from Charentes, preserved in the uppermost Albian amber from Archingeay-Les Nouillers (Perrichot et al., 2008). In the neighbour region of Poitou, another Cenomanian feather imprint has been discovered in the clay beds of Jaunay-Clan (Valentin et al., 2014).

The putative chordate found at Puy-Puy is a worm-like imprint, 27 mm long and 5 mm wide, with subparallel margins, the body being preserved with a sigmoid posture. Both extremities are missing. A chevron pattern, comparable to the myospetum–myomere arrangement of fossil cephalochordates (e.g., *Pikaia*; Conway Morris and Caron, 2012) and especially of the Recent lancelet *Asymmetron* (e.g., Kon et al., 2016), is visible on a large part of the fossil, with the angle of each chevron located at the mid-width (Fig. 11). Interestingly, the separation between the Caribbean and Southeast Asian clades of the *Asymmetron lucayanum* complex has been dated by molecular data to around 100 My and a dispersal route via the western Tethys has been proposed (Kon et al., 2016: fig. 4). This would be consistent with the presence of this lancelet in paralic environments of Western Europe. However, although the myoseptum–myomere arrangement and the body shape correspond more closely to lancelets than to annelids, the anterior part is lacking and consequently the cephalic and branchial regions cannot be observed. Our fossil is larger than the Early Permian cephalocordate *Palaeobranchiostoma hamatogergum* from South Africa and does not have the dorsal barbs and the ventral fin typical of the African species (Oelofsen and Loock, 1981). The Puy-Puy specimen can also be compared to the lamprey specimens described from the Lower Cretaceous of China (*Mesomyzon*; Chang et al., 2006, 2014). This alternative petromyzontid hypothesis is also compatible with the size, shape and anatomical features of the Puy-Puy specimen, as well as with the palaeoenvironment.

7. Discussion

7.1. Depositional environments

The sedimentological and palaeontological characteristics of the Puy-Puy clay show both continental (diverse plant and insect remains) and coastal marine (brachiopods, crustaceans) influences (Girard et al., 2011), in a protected area. Indeed, the sand/clay alternation of Puy-Puy is typical of coastal series (Néraudeau et al., 2005). Basal lignites (A1sl-A) with large pieces of wood and amber represent the same facies seen in other Charentese localities of latest Albian–early Cenomanian age, such as Archingeay-Les Nouillers (Néraudeau et al., 2002), Cadeuil (Néraudeau et al., 2008), or Fouras (Néraudeau et al., 2003) and were deposited in a hydrodynamic coastal environment.

The younger clay bed (A2sm), with plant and invertebrate imprints, without amber but dominated by angiosperms, probably belongs to a quieter and more protected environmental setting than the underlying lignite and sand accumulations, the fine laminations in the clay characterizing low energy (Moreau, 1993b). Although the angiosperm composition of the lower Cenomanian Puy-Puy Lagerstätte is concordant with most other coeval angiosperm floras in Europe (Coiffard et al., 2012), it contrasts markedly with other coastal fossil localities from the Charentese region. Cuticles from clays, silicified plants from flints as well as palynology suggest that Albian–Cenomanian coastal habitats of Charente-Maritime were dominated by conifers and ferns, with some taxa showing xeromorphic adaptations (e.g., Dejax and Masure, 2005; Néraudeau et al., 2005; Peyrot et al., 2005, 2019; Gomez et al., 2004, 2008; Moreau et al., 2014a, 2015). Gomez et al. (2008) have proposed that the local Albian–Cenomanian littoral palaeoenvironments were dominated by conifer mangrove-type vegetation. Thus, compared to other coeval littoral localities, the lower Cenomanian plant assemblage of Puy-Puy (P1) appears to be an exception, showing the highest abundance and diversity in angiosperm remains in a littoral environment from the lower Cenomanian of western France (Néraudeau et al., 2002; Gomez et al., 2004, 2008). In P1, the paucity of typical Charentese taxa adapted to halophytic conditions (e.g., *Brachyphyllum, Frenelopsis, Glenrosa carentonensis*) combined with the presence of *Ploufolia* leaves (probably related to the Nymphaeales) strongly suggests that the lower Cenomanian Puy-Puy flora was also heavily influenced by inland/continental freshwater inputs rather than solely autochthonous littoral inputs.

The combination in the same fossil plant assemblage of 1), a remarkable concentration of meso- and macroremains with absence of size and morphology sorting, 2), multiple branched shoots, and 3), an association of vegetative and reproductive structures strongly suggests that the production area (source vegetation) was relatively close to the deposit environment. Low fragmentation of leaves and leafy axes supports the hypothesis that plant remains were probably mixed during short-distance transport by air and/or water. Compared to the underlying cross-bedded sands (A1sl-S2 in Fig. 3), the clay laminations of plant beds P1 and P2 clearly reflect a decrease of the detrital discharge and low hydrodynamic energy in a protected area. This is also supported by connection and preservation of delicate structures such as flowers or perianth units. However, the presence of brackish to marine invertebrates (crustacean decapods, lingulid brachiopods) and hybodont shark egg capsules in the plant beds indicates that the deposit environment was a paralic basin connected to the sea (Vullo et al., 2013; Breton et al., 2015). All these elements suggest a para-autochthonous taphocoenosis where a continental plant assemblage was deposited in brackish water or in a confined coastal marine environment.

7.2. *Palaeoclimatic context*

Néraudeau and Moreau (1989) and Néraudeau et al. (1997) showed that the echinoid fauna from the lower Cenomanian of Tonnay-Charente region (with the quarries of Puy-Puy and Les Renardières) has Mediterranean–Tethyan affinities (e.g., an abundance of the echinoids *Archiacia* and *Mecaster*), and thus indicates a rather warm period. The same observation was made for the vertebrate assemblage, with the significant presence of low-latitude taxa (e.g., the hybodont shark *Tribodus*) (Néraudeau et al., 2005; Vullo et al., 2003; Vullo and Néraudeau, 2008). Moreover, Gomez et al. (2002b) found stomatal structures typical of xeric plants on *Frenelopsis* and *Glenrosa* leaves from the Albian–Cenomanian of Puy-Puy, like those observed on *Frenelopsis* from the Lower Cretaceous of Spain (Gomez et al., 2002a).

7.3. *Comparisons with other Cenomanian Lagerstatten*

Cenomanian Lagerstätten from France are mainly located in Charentes and are lignitic clay containing both fossiliferous amber (Perrichot et al., 2010) and plant cuticle accumulations, the most studied of which is Archingeay-Les Nouillers (Néraudeau et al., 2002; Gomez et al., 2008). However, although these amber and cuticle deposits show numerous cases of exquisite 3D preservation of arthropods, micro-organisms and plants, they do not contain clay laminae with diverse plant and animal prints, such as the famous lithographic limestones of Upper Jurassic Lagerstätten (Bernier et al., 2014; Peyer et al., 2014). Puy-Puy is the first French mid-Cretaceous Lagerstätte that presents some similarities with the Jurassic lithographic limestones: presence of exquisitely preserved plant-invertebrate-vertebrate associations in the same sediment lamina. A second one has been discovered recently at approximately 150 km from Puy-Puy, in the Poitou region (central-western France), at the Jaunay-Clan locality (Valentin et al., 2014; Nel et al., 2015). These two Cenomanian Lagerstätten have in common a rich plant assemblage with angiosperms, gymnosperms and pteridophytes with, locally, imprints of insects (e.g., odonatans, coleopterans, neuropterans, cockroaches), marine or brackish crustaceans (decapods) and isolated feathers. Unfortunately, the Jaunay-Clan deposit was a temporary outcrop corresponding at a railway building site that could be prospected for just one year only whilst the Puy-Puy quarry has been studied for 15 years. Consequently, the Puy-Puy palaeontological record is very diversified and still prospected. The presence of lingulid brachiopods and marine crustaceans in the plant accumulations indicates a connection between the quiet and protected area where leaves have been deposited in the close sea. However, the lack of marine molluscs at Puy-Puy contrasts with their abundance in other Cenomanian plant-bearing clay deposits (e.g., *Septifer* sp., *Protocardia* sp.), such as at Hucheloup, in Anjou (northwestern France) (Néraudeau et al., 2013b; Fleury et al., 2017) and their presence at Jaunay-Clan (Valentin et al., 2014). This probably means that, during deposition, the clayey sediments with plants were only temporarily connected to the sea, without a regular and massive input of marine shells. It is probably not a diagenetic bias because at Hucheloup and Jaunay-Clan, bivalves are preserved in the same lignitic clay as at Puy-Puy, and both Jaunay-Clan and Puy-Puy contains crustacean fossils. In these three Cenomanian plant-bearing clay deposits (Hucheloup, Jaunay-Clan, Puy-Puy), the most surprising observation is the lack of fishes, usually present and even abundant in Cenomanian lithographic limestones or shales. This is a major difference between the Puy-Puy Lagerstätte and other mid-Cretaceous Lagerstätten with more marine influences, such as Agoult (Gara Sbaa) in Morocco (Martill et al., 2011) and the famous Lebanese sites (Gayet et al., 2003). It is noteworthy that the preservation of delicate structures such as flowers is extremely rare in the French Cenomanian deposits; except the Puy-Puy quarry, only the Cenomanian Pauletian facies from Gard (southeastern France) yielded diverse inflorescences, flowers and fruits (Moreau et al., 2014b, 2016a, b).

8. Conclusions

Apart from its rich fossil plant content, the Puy-Puy Lagerstätte is noteworthy because the sedimentological series shows both lignites with amber and cuticles at the base, with exceptional 3D preservation, and clay laminae with exquisite 2D imprints in younger strata. In terms of sedimentology, fossil assemblage and palaeoenvironmental context, the Ingersoll shale Lagerstätte (Santonian in age) of Alabama (Bingham et al. 2008) seems to be the closest Late Cretaceous analogue to the Puy-Puy Lagerstätte. As at Puy-Puy, the Ingersoll shale biota includes invertebrate traces such as *Ophiomorpha* and numerous well-preserved plant remains, amber, feathers, all accumulated in a muddy paralic environment (Bingham et al., 2008).

Acknowledgments

We are greatly indebted to Patrick Chauvet, owner of the Puy-Puy quarry, who allowed our research team to work at Puy-Puy for several years. We thank Paul Tafforeau and Carmen

Soriano (ESRF) for the synchrotron imaging of the amber inclusion. Partial support was provided by grant OSUR from program AO2 2013 for visiting researchers (to V.P., enabling T.W.'s work at the Université de Rennes 1), and by the ESRF through attribution of inhouse beamtime on the beamline ID19. David M. Martill and an anonymous reviewer provided helpful comments and constructive remarks.

References

Arnaud, H., 1877. Mémoire sur le terrain crétacé du Sud-Ouest de la France. Mém. Soc. Géol. Fr. 10, 1–110.

Batten, D., Colin, J.-P., Néraudeau, D., 2010. Megaspores from mid Cretaceous deposits in western France and their biostratigraphic and palaeoenvironmental significance. Rev. Palaeobot. Palynol. 161, 151–167.

Bingham, P.S., Savrda, C.E., Knight, T.K., Lewis, R.D., 2008. Character and genesis of the Ingersoll Shale, a compact continental fossil Lagerstätte, Upper Cretaceous Eutaw Formation, Eastern Alabama. Palaios 23, 391–401.

Bernier, P. Barale, G., Bourseau, J.-P., Buffetaut, E., Gaillard, C., Gall, J.-C., Wenz, S., 2014. The lithographic limestones of Cerin (southern Jura Mountains, France). A synthetic approach and environmental interpretation. C. R. Palevol 13, 383–402.

Breton, G., Néraudeau, D., Dépré, E., 2015. Mecochiridae (Crustacea, Decapoda, Glypheidea) de l'Albien et du Cénomanien de France. Ann. Paléontol. 101, 55–64.

Chang, M.M., Zhang, J., Miao, D., 2006. A lamprey from the Cretaceous Jehol biota of China. Nature 441, 972–974.

Chang, M.M., Wu, F., Miao, D., Zhang, J., 2014. Discovery of fossil lamprey larva from the Lower Cretaceous reveals its three-phased life cycle. Proceedings N. Acad. Sci. 111, 15486–15490.

Coiffard, C., 2003. Applications de la parcimonie de Wagner à l'étude paléosynécologique de flores de l'Albien et du Cénomanien d'Europe. Université Claude Bernard–Lyon 1, France (Unpublished Master thesis, 26 pp.).

Coiffard, C., Gomez, B. Thévenard, F. Nel, A., Kvaček, J., Néraudeau, D., Thévenard, F., 2008. Application of the Wagner's Parsimony Method in fossil plant assemblages from the Cretaceous of Europe. Rev. Palaeobot. Palynol. 148, 1–12.

Coiffard, C., Gomez, B., Thiébaut, M., Kvaček, J., Thévenard, F., Néraudeau, D., 2009. Intramarginal veined Lauraceae leaves from the Albian–Cenomanian of Charente-Maritime (western France). Palaeontology 52, 323–336.

Coiffard, C., Gomez, B., Daviero-Gomez, V., Dilcher, D., 2012. Rise to dominance of angiosperm pioneers in European Cretaceous environments. Proceedings N. Acad. Sci. 109, 20955–20959.

Colin, J.-P., Néraudeau, D., Nel, A., Perrichot, V., 2011. Termite coprolites (Insecta: Isoptera) from the Cretaceous of western France: A palaeoecological insight. Rev. Micropaléontol. 54, 129–139.

Conway Morris, S., Caron, J.-B., 2012. *Pikaia gracilens* Walcott, a stem-group chordate from the Middle Cambrian of British Columbia. Biol. Rev. 87, 480–512.

Davidson, T., 1852. A monograph of the British Cretaceous Brachiopoda – Part II(1). Palaeontograph. Soc. Monogr. 6, 1–54.

Dejax, J., Masure, E., 2005. Analyse palynologique de l'argile lignitifère à ambre de l'Albien terminal d'Archingeay (Charente-Maritime, France). C. R. Palevol 4, 53–65.

Delmail, D., 2007. Morphologie comparée et paléoécophysiologie d'une Angiosperme du Cénomanien inférieur de la carrière de Puy-Puy (Tonnay-Charente, Charente-Maritime) par une approche morphométrique. Université de Rennes 1, France (Unpublished Master thesis, 32 pp.).

Ding, Q., Labandeira, C.C., Meng, Q., Ren, D., 2015. Insect herbivory, plant-host specialization and tissue partitioning on mid-Mesozoic broadleaved conifers of Northeastern China. Palaeogeogr., Palaeoclimatol., Palaeoecol. 440, 259–273.

Ding, Q., Labandeira, C.C., Ren, D., 2014. Biology of a leaf miner (Coleoptera) on *Liaoningocladus boii* (Coniferales) from the Early Cretaceous of northeastern China and the leaf-mining biology of possible insect culprit clades. Arthropod System. Phylog. 72, 281–308.

Fleury, R., Polette, F., Batten, D.J., Durand, M., Moreau, J.-D., Néraudeau, D., Strullu-Derrien, C., Redois, F., 2017. Palaeobotanical investigation of a Cenomanian clay lens in Hucheloup Quarry, Maine-et-Loire, NW France: Taxonomic, stratigraphic and palaeoenvironmental implications. Ann. Paléontol. 103, 235–250.

Frey, R.W., Howard, J.D., Pryor, W.A., 1978. *Ophiomorpha*: its morphologic, taxonomic, and environmental significance. Palaeogeogr., Palaeoclimatol., Palaeoecol. 23, 199–229.

Gayet, M., Belouze, A., Saad, P.A., 2003. Les Poissons fossiles. Mémoire du Temps. Désiris éd., 158 pp.

Girard, V., 2010. Microcénoses des ambres médio-crétacés français. Taphonomie, systématique, paléoécologie et reconstitution du paléoenvironnement. Mém. Géosci. Rennes 134, 1–334.

Girard, V., Breton, G., Brient, L., Néraudeau, D., 2009. Sheathed prokaryotic filaments, major components of Mid-Cretaceous French amber microcoenoses. J. Palaeolimnol. 42, 437–447.

Girard, V., Néraudeau, D., Adl, S., Breton, G., 2011. Protist-like inclusions in amber, as evidenced by Charentes amber. Eur. J. Protistol. 47, 59–66.

Goldring, R., Pollard, J.E., 1995. A re-evaluation of *Ophiomorpha* burrows in the Wealden Group (Lower Cretaceous) of southern England. Cretac. Res. 16, 665–680.

Golub, V.B., Popov, Y.A., 2008. A new species of Tingidae (Insecta: Hemiptera: Heteroptera) from the Lower Cretaceous of Transbaikalia. Paleontol. J. 42, 86–89.

Golub, V.B., Popov, Y.A., 2012. A new lace bug species of the genus *Sinaldocader* (Hemiptera: Heteroptera, Tingidae) from the Turonian of southwestern Kazakhstan. Paleontol. J. 46, 258–261.

Gomez, B., Coiffard, C., Dépré, E., Daviero-Gomez, V., Néraudeau, D., 2008. Diversity and histology of plant litter bed from the Cenomanian of Archingeay-Les Nouillers (southwestern France). C. R. Palevol 7, 135–144.

Gomez, B., Martin-Closas, C., Barale, G., Solé de Porta, N., Thévenard, F., Guignard, G., 2002a. *Frenelopsis* (Coniferales: Cheirolepidiaceae) and related male organ genera from the Lower Cretaceous of Spain. Palaeontology 45, 997–1036.

Gomez, B., Thévenard, F., Perrichot, V., Daviero-Gomez, V., Néraudeau, D., 2002b. Le conifère *Glenrosa* dans l'Albien-Cénomanien de Charentes: marqueur d'un climat à saison sèche. In : Actes du Colloque Environnement et Climat du Passé: Histoire et Evolution, oct. 2002, Paris, pp. 70.

Gomez, B., Daviero-Gomez, V., Perrichot, V., Thévenard, F., Coiffard, C., Philippe, M., Néraudeau, D., 2004. Assemblages floristiques de l'Albien-Cénomanien de Charente-Maritime (SO France). Ann. Paléontol. 90, 147–159.

Holmer, L.E., Bengtson, P., 2009. The first occurrence of a lingulid brachiopod from the Cretaceous of Sergipe, Brazil, with a restudy of « *Lingula* » *bagualensis* Wickens, 1905, from southern Patagonia. Paläontol. Zeit. 83, 255–266.

Holmer, L.E., Nakrem, H.A., 2012. The lingulid brachiopod *Lingularia* from lowermost Cretaceous hydrocarbon seep bodies, Sassenfjorden area, central Spitsbergen, Svalbard. Norw. J. Geol. 92, 167–174.

Kirkland, J.I., 1996. Paleontology of the Greenhorn Cyclothem (Cretaceous: Late Cenomanian to Middle Turonian) at Black Mesa, Northern Arizona. New Mexico Mus. Nat. Hist. 9, 1–131.

Kon, T., Nishida, M., Sterrer, W., 2016. Hidden ancient diversification in the circumtropical lancelet *Asymmetron lucayanum* complex. Mar. Biol. 149, 875–883.

Labandeira, C.C., Wilf, P., Johnson, K.R., Marsh, F., 2007. Guide to insects (and other) damage types on compressed plant fossils. Version 3.0, Smithsonian Institution, Washington, D.C.

Le Diouron, T., 2005. Les végétaux fossiles des argiles de l'Albien terminal et du Cénomanien basal de la carrière de Puy-Puy (Tonnay-Charente, Charente-Maritime). Implications paléoenvironnementales. Université de Rennes 1, France (Unpublished Master thesis, 30 pp.).

Longinelli, A., Nuti, S., 1973. Revised phosphate-water isotopic temperature scale. Earth Planet. Sci. Lett. 20, 373–376.

Martill, D.M., Ibrahim, N., Brito, P.M., Baider, L., Zhouri, S., Loveridge, R., Naish, D., Hing, R., 2011. A new Plattenkalk Lagerstätte in the Upper Cretaceous of Gara Sbaa, south-eastern Morocco. Cretac. Res. 32, 433–446.

Moreau, J.-D., Néraudeau, D., Gomez, B., Tafforeau, P., Dépré, É., 2014a. Plant inclusions from the Cenomanian flints of Archingeay-Les Nouillers, western France. Lethaia 47, 313–322.

Moreau, J.-D., Cloetens, P., Gomez, B., Daviero-Gomez, V., Néraudeau, D., Lafford T., Tafforeau, P., 2014b. Multiscale 3D virtual dissections of 100-million-year-old flowers using X-ray synchrotron micro- and nanotomography. Microsc. Microanal. 20, 305–312.

Moreau, J.-D., Néraudeau, D., Tafforeau, P., Dépré, É., 2015. Study of the histology of leafy axes and male cones of *Glenrosa carentonensis* sp. nov. (Cenomanian flints of Charente-Maritime, France) using synchrotron microtomography linked with palaeoecology. PloS One 10, e0134515.

Moreau, J.-D., Gomez, B., Coiffard, C., Daviero-Gomez, V., Tafforeau, P., Néraudeau, D., 2016a. *Verneda hermaphroditica* gen. et sp. nov.: A new flower head from the lower Upper Cretaceous (middle Cenomanian) of south-eastern France. Taxon 65, 823–838.

Moreau, J.-D., Gomez, B., Daviero-Gomez, V., Néraudeau, D., Tafforeau, P., 2016b. Inflorescences of *Mauldinia* sp. (Lauraceae) and associated fruits from the Cenomanian of Languedoc Roussillon, France. Cretac. Res. 59, 19–29.

Moreau, P., 1993a. *La transgression cénomanienne sur la marge septentrionale du bassin de l'Aquitaine (Charentes), flanc Nord du synclinal de Saintes et Angoumois. Modalités d'une invasion marine, aspects stratigraphiques, sédimentologiques et paléogéographiques. I. La sédimentaion terrigène et glauconieuse. Caractérisation et distribution des éléments*. Université de Poitiers, France (Thèse d'Etat, 672 pp, on deposit Soc. Géol. France).

Moreau, P., 1993b. *La transgression cénomanienne sur la marge septentrionale du bassin de l'Aquitaine (Charentes), flanc Nord du synclinal de Saintes et Angoumois. Modalités d'une invasion marine, aspects stratigraphiques, sédimentologiques et paléogéographiques. II. Paléontologie stratigraphique et biochronologique. Paléogéographie et structure*. France (Thèse d'Etat, 505 pp, on deposit Soc. Géol. France).

Nel, A., Fleck, G., Garcia, G., Gomez, B., Ferchaud, P., Valentin, X., 2015. New dragonflies from the lower Cenomanian of France enlighten the timing of the odonatan turnover at the Early–Late Cretaceous boundary. Cretac. Res. 52A, 108–117.

Nel, A., Néraudeau, D., Perrichot, V., Girard, V., Gomez, B., 2008. A new dragonfly family in the Upper Cretaceous of France (Insecta: Odonata: Aeshnoptera). Acta Paleontol. Pol. 53, 165–168.

Néraudeau, D., Moreau, P., 1989. Paléoécologie et paléogéographie des faunes d'échinides du Cénomanien nord-aquitain (Charente-Maritime, France). Geobios 22, 293–324.

Néraudeau, D., Mazan, P., Vullo, R., 2013a. Fossiles de la Préhistoire charentaise. Le Croît Vif, Saintes, 287 pp.

Néraudeau, D., Thierry, J., Moreau, P., 1997. Variation in echinoid biodiversity during the Cenomanian-early Turonian transgressive episode in Charentes (France). Bull. Soc. Géol. France 168, 51–61.

Néraudeau, D., Allain, R., Perrichot, V., Videt, B., De Lapparent De Broin, F., Guillocheau, F., Philippe, M., Rage, J.-C., Vullo, R., 2003. Découverte d'un dépôt paralique à bois fossiles, ambre insectifère et restes d'Iguanodontidae (Dinosauria, Ornithopoda) dans le Cénomanien inférieur de Fouras (Charente-Maritime, Sud-Ouest de la France). C. R. Palevol 2, 221–230.

Néraudeau, D., Perrichot, V., Dejax, J., Masure, E., Nel, A., Philippe, M., Moreau, P., Guillocheau, F., Guyot, T., 2002. Un nouveau gisement à ambre insectifère et à végétaux (Albien terminal probable): Archingeay (Charente-Maritime, France), Geobios 35, 233–240.

Néraudeau, D., Perrichot, V., Colin, J.-P., Girard, V., Gomez, B., Guillocheau, F., Masure, E., Peyrot, D., Tostain, F., Videt, B., Vullo, R., 2008. A new amber deposit from the Cretaceous (uppermost Albian-lowermost Cenomanian) of SW France. Cretac. Res. 29, 925–929.

Néraudeau, D., Redois, F., Ballèvre, M., Duplessis, B., Girard, V., Gomez, B., Daviero-Gomez, V., Mellier, B., Perrichot, V., 2013b. L'ambre cénomanien d'Anjou: stratigraphie et paléontologie des carrières du Brouillard et de Hucheloup (Ecouflant, Maine-et-Loire). Ann. Paléontol. 99, 361–374.

Néraudeau, D., Vullo, R., Gomez B., Perrichot, V., Videt, B., 2005. Stratigraphie et paléontologie (plantes, vertébrés) de la série paralique Albien terminal-Cénomanien basal de Tonnay-Charente (Charente-Maritime, France). C. R. Palevol 4, 79–93.

Nguyen Tu, T.T., Bocherens, H., Mariotti, A., Baudin, F., Pons, D., Broutin, J., Derenne, S., Largeau, C., 1999. Ecological distribution of Cenomanian terrestrial plants based on 13C/12C ratios. Palaeogeogr., Palaeoclimatol., Palaeoecol. 145, 79–93.

Oelofsen, B.W., Loock, J.C., 1981. A fossil cephalocordate from the Early Permian Whitehill Formation of South Africa. S. Afr. J. Sci. 77, 178–180.

Parry, L.A., Tanner, A., Vinther, J., 2015. The origins of annelids. Palaeontology 57, 1091–1103.

Perrichot, V., 2003. Environnements paraliques à ambre et à végétaux du Crétacé Nord-Aquitain (Charentes, Sud-Ouest de la France). Université de Rennes I, France (Unpublished PhD thesis, 295 pp.).

Perrichot, V., 2005. Environnements paraliques à ambre et à végétaux du Crétacé Nord-Aquitain (Charentes, Sud-Ouest de la France). Mém. Géosci. Rennes 118, 1–295.

Perrichot, V., Nel, A., Guilbert, E., Néraudeau, D., 2006. Fossil Tingoidea (Heteroptera: Cimicomorpha) from French Cretaceous amber, including Tingidae and a new family, Ebboidae. Zootaxa 1203, 57–68.

Perrichot, V., Néraudeau, D., Tafforeau, P., 2010. Charentese amber. In: Penney, D. (Ed.), Biodiversity of fossils in amber from the major world deposits. Siri Scientific Press, Manchester, pp. 192–207.

Perrichot,V., Marion, L., Néraudeau, D., Vullo, R., Tafforeau, P., 2008. The early evolution of feathers: fossil evidence from Cretaceous amber of France. Proceedings Roy. Soc. London B 275, 1197–1202.

Peyer, K., Charbonnier, S., Allain, R., Läng, E., Vacant, R., 2014. A new look at the Late Jurassic Canjuers conservation Lagerstätte (Tithonian, Var, France). C. R. Palevol 13, 403–420.

Peyrot, D., 2004. Caractérisation du contenu palynologique d’un gisement à ambre dans l’Albien-Cénomanien de Charente-Maritime (Sud-Ouest de la France). Université de Rennes 1, France (Unpublished Master thesis, 39 pp.).

Peyrot, D., Jolly, D., Barron, E., 2005. Apport de données palynologiques à la reconstruction paléoenvironnementale de l’Albo-Cénomanien des Charentes (Sud-Ouest de la France). C. R. Palevol 4, 151–165.

Peyrot, D., Barron, E., Polette, F., Batten, D.J., Néraudeau, D., 2019. Early Cenomanian palynofloras and inferred resiniferous forests and vegetation types in Charentes (southwestern France). Cretac. Res. 34, 168–189.

Philippe, M., Gomez, B., Girard, V., Coiffard, C., Daviero-Gomez, V., Thévenard, F., Billon-Bruyat, J.-P., Guiomar, M., Latil, J.-L., Le Loeuff, J., Néraudeau, D., Olivero, D., Schlögl, J., 2008. Woody or not woody ? Evidence for early angiosperm habit from the Early Cretaceous fossil wood record of Europe. Palaeoworld 17, 142–152.

Poinar, G., Jr., Buckley, R., 2006. Nematode (Nematoda: Mermithidae) and hairworm (Nematomorpha: Chordodidae) parasites in Early Cretaceous amber. J. Invertebr. Pathol. 93, 36–41.

Poinar, G. Jr, Acra, A., Acra, F., 1994. Earliest fosil nematode (Mermithidae) in Cretaceous Lebanese amber. Fundament. Applied Nematol. 17, 475–477.

Rogers, R.R., Krause, D.W., Kast, S.C., Marshall, M.S., Rahantarisoa, L., Robins, C.R., Sertich, J.J.W., 2013. A new, richly fossiliferous member comprised of tidal deposits in the Upper Cretaceous Maevarano Formation, northwestern Madagascar. Cretac. Res. 44, 12–29.

Stephenson, L.W., 1952. Larger invertebrate fossils of the Woodbine formation (Cenomanian) of Texas. U. S. Geol. Surv. Prof. Pap. 242, 1–211.

Tafforeau, P., Boistel, R., Boller, E. Bravin, A., Brunet, M., Chaimanee, Y., Cloetens, P., Feist, M., Hoszowska, J., Jaeger, J.-J., Kay, R.F., Lazzari, V., Marivaux, L., Nel, A., Nemoz, C., Thibault, X., Vignaud, P., Zabler, S., 2006. Applications of X-ray synchrotron microtomography for non-destructive 3D studies of paleontological specimens. Appl. Phys. A Mater. Sci. Process. 83, 195–202.

Valentin, X., Gomez, B., Daviero-Gomez, V., Charbonnier, S., Ferchaud, P., Kirejtshuk A., Licht, A., Néraudeau, D., Vullo, R., Garcia, G., 2014. Plant-dominated assemblge and invertebrates from the Lower Cenomanian of Jaunay-Clan, south-western France. C. R. Palevol 13, 443–454.

Vullo, R., Néraudeau, D., 2008. Cenomanian vertebrate assemblages from southwestern France: a new insight into the European mid-Cretaceous continental fauna. Cretac. Res. 29, 930–935.

Vullo, R., Néraudeau, D., Videt, B., 2003. Un faciès de type falun dans le Cénomanien basal de Charente-Maritime (France). Ann. Paléontol. 89, 171–189.

Vullo, R., Néraudeau, D., Dépré, E., 2013. Vertebrate remains from the Cenomanian (Late Cretaceous) plant-bearing Lagerstätte of Puy-Puy (Charente-Maritime, France). Cretac. Res. 45, 314–320.

Wilson, P., Parry, L.A., Vinther, J., Edgecombe, G.D., 2016. Unveiling biases in soft-tissue phosphatization: extensive preservation of musculature in the Cretaceous (Cenomanian) polychaete *Rollinschaeta myoplena* (Annelida: Amphinomidae). Palaeontology 59, 463–479.

Figure captions:

Fig. 1. Simplified geological map of the study area with uppermost Albian–Cenomanian outcrops represented in dark grey. The Puy-Puy Lagerstätte (white star) is located at Tonnay-Charente, near Rochefort. Scale bar: 10 km.

Fig. 2. The Puy-Puy quarry. View of the quarry in 2004 and interpretative sketch showing stratigraphical units and the position of the Lagerstätte within the series (asterisk); note that the illustrated deposits are no longer accessible, as the quarry has been filled. The white frame corresponds to the right-hand corner inset, showing the clay levels with plant accumulations; from the base to the top, the three arrows indicate the two main plant accumulations P1, P2 and a third fossiliferous level, respectively (see details in Fig. 3).

Fig. 3. Stratigraphical and sedimentological features of the Puy-Puy Lagerstätte. Two main fossiliferous level characterize the Lagerstätte: top of A1sl-A, uppermost Albian lignites with plant cuticles, wood and amber; mid-part P2 of A2 sm, lowermost Cenomanian clay with plant, invertebrate and vertebrate imprints. A, stratigraphic section, and positions of the two main plant beds, P1 and P2. B, details of A2sm. C, details of A1sl- S2, arrows indicate cross bedding. D, details of A1sl-A and A1sl-S2. Abbreviations: CO, basal conglomerate; F, Falun-like facies; GB, sandstones with horizontal bioturbations.

Fig. 4. Examples of plant fossils from the Puy-Puy Lagerstätte (Tonnay-Charente, Charente-Maritime, SW France). A, clay slab with conifer accumulation (*Geinitzia* sp.), IGR.90-061. B, clay slab with angiosperm (Type S) accumulation, IGR.90-062. C, opening of the clay lamination showing the imprint of an angiosperm leaf (Type R), IGR.90-063, on two adjacent clay laminae (C1) and close-up view of the leaf illustrated on the previous picture (C2). D, leaf of the angiosperm *Eucalyptolaurus depreii* Coiffard et al., 2009, IGR.90-064 (D1) and close-up view of the leaf illustrated on the previous picture, showing the venation (D2, D3). Scale bars: 10 mm (except C1: 20 mm).

Fig. 5. Flower fossils from the Puy-Puy Lagerstätte (Tonnay-Charente, Charente-Maritime, SW France). A, inflorescence, PUY-0065, displaying a peduncle bearing two pedicellate flowers in the distal part, and a third flower, attached slightly below the two flowers, suggested by an oval scar (A1) and interpretative drawing (A2). B, putative actinomorphic isolated flower, IGR.90-066 (B1) and interpretative drawing (B2). C-D, putative simple infructescences; first specimen IGR.90-067 (C), and second specimen IGR.90-068 (D1) with a close-up of a fruit (D2) and interpretative drawing (D3). Abbreviations: ca., carpel; fr, fruit;

p., pedicel; p.s., pedicel scar; p.r., pedicel receptacle; pe, perianth; re, receptacle; se, sepals; v.b., vascular bundles. Scale bars: 5 mm (except B: 2 mm).

Fig. 6. Fossils from the Puy-Puy Lagerstätte (Tonnay-Charente, Charente-Maritime, SW France). A-B, linguloid brachiopods (aff. *Lingula* sp.) from the Puy-Puy Lagerstätte; cast (A1) and imprint (A2) of a large specimen, IGR.90-069; second specimen preserved in a flattened imprint, IGR.90-070 (B). C, dense accumulation of small stick shaped coprolites, IGR.90-071. D, accumulations of large cigar-shaped coprolites, IGR.90-072. Scale bars: 10 mm.

Fig. 7. Crustacean and "worm" fossils from the Puy-Puy Lagerstätte (Tonnay-Charente, Charente-Maritime, SW France). A, crustacean burrow corresponding to a dense, subcylindrical, arrangement of crushed pellets (*Ophiomorpha*), IGR.90-074. B, mecochirid crustacean (*Mecochirus* sp.), IGR.90-073. C, indeterminate worm, IGR.90-075. Scale bars: 10 mm.

Fig. 8. Insect fossils from the Puy-Puy Lagerstätte (Tonnay-Charente, Charente-Maritime, SW France). A, microtomographic images of the lace bug *Ebboa areolata* Perrichot et al., 2006 (Heteroptera) from the late Albian amber, IGR.PUY-4.1, in dorsal (A1), ventral (A2), left lateral (A3) and right lateral (A4) views. B-C, cockroach wing imprints (Dictyoptera, stem group Blattodea), IGR.90-076 (B) and IGR.90-077 (C). D, net-winged imprint (Neuroptera), IGR.90-091. E, sand sheath of a caddisfly larva (Trichoptera), IGR.90-078. Scale bars: 10 mm.

Fig. 9. Plant-insect interactions from the Puy-Puy Lagerstätte (Tonnay-Charente, Charente-Maritime, SW France), represented by various damage types (DT). A, undetermined angiosperm leaf (Type R) (IGR.90-079) with circular, thick galls with a central region separated from the rim by a less thickened area, occuring throughout the leaf (DT163) (A1), with enlargement of one of the galled areas (A2). B, serial of cuspate margin excisions (black arrows) (DT143) on an undetermined angiosperm leaf (IGR.90-080). C–E, examples of surface feeding; C, Abrasion of surface tissue (DT30) on an undetermined woody angiosperm leaf (IGR.90-081); D, removal of surface tissue on *Eucalyptolaurus depreii* Coiffard et al., 2009 (DT30) (IGR.90-082); E, removal of surface tissue with weak reaction rim (DT29) on an undetermined angiosperm leaf (IGR.90-083). F, external foliage feeding (DT2, 12, 14) on an undetermined angiosperm leaf (IGR.90-084). G–K, damage types on *Eucalyptolaurus depreii* Coiffard et al., 2009. G, complete leaf (IGR.90-087) showing high frequency of consumption (DT12, 14); H, polylobate galling structures attached to the 1° vein with a thick outer rim (DT120) (IGR.90-088); I, serpentine mine, frass packed in sections (black arrow); white arrow indicates the position of the enlarged terminal chamber (DT44) and removal of surface tissue with a distinct reaction rim (DT31) (IGR.90-089); J, undulatory frass packed leaf mine with smooth margins (DT45); black arrow indicates oviposition site; white arrow points to the blotch-like mine terminus (IGR.90-086); K, cluster of overlapping, subparallel-orientated eggs (DT67) (IGR.90-090). L, distinctive, full-depth leaf mines, with intestiniform frass trails (DT280) occurring on the entire-margined, parallel-veined coniferous foliage *Dammarophyllum* sp. (IGR.90-085). Scale bars: A1, F–I, L: 10 mm; A2, B–D, K–K: 5 mm.

Fig. 10. Shark egg capsule (*Palaeoxyris* sp.) from the Puy-Puy Lagerstätte (Tonnay-Charente, Charente-Maritime, SW France), IGR.90-092. Fragmentary specimen consisting of the pedicle and the posterior part of the body. Scale bar: 10 mm.

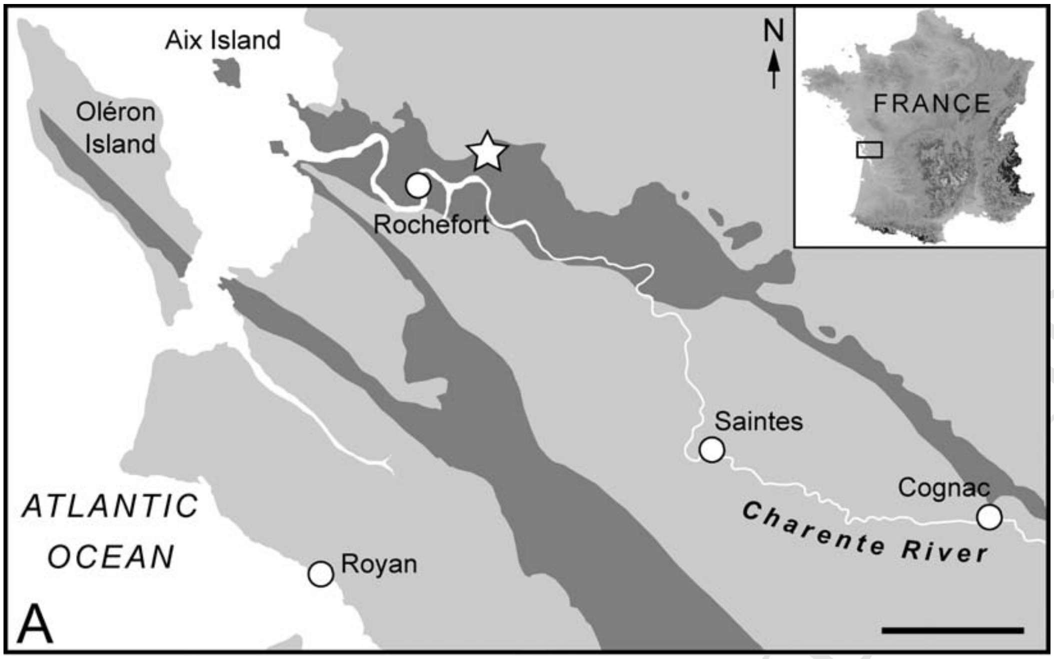
Fig. 11. Putative chordate from the Puy-Puy Lagerstätte (Tonnay-Charente, Charente-Maritime, SW France), IGR.90-065. Note the chevron pattern, comparable to the myoseptum–myomere arrangement of cephalochordate and lamprey fossils. Scale bar: 10 mm.

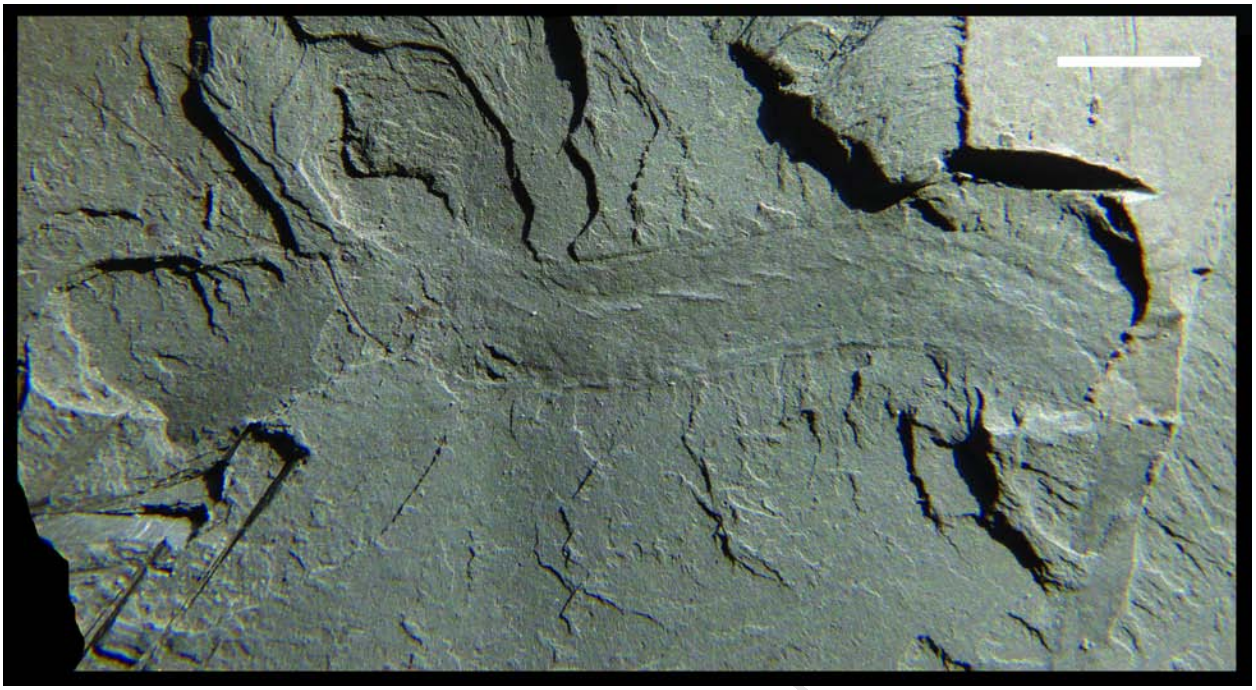
Taxonomical groups/ Types of ichnofossils	**Precise taxonomic assignment (genus and species when known)**	**References**	**Curatorial numbers**
PLANTS			
PTERIDOPHYTES			
(LEAVES)	Pteridophyte Type 2 (also named Pteridophyte Type C in Le Diouron, 2005)	Gomez et al., 2004 (Pl. 1B) Le Diouron, 2005 (Pl. 1.10-11)	PUY-0969 PUY-0970 + Numerous unnumbered specimens
(LEAVES)	Pteridophyte Type 3 (also named Pteridophyte Type D in Le Diouron, 2005)	Gomez et al., 2004 (Pl. 1C) Le Diouron, 2005 (Pl. 1.5)	PUY-0976 + Numerous unnumbered specimens
(LEAVES)	cf. *Osmunda cretacea* Samylina, 1964	Gomez et al., 2004 (Pl. 1A) Le Diouron, 2005 (Pl. 1.3) Néraudeau et al., 2005 (Fig. 4.1)	PUY-0972 + Numerous unnumbered specimens
(LEAVES)	*Weichselia reticulata* (Stokes and Webb) Fontaine in Ward emend. Alvin, 1971	Le Diouron, 2005 (Pl. 1.7)	PUY-0034 + Unnumbered specimens
EQUISETALES (LEAVES)	*Equisetites* sp.	**This study**	**IGR.90-93**
CONIFERS			
(LEAVES)	*Dammarophyllum striatum* Velen. 1889	Le Diouron, 2005 (Pl. 2.1-13) Néraudeau et al., 2005 (Fig. 4.4) Coiffard et al., 2006 **This study**	PUY-0083 PUY-1005 PUY-1011 PUY-1193 **IGR.90-85** + Numerous unnumbered specimens
(LEAVES)	*Dammarites albens* Presl in Sternberg, 1838	Unpublished data	Unnumbered specimens
(LEAFY AXES)	*Frenelopsis alata* (Feistmantel, 1881) E. Knobloch, 1971	Le Diouron, 2005	Numerous unnumbered specimens
(LEAFY AXES)	*Geinitzia reichenbachii* (Geintiz) Hollick and Jeffrey, 1909	Coiffard et al., 2004, 2006 Gomez et al., 2004 Le Diouron, 2005 (Pl. 3.2) Néraudeau et al., 2005 (Fig. 4.2) **This study**	PUY-1018 **IGR.90-061** + Numerous unnumbered specimens
(LEAFY AXES)	*Glenrosa carentonensis* Moreau et al., 2015	Unpublished data	Numerous unnumbered specimens
(WOOD)	*Agathoxylon gardoniense* (Crié, 1890) Philippe	Perrichot,	Numerous

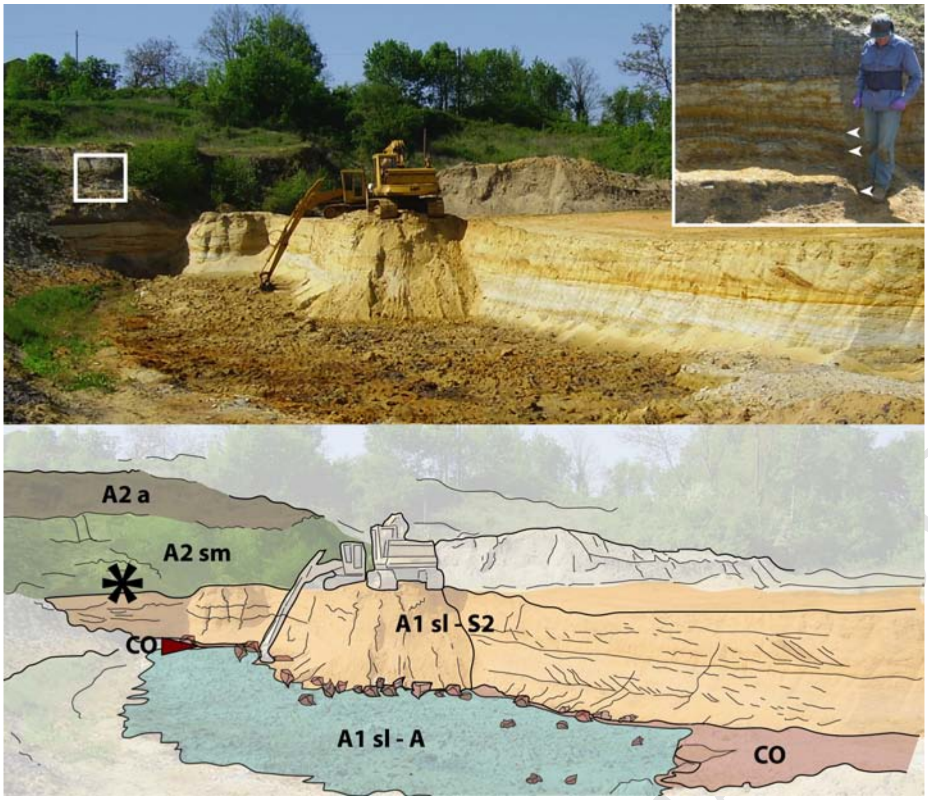
	in Néraudeau et al., 2002	2005 Philippe et al., 2008	unnumbered specimens
(WOOD)	*Protopodocarpoxylon* sp.	Perrichot, 2005 Philippe et al., 2008	Numerous unnumbered specimens
GINKGOPHYTES (LEAVES)	*Nehvizdya andegavense* (Pons et al., 1980) Gomez et al., 2000	Coiffard et al., 2004 Gomez et al., 2004 (Pl. 1G) Le Diouron, 2005 (Pl. 2.2) Néraudeau et al., 2005	PUY-0995 + Numerous unnumbered specimens
BENNETTITALEANS (LEAVES)	*Zamites* sp.	Gomez et al., 2004 (Pl. 1J) Le Diouron, 2005 (Pl. 9.5-7) Néraudeau et al., 2005 (Fig. 4.3)	PUY-0268 PUY-0968 + Numerous unnumbered specimens
(CONE)	*Classostrobus* sp.	Perrichot, 2005	
ANGIOSPERMS			
(LEAVES)	Angiosperm Types D to M, P to S (14 leaf morphological types)	Le Diouron, 2005	
(LEAVES)	Dicot Type 2	Gomez et al., 2004	
(LEAVES)	Angiosperm Type O in Le Diouron, 2005 (also named « Dicot Type 5 » in other publications)	Le Diouron, 2005 (Pl. 6.15) Néraudeau et al., 2005 (Fig. 4.8)	PUY-0105 + Numerous unnumbered specimens
(LEAVES)	Angiosperm Type R in Le Diouron, 2005	Le Diouron, 2005 (Pl. 7.6) **This study**	PUY-0493 **IGR.90-063** **IGR.90-079**
(LEAVES)	cf. *Grevillea dvoraki* Bayer, 1921 Angiosperm Type S in Le Diouron, 2005 (also named « Dicot Type 7 » in Néraudeau et al., 2005	Le Diouron, 2005 (Pl. 7.8-10) Néraudeau et al., 2005 (Fig. 4.7) **This study**	PUY-1235 PUY-0014 PUY-0015 **IGR.90-062** + Unnumbered specimens
(LEAVES)	Angiosperm Type T in Le Diouron, 2005 (trilobal leaves also named « Dicot Type 8 – Aceraceae ? » in other publications)	Gomez et al., 2004 (Pl. 1N) Néraudeau et al., 2005 (Fig. 4.9) Le Diouron, 2005 (Pl. 8.5)	PUY-1048 + Numerous unnumbered specimens
(LEAVES)	Angiosperm Type U in Le Diouron, 2005 (trilobal leaves also named «Dicot Type 9 – Araliaceae ? » in other publications)	Gomez et al., 2004 (Pl. 10) Néraudeau et al., 2005 (Fig. 4.10) Le Diouron,	**PUY-1047** **IGR.90-084** + Numerous unnumbered specimens

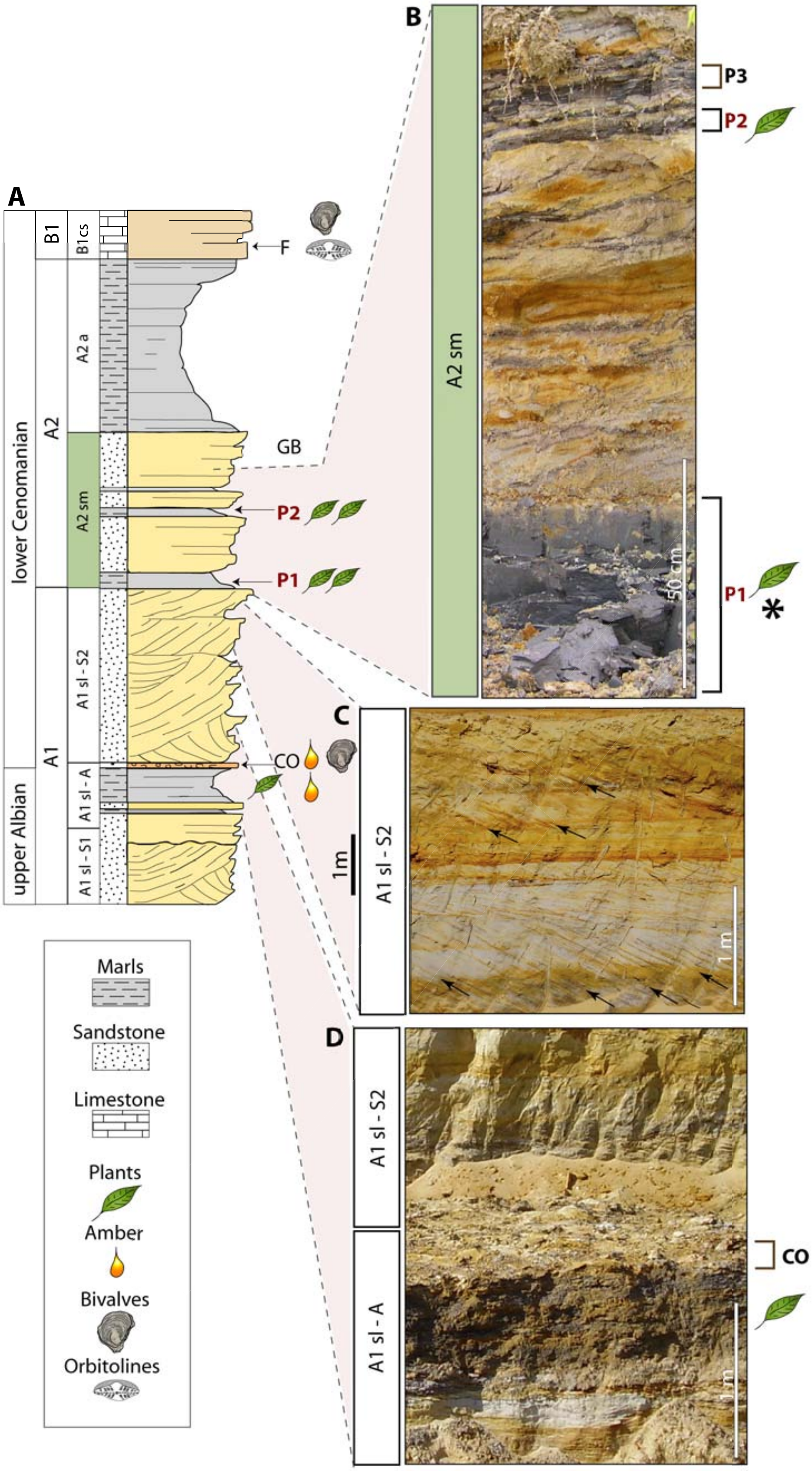
		2005 (Pl. 8.2) **This study**	
(LEAVES)	*Eucalyptolaurus depreii* Coiffard et al., 2009 (previously referred to *Myrtophyllum angustum* (Velen.) Berry, 1925 before 2009, especially in Coiffard et al., 2004, Gomez et al., 2004, Néraudeau et al., 2005 and Le Diouron, 2005; also named Angiosperm Type N in Le Diouron, 2005)	Coiffard et al. 2004, 2006, 2009 Gomez et al., 2004 (PL. 1M) Le Diouron, 2005 (PL. 6.7-11) Néraudeau et al., 2005 (FIG. 4.5) **This study**	PUY-1001 PUY-1002 PUY-0009 PUY-0010 PUY-1011 PUY-0039 PUY-0249 PUY-1030 PUY-1244 PUY-1245 PUY-1263 PUY-1264 PUY-1265 MA PUY 1243 **IGR.90-064** **IGR.90-082** **IGR.90-086** **IGR.90-087** **IGR.90-088** **IGR.90-089** **IGR.90-090** + Numerous unnumbered specimens
(LEAVES)	*Myrtophyllum geinitzii* Heer, 1874	Coiffard et al., 2006	Unnumbered specimens
(LEAVES)	cf. *Debeya coriacea* (Velen.) E. Knobloch, 1964 (previously named Angiosperm Type Q in Le Diouron, 2005 and Dicot Type 6 in Néraudeau et al., 2005)	Coiffard et al., 2004, 2006 Gomez et al., 2004 Le Diouron, 2005 (Pl. 7.2) Néraudeau et al ., 2005 (Fig. 4.6)	PUY-0012 PUY-0013 PUY-0080 + Unnumbered specimens
(LEAVES)	?*Sassafras* sp.	Le Diouron, 2005 Delmail, 2007	Unnumbered specimens
(LEAVES)	*Dicotylophyllum meeki* Heer in Meek and Hayden, 1858	Coiffard et al., 2006	Unnumbered specimens
(LEAVES)	*Araliphyllum daphnophyllum* /Vel./Vel. : Velen., 1889, Knobloch 1969, 1971 = *Aralia daphnophyllum* Velen., 1882	Coiffard et al., 2006	Unnumbered specimens
(LEAVES)	*Pseudoasterophyllites* cf. *cretaceus* (Feistm.) Velen., 1887	Unpublished data	Unnumbered specimens
(WOOD)	Dicotyledon wood	Philippe et al., 2008	Unnumbered specimens
(FLOWERS)	Flowers and inflorescences	Gomez et al., 2004 (Fig. 1P) Le Diouron, 2005 (Pl. 9.1, 9.2) Néraudeau et al., 2005 (Fig. 4.11) **This study**	PUY-0059 PUY-0065 **IGR.90-066** **IGR.90-067** **IGR.90-068**
(SEEDS)	Winged seeds	Le Diouron, 2005 (Pl. 9.3)	PUY-0208 **IGR.90-098**

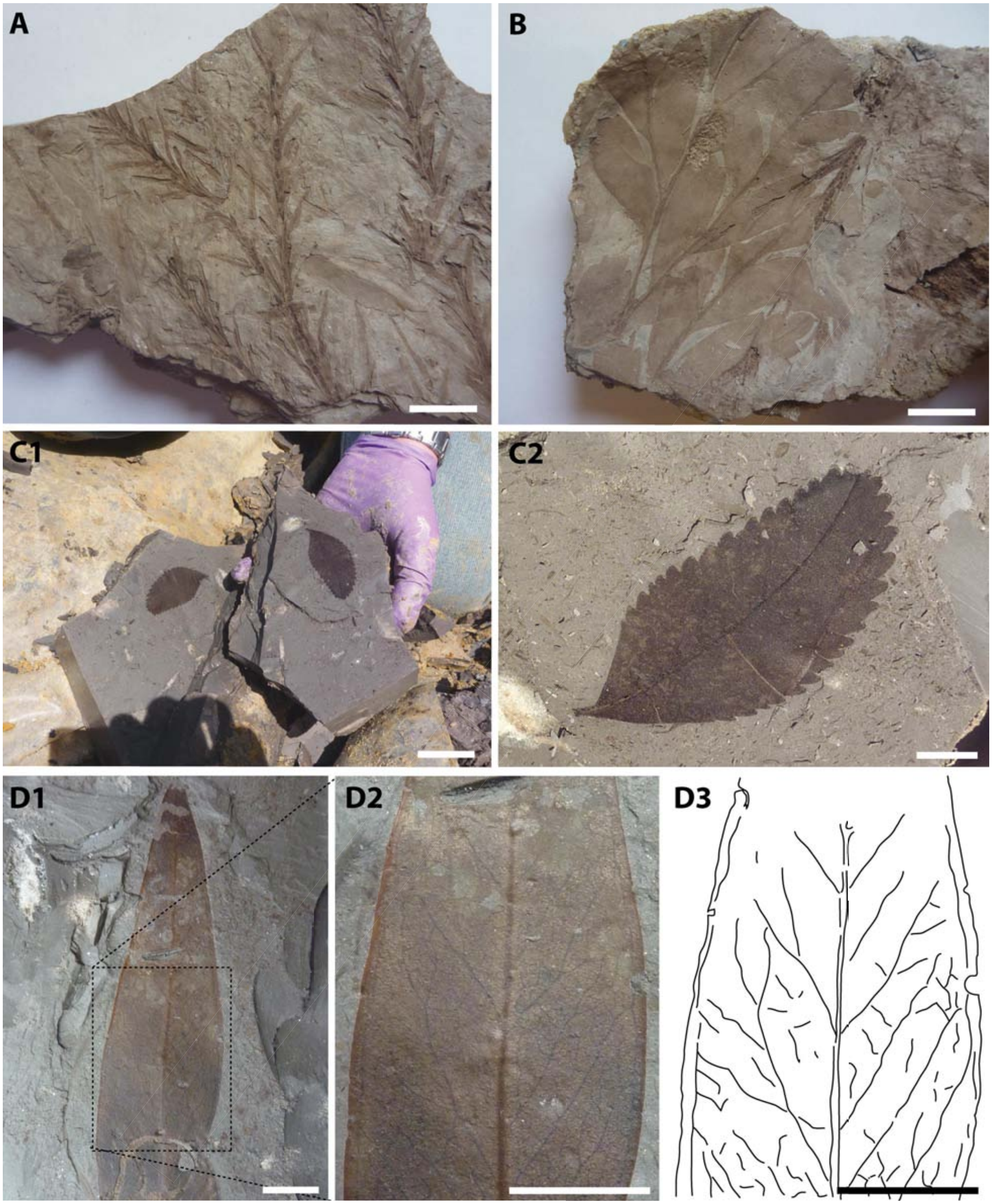
		Néraudeau et al., 2005 (Fig. 4.12) **This study**	
?NEMATODA			
	?Nematoda indet.	**This study**	**IGR.90-075**
LOPHOPHORA			
BRACHIOPODA	aff. *Lingula* sp.	**This study**	**IGR.90-069** **IGR.90-070** **IGR.90-094** **IGR.90-095**
ARTHROPODA			
CRUSTACEA	*Mecochirus* sp.	Breton et al., 2015 **This study**	LM2010.1.77 LM2010.1.79 LM2010.1.86 LM2010.1.783B **IGR.90-073** **IGR.90.096** **IGR.90-097**
HEXAPODA	Dictyoptera (Blattodea) indet.	**This study**	**IGR.90-76** **IGR.90-77** **IGR.PUY-4.3**
	Hemiptera Cimicomorpha Microphysidae : *Ebboa areolata* Perrichot et al., 2006	**This study**	**IGR.PUY-4.1**
	Neuroptera indet.	**This study**	**IGR.90-091**
	Odonata Enigmaeshnidae : *Enigmaeshna deprei* Nel et al., 2008	Nel et al., 2008	MNHN-LP-R 63889
	Trichoptera indet.	**This study**	**IGR.90-078**
CHORDATA			
?CEPHALOCHORDATA	?Cephalochordata indet.	**This study**	**IGR.90-087**
VERTEBRATA	Theropoda indet. (feather)	Vullo et al., 2013	MHNLR 2013.3.3
ICHNOFOSSILS			
BURROWS	Crustacean burrows : *Ophiomorpha* isp.	**This study**	**IGR.90-074**
COPROLITES	Crustacean coprolites	**This study**	**IGR.90-071** **IGR.90-072**
	Termite coprolites : *Microcarpolithes hexagonalis* Vangerow, 1954	Colin et al., 2011	Numerous unnumbered specimens
EGGS	Shark egg capsules: *Palaeoxyris* sp.	Vullo et al., 2013 **This study**	MHNLR 2013.3.1 **IGR.90-92**
INSECT DAMAGES ON PLANTS	71 kinds of insect damages on plants, corresponding to morphological types defined in the « Damage type system » of Labandeira et al., 2007 (e.g., types DT2, DT12, DT30, DT31, DT80, DT280)	**This study**	**IGR.90-79** **IGR.90-80** **IGR.90-81** **IGR.90-82** **IGR.90-83** **IGR.90-84** **IGR.90-85** **IGR.90-86** **IGR.90-87** **IGR.90-88**

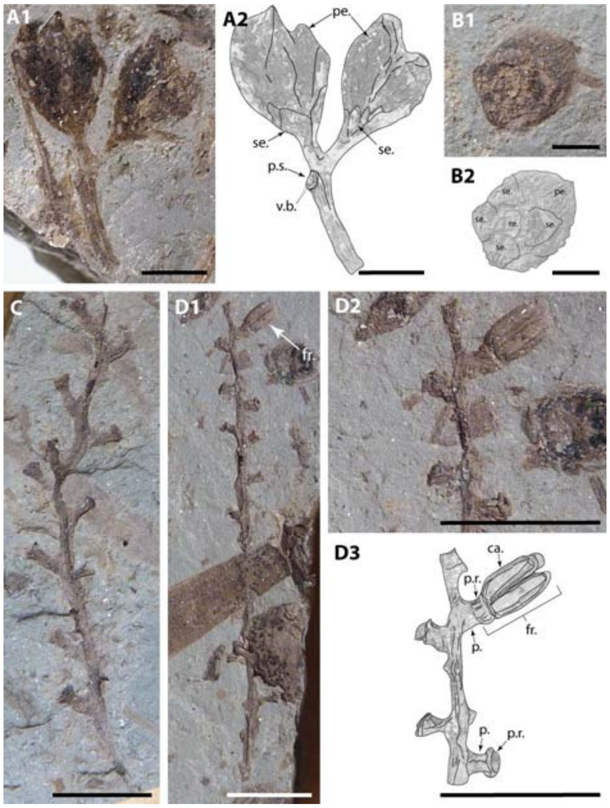

Aix Island
Oléron
Island
N
FRANCE
Rochefort
Saintes
Cognac
ATLANTIC
OCEAN
Charente River
Royan
A

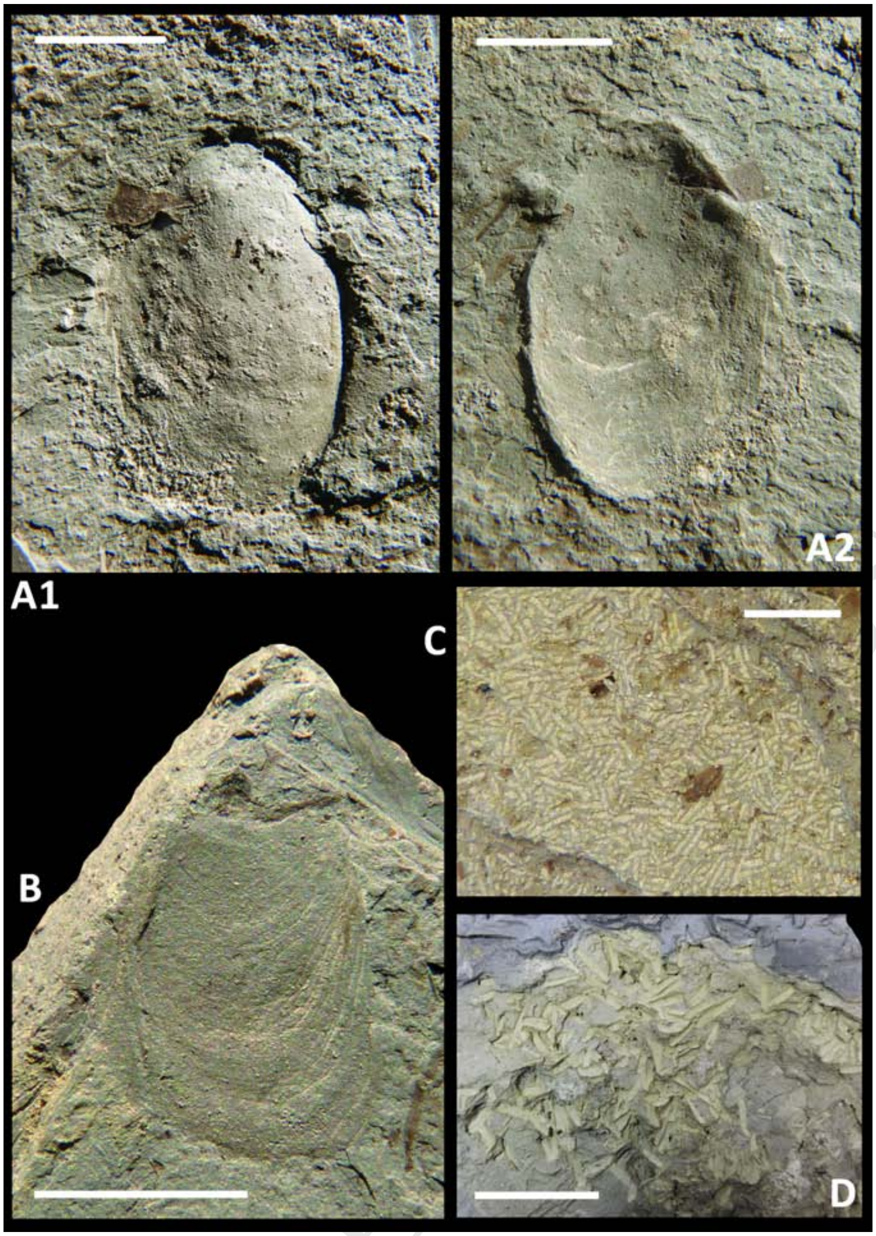


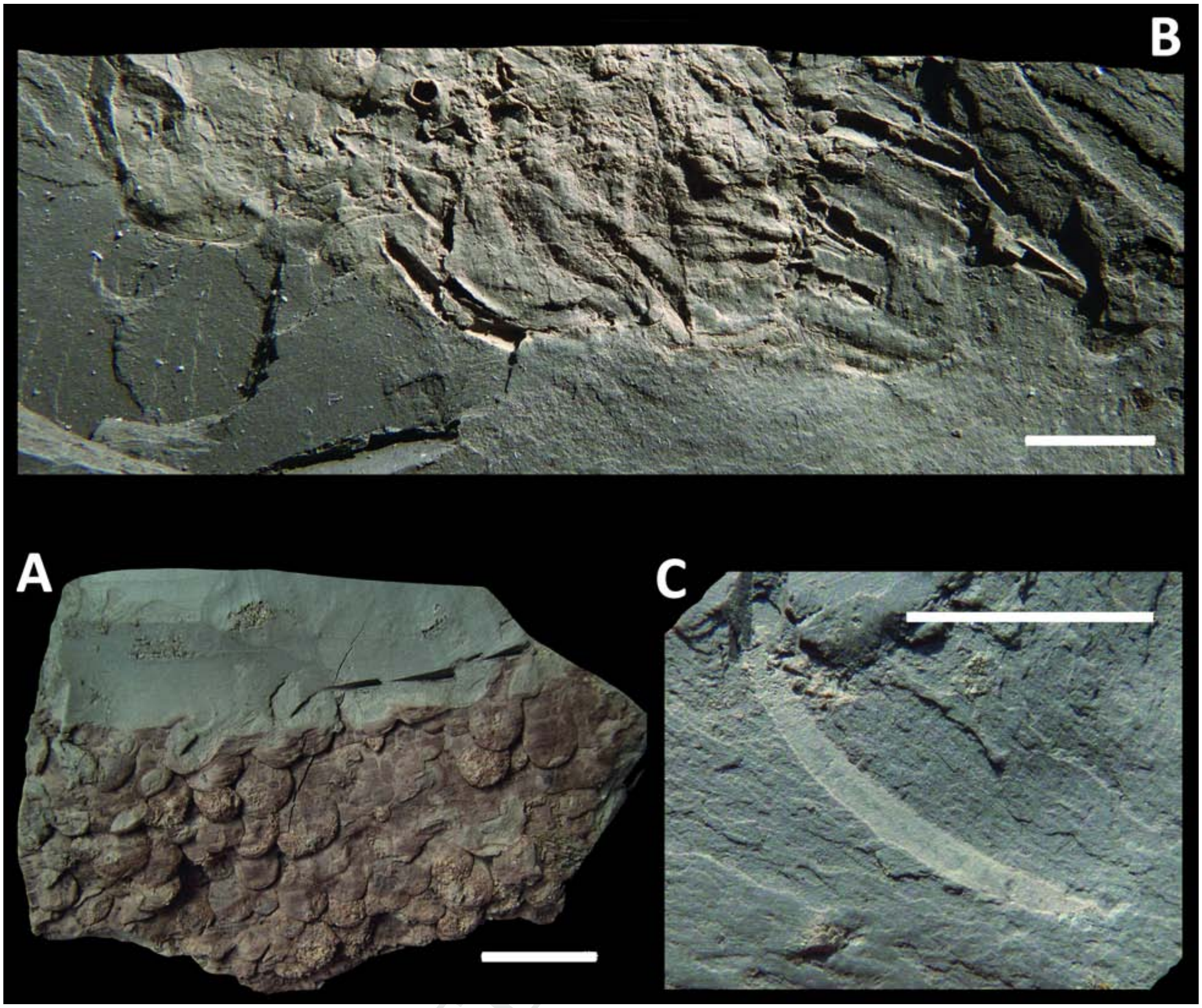

A2 a
A2 sm
*
CO
A1 sl - S2
A1 sl - A
CO

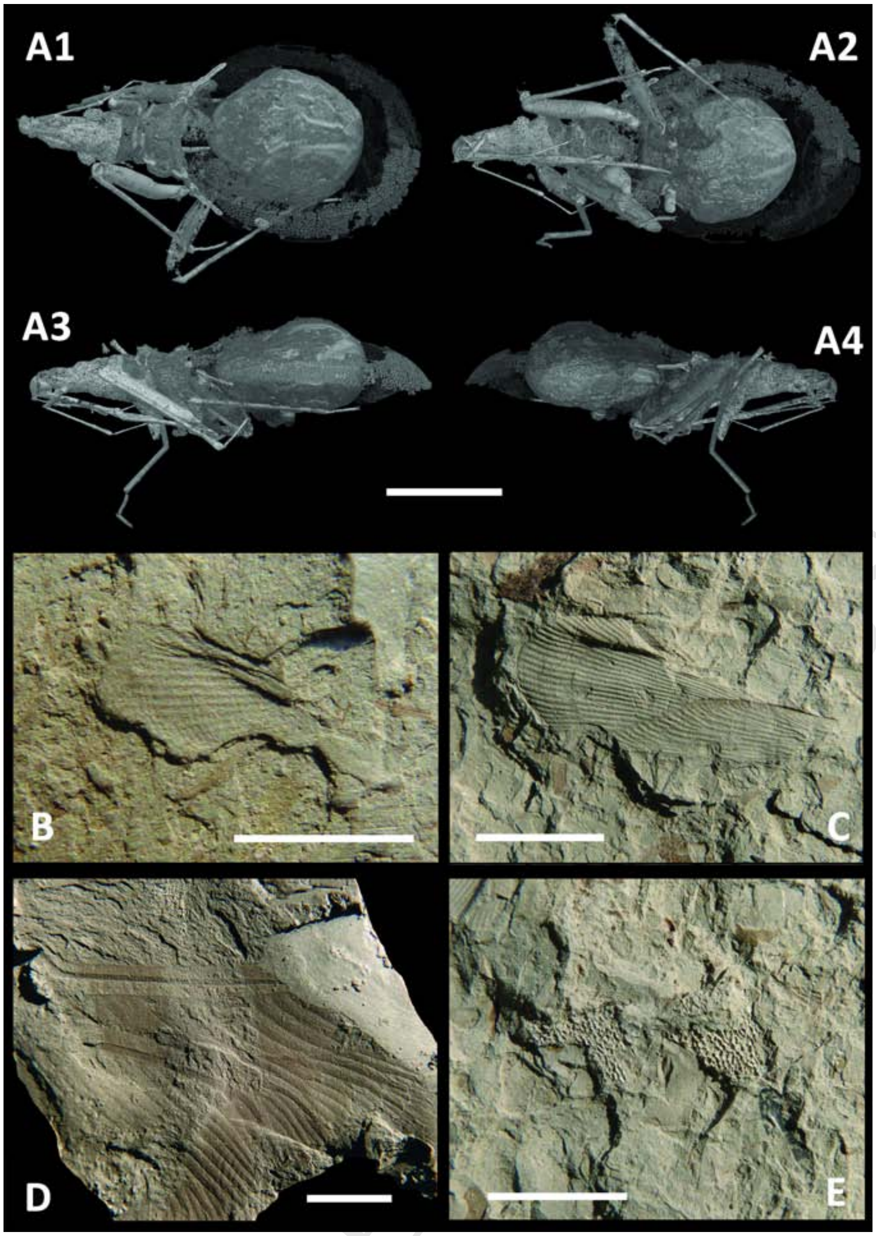

A
B1
B1cs
A2
A2 a
A2 sm
lower Cenomanian
upper Albian
A1
A1 sl - S2
A1 sl - A
A1 sl - S1
F
GB
P2
P1
CO
Marls
Sandstone
Limestone
Plants
Amber
Bivalves
Orbitolines
B
A2 sm
P3
P2
50 cm
P1
*
C
A1 sl - S2
1m
1 m
D
A1 sl - S2
A1 sl - A
CO
1 m

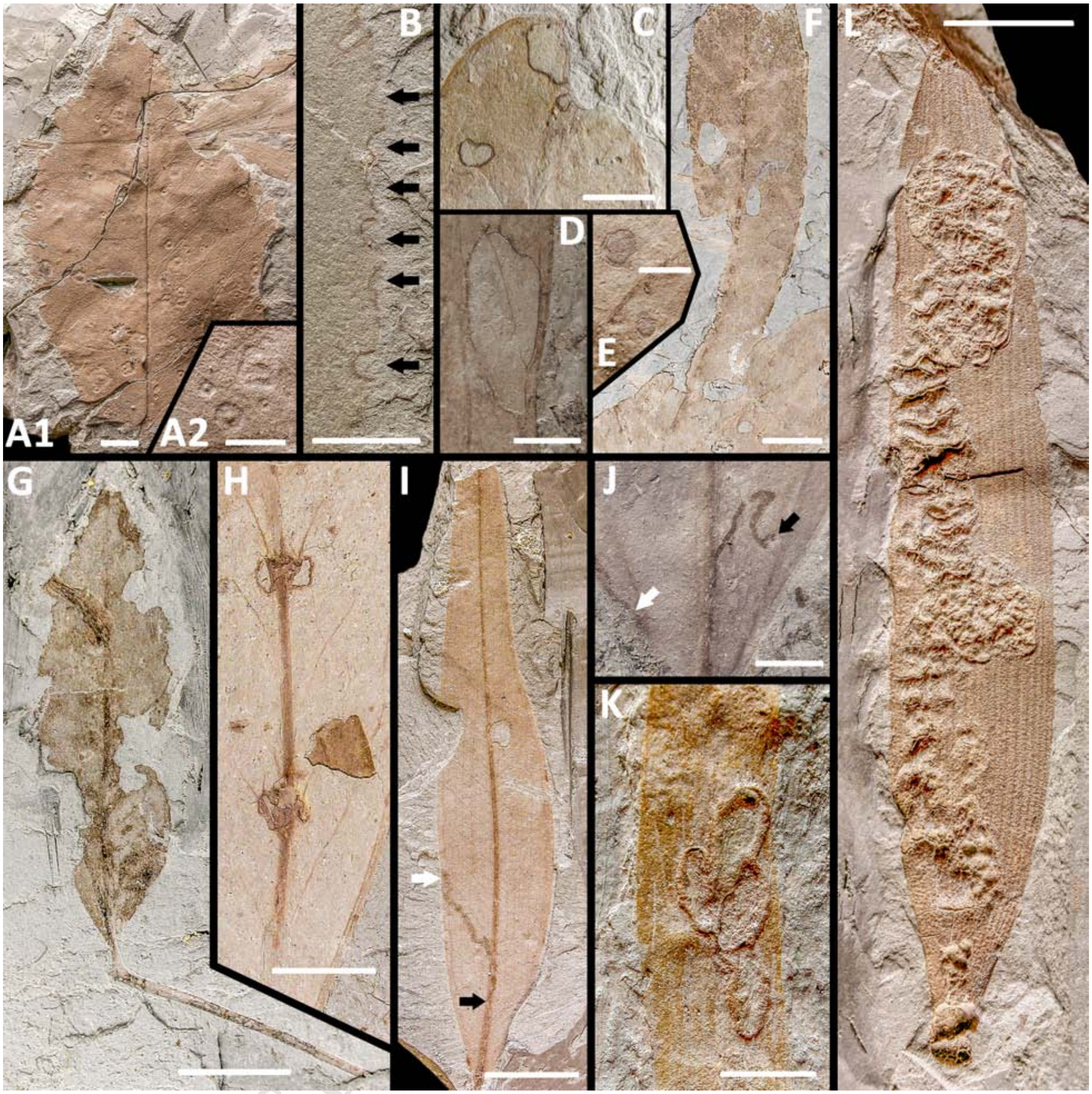

A
B
C1
C2
D1
D2
D3


A1
A2
pe.
se.
se.
p.s.
v.b.
B1
B2
se.
pe.
se.
pe.
se.
se.
C
D1
fr.
D2
D3
ca.
p.r.
fr.
p.
p.
p.r.


A1
A2
B
C
D


B
A
C


A1
A2
A3
A4
B
C
D
E


A1
A2
B
C
D
E
F
L
G
H
I
J
K

- Stratigraphy, palaeontology and palaeoecology of the Puy-Puy Lagerstätte, France.
- Mid-Cretaceous Konservat-Lagerstätte formed in a quiet paralic environment.
- Rich plant assemblage with diverse insect damages on angiosperm leaves.
- Lagerstätte with insects preserved in both amber and lignitic clay.
- Co-occurrence of marine, brackish, freshwater and terrestrial organisms.