



HAL
open science

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-02088578v1>

Submitted on 3 Apr 2019

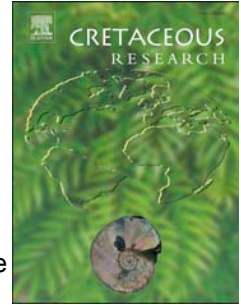
HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Accepted Manuscript

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>.

This is a PDF file of an unedited manuscript that has been accepted for publication. As a service to our customers we are providing this early version of the manuscript. The manuscript will undergo copyediting, typesetting, and review of the resulting proof before it is published in its final form. Please note that during the production process errors may be discovered which could affect the content, and all legal disclaimers that apply to the journal pertain.

1 The paralic Albian–Cenomanian Puy-Puy Lagerstätte (Aquitaine Basin, France):

2 An overview and new data

3

4 Didier Néraudeau^a, Romain Vullo^{a,*}, Pierre Bénéfice^b, Gérard Breton^a, Éric

5 Dépré^c, Danièle Gaspard^d, Vincent Girard^e, Matthieu Le Couls^a, Jean-David

6 Moreau^{f, g}, André Nel^h, Vincent Perrichot^a, Mónica M. Solórzano-Kraemer^{i, j},

7 Torsten Wappler^k

8

9 ^a*Univ Rennes, CNRS, Géosciences Rennes, UMR 6118, 263 avenue du Général Leclerc, F-35000 Rennes,*

10 *France*

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

12 ^c*GIP-GEVES (Groupement d'Étude et de Contrôle des Variétés et Semences), Le Magneraud, F-17700*

13 *Surgères, France*

14 ^d*CR2P, Centre de Recherche sur la Paléodiversité et les Paléoenvironnements, UMR CNRS 7207, Muséum*

15 *National d'Histoire Naturelle, EPHE, UPMC, Sorbonne Université, CP 38, 8 Rue Buffon, F-75005 Paris,*

16 *France*

17 ^e*Institut des Sciences de l'Évolution de Montpellier, Université Montpellier, UMR CNRS 5554, EPHE, IRD,*

18 *Place Eugène Bataillon, F-34095 Montpellier, France*

19 ^f*Université Bretagne Sud, CNRS, Centre de Recherche Yves Coppens, Laboratoire Géosciences Océan, UMR*

20 *6538, rue André Lwoff, F-56017 Vannes, France*

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

22 ^h*ISYEB, Institut de Systématique, Évolution, Biodiversité, UMR CNRS 7205, Muséum National d'Histoire*

23 *Naturelle, EPHE, UPMC, Sorbonne Université, CP 50, Entomologie, 45 rue Buffon, F-75005 Paris, France*

24 ⁱSenckenberg Forschungsinstitut und Naturmuseum, Paläontologie und Historische Geologie-Berstein Sektion,
25 Senckenberganlage 25, D-60325 Frankfurt am Main, Germany

26 ^jSteinmann Institut für Geologie, Mineralogie und Paläontologie, Universität Bonn, Nussallee 8, D-53115 Bonn,
27 Germany

28 ^kHessisches Landesmuseum Darmstadt, Friedensplatz 1, D-64283 Darmstadt, Germany

29

30 *Corresponding author.

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

32

33 ABSTRACT

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

48

49 *Keywords:*

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

51

52

53 **1. Introduction**

54

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

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

84

85

86 **2. Geological setting**

87

88 The Puy-Puy quarry is located near Tonnay-Charente town, about twenty kilometres
89 from the Charente river estuary (Fig. 1). The uppermost Albian–lower Cenomanian deposits
90 mainly consist of fluviatile and paralic sand, but contain several clay intercalations with local
91 concentrations of plant fossils or lignite and amber (Néraudeau et al., 2005) (Figs. 2, 3). These
92 alternations of sand and clay correspond to the lithological unit A, subdivided in two
93 lithological subunits (Néraudeau et al., 1997): A1 for heterometric sand, with large-scale cross
94 bedding and rich in lignite and amber (Girard, 2010), dated palynologically as latest Albian–
95 earliest Cenomanian (Néraudeau et al., 2002; Batten et al., 2010); A2 for more homometric
96 fine sand, mainly arranged in horizontal beds and poor in wood remains, dated as earliest
97 Cenomanian (Néraudeau et al., 2002). The sand and clay of unit A are overlain by shelly sand
98 (Vullo et al., 2003; level F in Fig. 3A), rich in orbitoline foraminifera and oysters, which

99 marks the base of lithological unit B (subunit B1). In the Puy-Puy quarry, the outstanding
100 fossiliferous facies (Lagerstätte) is located in the clay from the mid part of A2 (facies P1 and
101 P2, level A2sm; Figs. 2, 3), exceptional preservation is also present in the basal uppermost
102 Albian lignites and amber (level A1sl-A), but to a lesser extent.

103 The detailed description of the Puy-Puy section (Figs. 2, 3) shows at the base
104 (uppermost Albian part of subunit A1) sand deposits (A1sl-S1) overlain by an approximately
105 1-m-thick clay bed (A1sl-A) with cuticle compressions (e.g., *Frenelopsis* and *Glenrosa*),
106 lignites and amber. The lowermost Cenomanian bed consists a fine conglomerate (bed CO in
107 Figs. 2, 3A), containing rare small examples of the oyster *Ceratostreon flabellatum* and
108 reworked altered amber. This conglomerate is overlain by a 2–3-m-thick coarse sand layer
109 with large-scale cross bedding (A1sl-S2). Within the basal sand of A1sl-S2, a few lenses of
110 coarse sand contain juveniles of *C. flabellatum*, serpulids and small reptile bone pebbles. This
111 sandy facies of subunit A1 is overlain by the sand and clay alternation of subunit A2; the
112 laminated clay bed of A2sm contains abundant plant and invertebrate imprints, and
113 ichnofossils. The thickest clay level (about 30 cm thick), bed P1, constitutes the Lagerstätte
114 (Fig. 3C). Above P1, the facies A2sm continues with a 2.5-m-thick alternation of clay and
115 fine sand. At its top, the alternation contains fewer and thinner clay layers when sand
116 progressively becomes a more cemented sandstone with ripple marks and isopod tracks (level
117 GB in Fig. 3A). The top of the sand and clay series is marked by a 2–3-m-thick bed of
118 brackish lagoonal clay (A2a) very poor in plant remains, apart from millimetric fragments of
119 cuticles. The top of the section corresponds to about 1 m thick of shallow marine carbonate
120 facies (B1cs), enriched in the orbitoline *Orbitolina conica* and the small oyster *Rhynchostreon*
121 *suborbiculatum* at the base (F), and overlain by a limestone with diverse marine invertebrates,
122 especially large rudists such as *Ichthyosarcolithes triangularis*.

123

124

125 **3. Material and methods**

126

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

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

143 The only complete insect specimen preserved in amber was scanned on the BM5
144 beamline (European Synchrotron Radiation Facility, Grenoble, France; Tafforeau et al., 2006)
145 using propagation phase contrast in 2009. The scans of the specimen were performed using a
146 voxel size of 0.702 μm . The radiographs were acquired using a beam set at energy of 20 keV
147 using a double Ru/B4C multilayer monochromator and a propagation distance of 7 cm
148 between the specimen and the detector. We used a FReLoN CCD e2V camera mounted on

149 lens-based optical system coupled with a 25- μm -thick YAG(Ce) scintillator. Scans were
150 performed using 1500 projections and an exposure time of 2s per projection. The scans were
151 reconstructed using a back-projection algorithm implemented in the PyHST2 software (High
152 Speed Tomography in python version, ESRF, Mirone et al., 2014). Data were finally
153 converted into a 16 bit tiff stack of slices using 0.001% saturation values on the whole 32 bits
154 3D histogram, corrected for residual ring artefacts and cropped. The three dimensional
155 reconstructions of specimens were achieved with the software VG Studio Max 2.2 (Volume
156 Graphics, Heidelberg, Germany).

157 The main part of the fossil material collected at Puy-Puy (Appendix 1) and the
158 specimens illustrated here are housed in the Geology Department and Museum of the
159 University of Rennes 1 (UMR CNRS 6118 Géosciences Rennes), under the collection
160 numbers IGR.90-061 to IGR.90-098, plus IGR.PUY-4.1 and IGR.PUY-4.3. A few specimens,
161 previously published, are housed in other institutions: the holotype (MNHN-LP-R 63889) of
162 the odonatan *Enigmaeshna deprei*, housed at the National Museum of Natural History; the
163 crustacean specimens, housed at the “Musée Vert” of Le Mans (Breton et al., 2015:
164 LM2010.1.77; LM2010.1.79; LM2010.1.86; LM2010.1.783B); the vertebrate remains housed
165 at the Museum of Natural History of La Rochelle (Vullo et al., 2013: MHNLR 2013.3.1,
166 MNHLR 2313.3.2, MNHLR 2013.3.3); an inflorescence with two pedicellate flowers (Gomez
167 et al., 2004, Le Diouron, 2005; Néraudeau et al., 2005: PUY-0065), a winged seed
168 (Néraudeau et al., 2005; Le Diouron, 2005: PUY-0208) and the type specimens or previously
169 figured specimens of the angiosperm *Eucalyptolaurus depreii* (Coiffard et al., 2009: PUY-
170 0009/10, PUY-0039, PUY-0249, PUY-1244/45, PUY-1263/64/65), housed in the collections
171 of palaeobotany of the University Claude Bernard-Lyon (UCBL); numerous other specimens
172 of plants from Puy-Puy are housed in the UCBL collections, with curatory numbers beginning
173 by the prefix “PUY-“ followed by the numbers mentioned in Appendix 1; an additional

174 specimen of *Eucalyptolaurus depreii* is housed at the Musée of Angoulême (Coiffard et al.,
175 2009: MA PUY 1243).

176

177

178 **4. Plant assemblage**

179

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

186 In the P1 clay lens, after conifers, angiosperms constitute the second most abundant
187 plant macroremains. About twenty different leaf morphologies have been distinguished (Le
188 Diouron, 2005; Delmail, 2007). They have been variously assigned to cf. *Grevillea dvorakii*,
189 cf. *Debeya coriacea*, platanophyll leaves tentatively assigned to the Proteales (Néraudeau et
190 al., 2005) and *Eucalyptolaurus depreii* considered close to the Lauraceae (Coiffard et al.,
191 2009) (Fig. 4D). All indicate that the lower Cenomanian angiosperm assemblage (Fig. 4B–D)
192 of the Puy-Puy Lagerstätte was dominated by magnoliids, mainly Lauraceae, and some
193 possible basal eudicots (Proteales such as some Platanaceae).

194 The angiosperm remains from Puy-Puy also include exquisitely preserved
195 reproductive structures. A simple inflorescence (cymose?) was illustrated, but not described,
196 by Gomez et al. (2004) and Néraudeau et al. (2005). The inflorescence displays a peduncle
197 bearing two pedicellate flowers in the distal part (Fig. 5A); a third flower, attached below the
198 two flowers, is suggested by an oval scar. The specimen is 21 mm long. Flowers are 9 mm

199 long and 7 mm wide. The peduncle measures 8 mm long and is 1.4 mm in diameter. The
200 distal-most pedicellate flower terminates at the inflorescence axis; the second flower branches
201 off slightly below at an angle of *c.* 50°. The two pedicels are 2.2 and 2.6 mm long and 0.9 and
202 1.2 mm in diameter respectively. The top of the pedicel is flared, with no distinction from the
203 receptacle. Flowers are globular, cup-shaped, and seem to be actinomorphic. Perianth is well-
204 developed. The sepals seem to be free, are 2.2–2.3 mm long and their apices are obtuse to
205 acute. The petals seem to be free, account for the entire length of the flower. Insertion of
206 floral organs seems to be hypogynous.

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

213 Plant remains from Puy-Puy also include putative simple infructescences. They
214 display up to 16 spirally arranged pedicels and a single fruit borne distally (Fig. 5C, D).
215 Infructescence stems are up to 31 mm long and range between 0.35–0.60 mm in diameter.
216 Pedicels are short, stocky, usually concaved, with either a pentagonal and keeled or
217 cylindrical transversal section. They are regularly spaced, 1.6–2.3 mm long, and form angles
218 of 42–90° with the infructescence stem measuring 0.9–1.1 mm long and 0.4–1.0 mm wide.
219 Distally, the pedicels form an enlarged receptacle. Each pedicel bears a single fruit. The single
220 fruit observed is 2.4 mm long and 1.3 mm wide. The pedicels remain attached to the stem
221 after the fruits fall thereby leaving a star-shaped scar where they meet the pedicels. The
222 perianth and the androecium are lacking. The carpels seem to number four or five per fruit but

223 this cannot be confirmed (Fig. 5D). Carpels are elongate, oval and typically measure 2.1 mm
224 long and 0.5 mm wide.

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

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

236 Fossil wood of conifers is relatively uncommon in the clay P1 and restricted generally
237 to infracentimetric fragments ascribed to *Agathoxylon* and *Protopodocarpoxyton* (Perrichot,
238 2005; Philippe et al., 2008). A single type of underminable heteroaxylous wood (basal
239 angiosperm or eudicot) has been found (Philippe et al., 2008).

240

241

242 **5. Invertebrates**

243

244 Compared to the myriad plant remains found at Puy-Puy in the Cenomanian clay,
245 invertebrate fossils are much rarer, totaling no more than thirty specimens after more than
246 fifteen years of sampling. Some specimens are poorly preserved and too incomplete for a
247 systematic assignment, and even distinguishing between fragments of crustaceans and insects

248 can be difficult. Identified specimens include three putative brachiopods, seven insects, and
249 nine crustaceans. So far, no molluscs have yet been found.

250

251 5.1. Putative brachiopods

252

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

266 The Puy-Puy specimens are larger and more rounded in outline than the *Lingula* sp.
267 found in the upper Cenomanian clay of Roullet-Saint-Estèphe, in Charente (Néraudeau et al.,
268 2013a) and a single specimen previously found (but unpublished) in the uppermost Albian–
269 lowermost Cenomanian lignitic clay of Les Renardières, another quarry of Tonny-Charente,
270 located at 4 km from Puy-Puy (Néraudeau et al., 2005).

271

272 5.2. Crustaceans

273

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

283 *Burrows*. Two fossils are interpreted as crustacean burrows. They correspond to a
284 dense, subcylindrical arrangement of crushed pellets (Fig. 7A), each one being 4 to 5 mm in
285 diameter. These traces clearly belong to the widespread ichnogenus *Ophiomorpha*, well
286 known in Mesozoic and Cenozoic deposits, including Cretaceous rocks (Goldring and Pollard,
287 1995; Rogers et al., 2013). In Recent aquatic environments, the crustacean *Callianassa*
288 produces similar structures (Frey et al., 1978) and this group of decapods is therefore
289 considered as the trace maker of the ichnogenus *Ophiomorpha*.

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

297

298 5.3. Indeterminate “worms”

299

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

310

311 5.4. Insects

312

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

316 *Insect remains.* Two insect inclusions (Hemiptera and Dictyoptera) have been found in
317 a single piece of amber from the upper Albian lignitic clay, at the base of the Puy-Puy series,
318 albeit investigation was limited by the small amount and poor quality of the amber. A
319 cockroach is represented by a single leg; the single hemipteran (Fig. 8A) is represented by a
320 lace bug (Cimicomorpha) assignable to *Ebboa areolata*, a species known from the coeval
321 Charentese amber of Archingeay-Les Nouillers and the Cenomanian Alpine amber (Perrichot

322 et al., 2006). *Ebboa areolata*, originally placed in its own extinct family (Ebboidae; Perrichot
323 et al., 2006), was subsequently transferred to Microphysidae (Golub and Popov, 2008, 2012).

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

333 *Insect damages on plants.* Insect mediated damages were examined on 1605
334 specimens of plants. 357 leaves or leaf fragments, representing 22.1% of the material
335 examined, exhibit some kind of damage (Fig. 9). Of these, 301 (84.3%) were damaged in one
336 way, while the remaining 56 (15.7%) showed two or more forms of damage. Seventy-one
337 damage types (DTs) attributable to insect herbivory and oviposition were identified and
338 allocated to the seven functional feeding groups (FFGs) based on the widely used damage
339 type system of Labandeira et al. (2007). In terms of abundance, herbivory on the Puy-Puy
340 flora is dominated by external foliage feeding, particularly surface feeding (Fig. 9B–F),
341 represented by several damage types (DTs), especially DT30 and DT31, comprising one-third
342 of all recorded damage type occurrences. Galling is next highest at Puy-Puy, characterized
343 mostly by featureless, small, hemispherical galls (DT80) (Fig. 9A). Hole feeding (DT2) and
344 margin feeding (DT12) is found in approximately equal abundances at Puy-Puy (Fig. 9B–F).
345 Nevertheless, the abundance data indicates a dominance of generalized damage (89.1%),
346 when compared to specialized damage (10.9%). For the Puy-Puy Flora dicotylodorous

347 angiosperms were the most herbivorized (33.1%), followed by conifers (17.8%),
348 pteridophytes (6.2%), and cycadophytes (~1%). Particularly, the lauraceous taxon
349 *Eucalyptolaurus depreii* exhibits the most diverse component community of herbivore
350 activities (Fig. 9D, G–K), with a corresponding diversity of 40 DTs being the highest in the
351 entire assemblage, including 23 specialized DTs. Second in rank order is the broad-leaved
352 coniferous foliage *Dammarophyllum* sp. (Fig. 9L), representing a lower proportion of
353 damaged leaves (23.4%) but also with an elevated level of consumption (34 DTs).
354 Interestingly, there is one harboring specialized interaction (DT280), representing a leaf miner
355 targeting the parenchyma. So far, this is only known from the broad-leaved conifer
356 *Liaoningcladus boii* Sun, Zheng and Mai, 2000 from the mid Lower Cretaceous Yixian
357 Formation (Ding et al., 2014, 2015).

358

359

360 **6. Vertebrates and putative chordate**

361

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

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

374 The second vertebrate fossil is a well-preserved body contour feather, which is one of
375 only a few very rare mid-Cretaceous feathers known from Europe (Vullo et al., 2013). Fossil
376 feathers have been previously discovered in the mid-Cretaceous deposits from Charentes,
377 preserved in the uppermost Albian amber from Archingeay-Les Nouillers (Perrichot et al.,
378 2008). In the neighbour region of Poitou, another Cenomanian feather imprint has been
379 discovered in the clay beds of Jaunay-Clan (Valentin et al., 2014).

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

397 petromyzontid hypothesis is also compatible with the size, shape and anatomical features of
398 the Puy-Puy specimen, as well as with the palaeoenvironment.

399

400

401 **7. Discussion**

402

403 *7.1. Depositional environments*

404

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

413 The younger clay bed (A2sm), with plant and invertebrate imprints, without amber but
414 dominated by angiosperms, probably belongs to a quieter and more protected environmental
415 setting than the underlying lignite and sand accumulations, the fine laminations in the clay
416 characterizing low energy (Moreau, 1993b). Although the angiosperm composition of the
417 lower Cenomanian Puy-Puy Lagerstätte is concordant with most other coeval angiosperm
418 floras in Europe (Coiffard et al., 2012), it contrasts markedly with other coastal fossil
419 localities from the Charentese region. Cuticles from clays, silicified plants from flints as well
420 as palynology suggest that Albian–Cenomanian coastal habitats of Charente-Maritime were
421 dominated by conifers and ferns, with some taxa showing xeromorphic adaptations (e.g.,

422 Dejax and Masure, 2005; Néraudeau et al., 2005; Peyrot et al., 2005, 2019; Gomez et al.,
423 2004, 2008; Moreau et al., 2014a, 2015). Gomez et al. (2008) have proposed that the local
424 Albian–Cenomanian littoral palaeoenvironments were dominated by conifer mangrove-type
425 vegetation. Thus, compared to other coeval littoral localities, the lower Cenomanian plant
426 assemblage of Puy-Puy (P1) appears to be an exception, showing the highest abundance and
427 diversity in angiosperm remains in a littoral environment from the lower Cenomanian of
428 western France (Néraudeau et al., 2002; Gomez et al., 2004, 2008). In P1, the paucity of
429 typical Charentese taxa adapted to halophytic conditions (e.g., *Brachyphyllum*, *Frenelopsis*,
430 *Glenrosa carentonensis*) combined with the presence of *Ploufolia* leaves (probably related to
431 the Nymphaeales) strongly suggests that the lower Cenomanian Puy-Puy flora was also
432 heavily influenced by inland/continental freshwater inputs rather than solely autochthonous
433 littoral inputs.

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

447 where a continental plant assemblage was deposited in brackish water or in a confined coastal
448 marine environment.

449

450 7.2. Palaeoclimatic context

451

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

462

463 7.3. Comparisons with other Cenomanian Lagerstätten

464

465 Cenomanian Lagerstätten from France are mainly located in Charentes and are lignitic
466 clay containing both fossiliferous amber (Perrichot et al., 2010) and plant cuticle
467 accumulations, the most studied of which is Archingeay-Les Nouillers (Néraudeau et al.,
468 2002; Gomez et al., 2008). However, although these amber and cuticle deposits show
469 numerous cases of exquisite 3D preservation of arthropods, micro-organisms and plants, they
470 do not contain clay laminae with diverse plant and animal prints, such as the famous
471 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., odonatan, 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

497 and other mid-Cretaceous Lagerstätten with more marine influences, such as Agoult (Gara
498 Sbaa) in Morocco (Martill et al., 2011) and the famous Lebanese sites (Gayet et al., 2003). It
499 is noteworthy that the preservation of delicate structures such as flowers is extremely rare in
500 the French Cenomanian deposits; except the Puy-Puy quarry, only the Cenomanian Pauletian
501 facies from Gard (southeastern France) yielded diverse inflorescences, flowers and fruits
502 (Moreau et al., 2014b, 2016a, b).

503

504

505 **8. Conclusions**

506

507 Apart from its rich fossil plant content, the Puy-Puy Lagerstätte is noteworthy because
508 the sedimentological series shows both lignites with amber and cuticles at the base, with
509 exceptional 3D preservation, and clay laminae with exquisite 2D imprints in younger strata. In
510 terms of sedimentology, fossil assemblage and palaeoenvironmental context, the Ingersoll
511 shale Lagerstätte (Santonian in age) of Alabama (Bingham et al. 2008) seems to be the closest
512 Late Cretaceous analogue to the Puy-Puy Lagerstätte. As at Puy-Puy, the Ingersoll shale biota
513 includes invertebrate traces such as *Ophiomorpha* and numerous well-preserved plant
514 remains, amber, feathers, all accumulated in a muddy paralic environment (Bingham et al.,
515 2008).

516

517

518 **Acknowledgments**

519

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

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

527

528

529 **References**

530

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

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

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

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

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

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

- 546 Chang, M.M., Wu, F., Miao, D., Zhang, J., 2014. Discovery of fossil lamprey larva from the
547 Lower Cretaceous reveals its three-phased life cycle. *Proceedings N. Acad. Sci.* 111,
548 15486–15490.
- 549 Coiffard, C., 2003. Applications de la parcimonie de Wagner à l'étude paléosynécologique de
550 flores de l'Albien et du Cénomaniens d'Europe. Université Claude Bernard–Lyon 1,
551 France (Unpublished Master thesis, 26 pp.).
- 552 Coiffard, C., Gomez, B., Thévenard, F., Nel, A., Kvaček, J., Néraudeau, D., Thévenard, F.,
553 2008. Application of the Wagner's Parsimony Method in fossil plant assemblages
554 from the Cretaceous of Europe. *Rev. Palaeobot. Palynol.* 148, 1–12.
- 555 Coiffard, C., Gomez, B., Thiébaud, M., Kvaček, J., Thévenard, F., Néraudeau, D., 2009.
556 Intramarginal veined Lauraceae leaves from the Albien–Cenomanian of Charente-
557 Maritime (western France). *Palaeontology* 52, 323–336.
- 558 Coiffard, C., Gomez, B., Daviero-Gomez, V., Dilcher, D., 2012. Rise to dominance of
559 angiosperm pioneers in European Cretaceous environments. *Proceedings N. Acad.*
560 *Sci.* 109, 20955–20959.
- 561 Colin, J.-P., Néraudeau, D., Nel, A., Perrichot, V., 2011. Termite coprolites (Insecta: Isoptera)
562 from the Cretaceous of western France: A palaeoecological insight. *Rev.*
563 *Micropaléontol.* 54, 129–139.
- 564 Conway Morris, S., Caron, J.-B., 2012. *Pikaia gracilens* Walcott, a stem-group chordate from
565 the Middle Cambrian of British Columbia. *Biol. Rev.* 87, 480–512.
- 566 Davidson, T., 1852. A monograph of the British Cretaceous Brachiopoda – Part II(1).
567 *Palaeontograph. Soc. Monogr.* 6, 1–54.
- 568 Dejax, J., Masure, E., 2005. Analyse palynologique de l'argile lignifère à ambre de l'Albien
569 terminal d'Archingeay (Charente-Maritime, France). *C. R. Palevol* 4, 53–65.

- 570 Delmail, D., 2007. Morphologie comparée et paléocophysiologie d'une Angiosperme du
571 Cénomaniens inférieur de la carrière de Puy-Puy (Tonny-Charente, Charente-
572 Maritime) par une approche morphométrique. Université de Rennes 1, France
573 (Unpublished Master thesis, 32 pp.).
- 574 Ding, Q., Labandeira, C.C., Meng, Q., Ren, D., 2015. Insect herbivory, plant-host
575 specialization and tissue partitioning on mid-Mesozoic broadleaved conifers of
576 Northeastern China. *Palaeogeogr., Palaeoclimatol., Palaeoecol.* 440, 259–273.
- 577 Ding, Q., Labandeira, C.C., Ren, D., 2014. Biology of a leaf miner (Coleoptera) on
578 *Liaoningocladus boii* (Coniferales) from the Early Cretaceous of northeastern China
579 and the leaf-mining biology of possible insect culprits clades. *Arthropod System.*
580 *Phylog.* 72, 281–308.
- 581 Fleury, R., Polette, F., Batten, D.J., Durand, M., Moreau, J.-D., Néraudeau, D., Strullu-
582 Derrien, C., Redois, F., 2017. Palaeobotanical investigation of a Cenomanian clay
583 lens in Hucheloup Quarry, Maine-et-Loire, NW France: Taxonomic, stratigraphic
584 and palaeoenvironmental implications. *Ann. Paléontol.* 103, 235–250.
- 585 Frey, R.W., Howard, J.D., Pryor, W.A., 1978. *Ophiomorpha*: its morphologic, taxonomic, and
586 environmental significance. *Palaeogeogr., Palaeoclimatol., Palaeoecol.* 23, 199–
587 229.
- 588 Gayet, M., Belouze, A., Saad, P.A., 2003. Les Poissons fossiles. Mémoire du Temps. Désiris
589 éd., 158 pp.
- 590 Girard, V., 2010. Microcénoses des ambres médio-crétacés français. Taphonomie,
591 systématique, paléocologie et reconstitution du paléoenvironnement. *Mém. Géosci.*
592 Rennes 134, 1–334.

- 593 Girard, V., Breton, G., Brient, L., Néraudeau, D., 2009. Sheathed prokaryotic filaments, major
594 components of Mid-Cretaceous French amber microcoenoses. *J. Palaeolimnol.* 42,
595 437–447.
- 596 Girard, V., Néraudeau, D., Adl, S., Breton, G., 2011. Protist-like inclusions in amber, as
597 evidenced by Charentes amber. *Eur. J. Protistol.* 47, 59–66.
- 598 Goldring, R., Pollard, J.E., 1995. A re-evaluation of *Ophiomorpha* burrows in the Wealden
599 Group (Lower Cretaceous) of southern England. *Cretac. Res.* 16, 665–680.
- 600 Golub, V.B., Popov, Y.A., 2008. A new species of Tingidae (Insecta: Hemiptera: Heteroptera)
601 from the Lower Cretaceous of Transbaikalia. *Paleontol. J.* 42, 86–89.
- 602 Golub, V.B., Popov, Y.A., 2012. A new lace bug species of the genus *Sinaldocader*
603 (Hemiptera: Heteroptera, Tingidae) from the Turonian of southwestern Kazakhstan.
604 *Paleontol. J.* 46, 258–261.
- 605 Gomez, B., Coiffard, C., Dépré, E., Daviero-Gomez, V., Néraudeau, D., 2008. Diversity and
606 histology of plant litter bed from the Cenomanian of Archingeay-Les Nouillers
607 (southwestern France). *C. R. Palevol* 7, 135–144.
- 608 Gomez, B., Martin-Closas, C., Barale, G., Solé de Porta, N., Thévenard, F., Guignard, G.,
609 2002a. *Frenelopsis* (Coniferales: Cheirolepidiaceae) and related male organ genera
610 from the Lower Cretaceous of Spain. *Palaeontology* 45, 997–1036.
- 611 Gomez, B., Thévenard, F., Perrichot, V., Daviero-Gomez, V., Néraudeau, D., 2002b. Le
612 conifère *Glenrosa* dans l'Albien-Cénomaniens de Charentes: marqueur d'un climat à
613 saison sèche. In : Actes du Colloque Environnement et Climat du Passé: Histoire et
614 Evolution, oct. 2002, Paris, pp. 70.
- 615 Gomez, B., Daviero-Gomez, V., Perrichot, V., Thévenard, F., Coiffard, C., Philippe, M.,
616 Néraudeau, D., 2004. Assemblages floristiques de l'Albien-Cénomaniens de
617 Charente-Maritime (SO France). *Ann. Paléontol.* 90, 147–159.

- 618 Holmer, L.E., Bengtson, P., 2009. The first occurrence of a lingulid brachiopod from the
619 Cretaceous of Sergipe, Brazil, with a restudy of « *Lingula* » *bagualensis* Wickens,
620 1905, from southern Patagonia. *Paläontol. Zeit.* 83, 255–266.
- 621 Holmer, L.E., Nakrem, H.A., 2012. The lingulid brachiopod *Lingularia* from lowermost
622 Cretaceous hydrocarbon seep bodies, Sassenfjorden area, central Spitsbergen,
623 Svalbard. *Norw. J. Geol.* 92, 167–174.
- 624 Kirkland, J.I., 1996. Paleontology of the Greenhorn Cyclothem (Cretaceous: Late
625 Cenomanian to Middle Turonian) at Black Mesa, Northern Arizona. *New Mexico*
626 *Mus. Nat. Hist.* 9, 1–131.
- 627 Kon, T., Nishida, M., Sterrer, W., 2016. Hidden ancient diversification in the circumtropical
628 lancelet *Asymmetron lucayanum* complex. *Mar. Biol.* 149, 875–883.
- 629 Labandeira, C.C., Wilf, P., Johnson, K.R., Marsh, F., 2007. Guide to insects (and other)
630 damage types on compressed plant fossils. Version 3.0, Smithsonian Institution,
631 Washington, D.C.
- 632 Le Diouron, T., 2005. Les végétaux fossiles des argiles de l'Albien terminal et du
633 Cénomanién basal de la carrière de Puy-Puy (Tonny-Charente, Charente-Maritime).
634 Implications paléoenvironnementales. Université de Rennes 1, France (Unpublished
635 Master thesis, 30 pp.).
- 636 Longinelli, A., Nuti, S., 1973. Revised phosphate-water isotopic temperature scale. *Earth*
637 *Planet. Sci. Lett.* 20, 373–376.
- 638 Martill, D.M., Ibrahim, N., Brito, P.M., Baider, L., Zhou, S., Loveridge, R., Naish, D., Hing,
639 R., 2011. A new Plattenkalk Lagerstätte in the Upper Cretaceous of Gara Sbaa,
640 south-eastern Morocco. *Cretac. Res.* 32, 433–446.

- 641 Moreau, J.-D., Néraudeau, D., Gomez, B., Tafforeau, P., Dépré, É., 2014a. Plant inclusions
642 from the Cenomanian flints of Archingeay-Les Nouillers, western France. *Lethaia*
643 47, 313–322.
- 644 Moreau, J.-D., Cloetens, P., Gomez, B., Daviero-Gomez, V., Néraudeau, D., Lafford T.,
645 Tafforeau, P., 2014b. Multiscale 3D virtual dissections of 100-million-year-old
646 flowers using X-ray synchrotron micro- and nanotomography. *Microsc. Microanal.*
647 20, 305–312.
- 648 Moreau, J.-D., Néraudeau, D., Tafforeau, P., Dépré, É., 2015. Study of the histology of leafy
649 axes and male cones of *Glenrosa carentonensis* sp. nov. (Cenomanian flints of
650 Charente-Maritime, France) using synchrotron microtomography linked with
651 palaeoecology. *PloS One* 10, e0134515.
- 652 Moreau, J.-D., Gomez, B., Coiffard, C., Daviero-Gomez, V., Tafforeau, P., Néraudeau, D.,
653 2016a. *Verneda hermaphroditica* gen. et sp. nov.: A new flower head from the lower
654 Upper Cretaceous (middle Cenomanian) of south-eastern France. *Taxon* 65, 823–
655 838.
- 656 Moreau, J.-D., Gomez, B., Daviero-Gomez, V., Néraudeau, D., Tafforeau, P., 2016b.
657 Inflorescences of *Mauldinia* sp. (Lauraceae) and associated fruits from the
658 Cenomanian of Languedoc Roussillon, France. *Cretac. Res.* 59, 19–29.
- 659 Moreau, P., 1993a. *La transgression cénomanienne sur la marge septentrionale du bassin de*
660 *l'Aquitaine (Charentes), flanc Nord du synclinal de Saintes et Angoumois. Modalités*
661 *d'une invasion marine, aspects stratigraphiques, sédimentologiques et*
662 *paléogéographiques. I. La sédimentation terrigène et glauconieuse. Caractérisation*
663 *et distribution des éléments.* Université de Poitiers, France (Thèse d'Etat, 672 pp, on
664 deposit Soc. Géol. France).

- 665 Moreau, P., 1993b. *La transgression cénomaniennne sur la marge septentrionale du bassin de*
666 *l'Aquitaine (Charentes), flanc Nord du synclinal de Saintes et Angoumois. Modalités*
667 *d'une invasion marine, aspects stratigraphiques, sédimentologiques et*
668 *paléogéographiques. II. Paléontologie stratigraphique et biochronologique.*
669 *Paléogéographie et structure.* France (Thèse d'Etat, 505 pp, on deposit Soc. Géol.
670 France).
- 671 Nel, A., Fleck, G., Garcia, G., Gomez, B., Ferchaud, P., Valentin, X., 2015. New dragonflies
672 from the lower Cenomanian of France enlighten the timing of the odonatan turnover
673 at the Early–Late Cretaceous boundary. *Cretac. Res.* 52A, 108–117.
- 674 Nel, A., Néraudeau, D., Perrichot, V., Girard, V., Gomez, B., 2008. A new dragonfly family
675 in the Upper Cretaceous of France (Insecta: Odonata: Aeshnoptera). *Acta Paleontol.*
676 *Pol.* 53, 165–168.
- 677 Néraudeau, D., Moreau, P., 1989. Paléoécologie et paléogéographie des faunes d'échinides du
678 Cénomanienn nord-aquitain (Charente-Maritime, France). *Geobios* 22, 293–324.
- 679 Néraudeau, D., Mazan, P., Vullo, R., 2013a. Fossiles de la Préhistoire charentaise. *Le Croît*
680 *Vif, Saintes*, 287 pp.
- 681 Néraudeau, D., Thierry, J., Moreau, P., 1997. Variation in echinoid biodiversity during the
682 Cenomanian–early Turonian transgressive episode in Charentes (France). *Bull. Soc.*
683 *Géol. France* 168, 51–61.
- 684 Néraudeau, D., Allain, R., Perrichot, V., Videt, B., De Lapparent De Broin, F., Guillocheau,
685 F., Philippe, M., Rage, J.-C., Vullo, R., 2003. Découverte d'un dépôt paralique à bois
686 fossiles, ambre insectifère et restes d'Iguanodontidae (Dinosauria, Ornithopoda) dans
687 le Cénomanienn inférieur de Fouras (Charente-Maritime, Sud-Ouest de la France). *C.*
688 *R. Palevol* 2, 221–230.

- 689 Néraudeau, D., Perrichot, V., Dejax, J., Masure, E., Nel, A., Philippe, M., Moreau, P.,
690 Guillocheau, F., Guyot, T., 2002. Un nouveau gisement à ambre insectifère et à
691 végétaux (Albien terminal probable): Archingeay (Charente-Maritime, France),
692 *Geobios* 35, 233–240.
- 693 Néraudeau, D., Perrichot, V., Colin, J.-P., Girard, V., Gomez, B., Guillocheau, F., Masure, E.,
694 Peyrot, D., Tostain, F., Videt, B., Vullo, R., 2008. A new amber deposit from the
695 Cretaceous (uppermost Albian-lowermost Cenomanian) of SW France. *Cretac. Res.*
696 29, 925–929.
- 697 Néraudeau, D., Redois, F., Ballèvre, M., Duplessis, B., Girard, V., Gomez, B., Daviero-
698 Gomez, V., Mellier, B., Perrichot, V., 2013b. L'ambre cénomanien d'Anjou:
699 stratigraphie et paléontologie des carrières du Brouillard et de Hucheloup (Ecouflant,
700 Maine-et-Loire). *Ann. Paléontol.* 99, 361–374.
- 701 Néraudeau, D., Vullo, R., Gomez B., Perrichot, V., Videt, B., 2005. Stratigraphie et
702 paléontologie (plantes, vertébrés) de la série paralique Albien terminal-Cénomanien
703 basal de Tonnay-Charente (Charente-Maritime, France). *C. R. Palevol* 4, 79–93.
- 704 Nguyen Tu, T.T., Bocherens, H., Mariotti, A., Baudin, F., Pons, D., Broutin, J., Derenne, S.,
705 Largeau, C., 1999. Ecological distribution of Cenomanian terrestrial plants based on
706 $^{13}\text{C}/^{12}\text{C}$ ratios. *Palaeogeogr., Palaeoclimatol., Palaeoecol.* 145, 79–93.
- 707 Oelofsen, B.W., Loock, J.C., 1981. A fossil cephalocordate from the Early Permian Whitehill
708 Formation of South Africa. *S. Afr. J. Sci.* 77, 178–180.
- 709 Parry, L.A., Tanner, A., Vinther, J., 2015. The origins of annelids. *Palaeontology* 57, 1091–
710 1103.
- 711 Perrichot, V., 2003. Environnements paraliques à ambre et à végétaux du Crétacé Nord-
712 Aquitain (Charentes, Sud-Ouest de la France). Université de Rennes I, France
713 (Unpublished PhD thesis, 295 pp.).

- 714 Perrichot, V., 2005. Environnements paraliques à ambre et à végétaux du Crétacé Nord-
715 Aquitain (Charentes, Sud-Ouest de la France). *Mém. Géosci. Rennes* 118, 1–295.
- 716 Perrichot, V., Nel, A., Guilbert, E., Néraudeau, D., 2006. Fossil Tingioidea (Heteroptera:
717 Cimicomorpha) from French Cretaceous amber, including Tingidae and a new
718 family, Ebboidea. *Zootaxa* 1203, 57–68.
- 719 Perrichot, V., Néraudeau, D., Tafforeau, P., 2010. Charentese amber. In: Penney, D. (Ed.),
720 Biodiversity of fossils in amber from the major world deposits. Siri Scientific Press,
721 Manchester, pp. 192–207.
- 722 Perrichot, V., Marion, L., Néraudeau, D., Vullo, R., Tafforeau, P., 2008. The early evolution
723 of feathers: fossil evidence from Cretaceous amber of France. *Proceedings Roy. Soc.*
724 *London B* 275, 1197–1202.
- 725 Peyer, K., Charbonnier, S., Allain, R., Läng, E., Vacant, R., 2014. A new look at the Late
726 Jurassic Canjuers conservation Lagerstätte (Tithonian, Var, France). *C. R. Palevol*
727 13, 403–420.
- 728 Peyrot, D., 2004. Caractérisation du contenu palynologique d'un gisement à ambre dans
729 l'Albien-Cénomaniens de Charente-Maritime (Sud-Ouest de la France). Université de
730 Rennes 1, France (Unpublished Master thesis, 39 pp.).
- 731 Peyrot, D., Jolly, D., Barron, E., 2005. Apport de données palynologiques à la reconstruction
732 paléoenvironnementale de l'Albo-Cénomaniens des Charentes (Sud-Ouest de la
733 France). *C. R. Palevol* 4, 151–165.
- 734 Peyrot, D., Barron, E., Polette, F., Batten, D.J., Néraudeau, D., 2019. Early Cenomanian
735 palynofloras and inferred resiniferous forests and vegetation types in Charentes
736 (southwestern France). *Cretac. Res.* 34, 168–189.
- 737 Philippe, M., Gomez, B., Girard, V., Coiffard, C., Daviero-Gomez, V., Thévenard, F., Billon-
738 Bruyat, J.-P., Guiomar, M., Latil, J.-L., Le Loeuff, J., Néraudeau, D., Olivero, D.,

- 739 Schlögl, J., 2008. Woody or not woody ? Evidence for early angiosperm habit from
740 the Early Cretaceous fossil wood record of Europe. *Palaeoworld* 17, 142–152.
- 741 Poinar, G., Jr., Buckley, R., 2006. Nematode (Nematoda: Mermithidae) and hairworm
742 (Nematomorpha: Chordodidae) parasites in Early Cretaceous amber. *J. Invertebr.*
743 *Pathol.* 93, 36–41.
- 744 Poinar, G. Jr, Acra, A., Acra, F., 1994. Earliest fossil nematode (Mermithidae) in Cretaceous
745 Lebanese amber. *Fundament. Applied Nematol.* 17, 475–477.
- 746 Rogers, R.R., Krause, D.W., Kast, S.C., Marshall, M.S., Rahantarisoa, L., Robins, C.R.,
747 Sertich, J.J.W., 2013. A new, richly fossiliferous member comprised of tidal deposits
748 in the Upper Cretaceous Maevarano Formation, northwestern Madagascar. *Cretac.*
749 *Res.* 44, 12–29.
- 750 Stephenson, L.W., 1952. Larger invertebrate fossils of the Woodbine formation (Cenomanian)
751 of Texas. *U. S. Geol. Surv. Prof. Pap.* 242, 1–211.
- 752 Tafforeau, P., Boistel, R., Boller, E. Bravin, A., Brunet, M., Chaimanee, Y., Cloetens, P.,
753 Feist, M., Hoszowska, J., Jaeger, J.-J., Kay, R.F., Lazzari, V., Marivaux, L., Nel, A.,
754 Nemoz, C., Thibault, X., Vignaud, P., Zabler, S., 2006. Applications of X-ray
755 synchrotron microtomography for non-destructive 3D studies of paleontological
756 specimens. *Appl. Phys. A Mater. Sci. Process.* 83, 195–202.
- 757 Valentin, X., Gomez, B., Daviero-Gomez, V., Charbonnier, S., Ferchaud, P., Kirejtshuk A.,
758 Licht, A., Néraudeau, D., Vullo, R., Garcia, G., 2014. Plant-dominated assemblage
759 and invertebrates from the Lower Cenomanian of Jaunay-Clan, south-western
760 France. *C. R. Palevol* 13, 443–454.
- 761 Vullo, R., Néraudeau, D., 2008. Cenomanian vertebrate assemblages from southwestern
762 France: a new insight into the European mid-Cretaceous continental fauna. *Cretac.*
763 *Res.* 29, 930–935.

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

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

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

773

774

775 Figure captions:

776

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

780

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

787

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

795
796 **Fig. 4.** Examples of plant fossils from the Puy-Puy Lagerstätte (Tonny-Charente, Charente-
797 Maritime, SW France). A, clay slab with conifer accumulation (*Geinitzia* sp.), IGR.90-061. B,
798 clay slab with angiosperm (Type S) accumulation, IGR.90-062. C, opening of the clay
799 lamination showing the imprint of an angiosperm leaf (Type R), IGR.90-063, on two adjacent
800 clay laminae (C1) and close-up view of the leaf illustrated on the previous picture (C2). D,
801 leaf of the angiosperm *Eucalyptolaurus depreii* Coiffard et al., 2009, IGR.90-064 (D1) and
802 close-up view of the leaf illustrated on the previous picture, showing the venation (D2, D3).
803 Scale bars: 10 mm (except C1: 20 mm).

804
805 **Fig. 5.** Flower fossils from the Puy-Puy Lagerstätte (Tonny-Charente, Charente-Maritime,
806 SW France). A, inflorescence, PUY-0065, displaying a peduncle bearing two pedicellate
807 flowers in the distal part, and a third flower, attached slightly below the two flowers,
808 suggested by an oval scar (A1) and interpretative drawing (A2). B, putative actinomorphic
809 isolated flower, IGR.90-066 (B1) and interpretative drawing (B2). C-D, putative simple
810 infructescences; first specimen IGR.90-067 (C), and second specimen IGR.90-068 (D1) with
811 a close-up of a fruit (D2) and interpretative drawing (D3). Abbreviations: ca., carpel; fr, fruit;

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

814

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

821

822 **Fig. 7.** Crustacean and “worm” fossils from the Puy-Puy Lagerstätte (Tonny-Charente,
823 Charente-Maritime, SW France). A, crustacean burrow corresponding to a dense,
824 subcylindrical, arrangement of crushed pellets (*Ophiomorpha*), IGR.90-074. B, mecochirid
825 crustacean (*Mecochirus* sp.), IGR.90-073. C, indeterminate worm, IGR.90-075. Scale bars:
826 10 mm.

827

828 **Fig. 8.** Insect fossils from the Puy-Puy Lagerstätte (Tonny-Charente, Charente-Maritime,
829 SW France). A, microtomographic images of the lace bug *Ebboa areolata* Perrichot et al.,
830 2006 (Heteroptera) from the late Albian amber, IGR.PUY-4.1, in dorsal (A1), ventral (A2),
831 left lateral (A3) and right lateral (A4) views. B-C, cockroach wing imprints (Dictyoptera,
832 stem group Blattodea), IGR.90-076 (B) and IGR.90-077 (C). D, net-winged imprint
833 (Neuroptera), IGR.90-091. E, sand sheath of a caddisfly larva (Trichoptera), IGR.90-078.
834 Scale bars: 10 mm.

835

836 **Fig. 9.** Plant-insect interactions from the Puy-Puy Lagerstätte (Tonny-Charente, Charente-
837 Maritime, SW France), represented by various damage types (DT). A, undetermined
838 angiosperm leaf (Type R) (IGR.90-079) with circular, thick galls with a central region
839 separated from the rim by a less thickened area, occurring throughout the leaf (DT163) (A1),
840 with enlargement of one of the galled areas (A2). B, serial of cusped margin excisions (black
841 arrows) (DT143) on an undetermined angiosperm leaf (IGR.90-080). C–E, examples of
842 surface feeding; C, Abrasion of surface tissue (DT30) on an undetermined woody angiosperm
843 leaf (IGR.90-081); D, removal of surface tissue on *Eucalyptolaurus depreii* Coiffard et al.,
844 2009 (DT30) (IGR.90-082); E, removal of surface tissue with weak reaction rim (DT29) on
845 an undetermined angiosperm leaf (IGR.90-083). F, external foliage feeding (DT2, 12, 14) on
846 an undetermined angiosperm leaf (IGR.90-084). G–K, damage types on *Eucalyptolaurus*
847 *depreii* Coiffard et al., 2009. G, complete leaf (IGR.90-087) showing high frequency of
848 consumption (DT12, 14); H, polylobate galling structures attached to the 1° vein with a thick
849 outer rim (DT120) (IGR.90-088); I, serpentine mine, frass packed in sections (black arrow);
850 white arrow indicates the position of the enlarged terminal chamber (DT44) and removal of
851 surface tissue with a distinct reaction rim (DT31) (IGR.90-089); J, undulatory frass packed
852 leaf mine with smooth margins (DT45); black arrow indicates oviposition site; white arrow
853 points to the blotch-like mine terminus (IGR.90-086); K, cluster of overlapping, subparallel-
854 orientated eggs (DT67) (IGR.90-090). L, distinctive, full-depth leaf mines, with intestiniform
855 frass trails (DT280) occurring on the entire-margined, parallel-veined coniferous foliage
856 *Dammarophyllum* sp. (IGR.90-085). Scale bars: A1, F–I, L: 10 mm; A2, B–D, K–K: 5 mm.

857
858 **Fig. 10.** Shark egg capsule (*Palaeoxyris* sp.) from the Puy-Puy Lagerstätte (Tonny-Charente,
859 Charente-Maritime, SW France), IGR.90-092. Fragmentary specimen consisting of the
860 pedicle and the posterior part of the body. Scale bar: 10 mm.

861

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

866

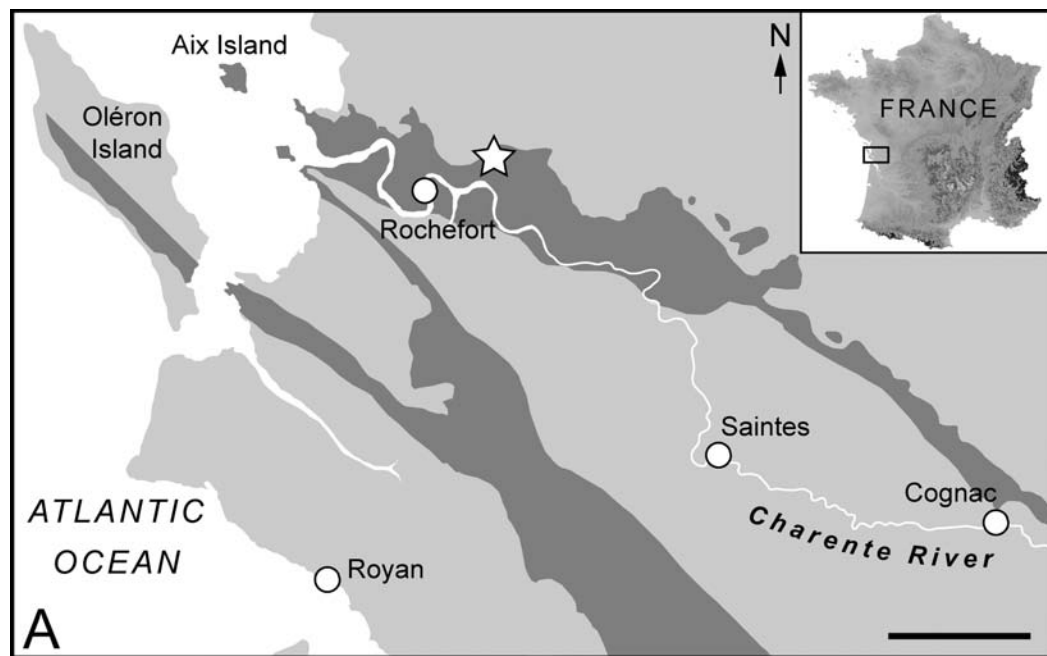
ACCEPTED MANUSCRIPT

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. <i>Osmunda cretacea</i> Samylin, 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)	<i>Weichselia reticulata</i> (Stokes and Webb) Fontaine in Ward emend. Alvin, 1971	Le Diouron, 2005 (Pl. 1.7)	PUY-0034 + Unnumbered specimens
EQUISETALES (LEAVES)	<i>Equisetites</i> sp.	This study	IGR.90-93
CONIFERS			
(LEAVES)	<i>Dammarophyllum striatum</i> 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)	<i>Dammarites albens</i> Presl in Sternberg, 1838	Unpublished data	Unnumbered specimens
(LEAFY AXES)	<i>Frenelopsis alata</i> (Feistmantel, 1881) E. Knobloch, 1971	Le Diouron, 2005	Numerous unnumbered specimens
(LEAFY AXES)	<i>Geinitzia reichenbachii</i> (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)	<i>Glenrosa carentonensis</i> Moreau et al., 2015	Unpublished data	Numerous unnumbered specimens
(WOOD)	<i>Agathoxylon gardoniense</i> (Crié, 1890) Philippe	Perrichot,	Numerous

	in Néraudeau et al., 2002	2005 Philippe et al., 2008	unnumbered specimens
(WOOD)	<i>Protopodocarpoxylon</i> sp.	Perrichot, 2005 Philippe et al., 2008	Numerous unnumbered specimens
GINKGOPHYTES (LEAVES)	<i>Nehvizdya andegavense</i> (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)	<i>Zamites</i> 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)	<i>Classostrobus</i> 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. <i>Grevillea dvoraki</i> 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)	<i>Eucalyptolaurus depreii</i> Coiffard et al., 2009 (previously referred to <i>Myrtophyllum angustum</i> (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)	<i>Myrtophyllum geinitzii</i> Heer, 1874	Coiffard et al., 2006	Unnumbered specimens
(LEAVES)	cf. <i>Debeya coriacea</i> (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)	? <i>Sassafras</i> sp.	Le Diouron, 2005 Delmail, 2007	Unnumbered specimens
(LEAVES)	<i>Dicotylophyllum meeki</i> Heer in Meek and Hayden, 1858	Coiffard et al., 2006	Unnumbered specimens
(LEAVES)	<i>Araliphyllum daphnophyllum</i> Velen./Vel. : Velen., 1889, Knobloch 1969, 1971 = <i>Aralia daphnophyllum</i> Velen., 1882	Coiffard et al., 2006	Unnumbered specimens
(LEAVES)	<i>Pseudoasterophyllites</i> cf. <i>cretaceus</i> (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

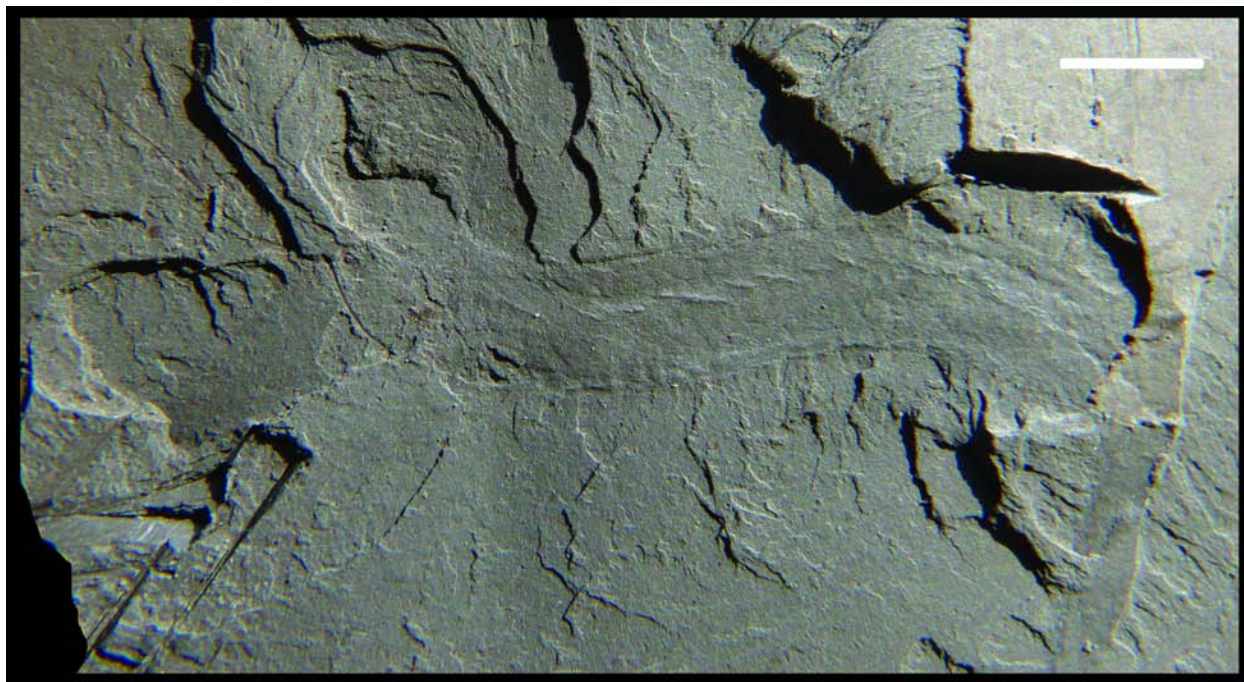
		Néraudeau et al., 2005 (Fig. 4.12) This study	
?NEMATODA			
	?Nematoda indet.	This study	IGR.90-075
LOPHOPHORA			
BRACHIOPODA	aff. <i>Lingula</i> sp.	This study	IGR.90-069 IGR.90-070 IGR.90-094 IGR.90-095
ARTHROPODA			
CRUSTACEA	<i>Mecochirus</i> sp.	Breton et al., 2015 This study	LM2010.1.77 LM2010.1.79 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 : <i>Ebboa areolata</i> Perrichot et al., 2006	This study	IGR.PUY-4.1
	Neuroptera indet.	This study	IGR.90-091
	Odonata Enigmaeshnidae : <i>Enigmaeshna deprei</i> 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
ICHTHOFOSSILS			
BURROWS	Crustacean burrows : <i>Ophiomorpha</i> isp.	This study	IGR.90-074
COPROLITES	Crustacean coprolites	This study	IGR.90-071 IGR.90-072
	Termite coprolites : <i>Microcarpolithes hexagonalis</i> Vangerow, 1954	Colin et al., 2011	Numerous unnumbered specimens
EGGS	Shark egg capsules: <i>Palaeoxyris</i> 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



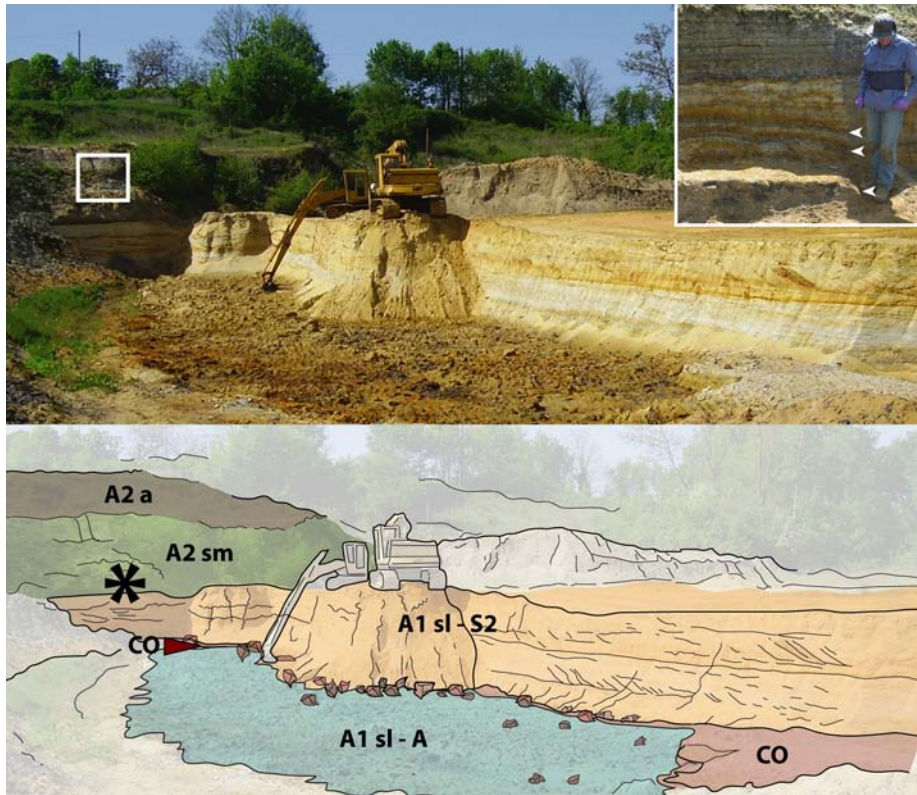


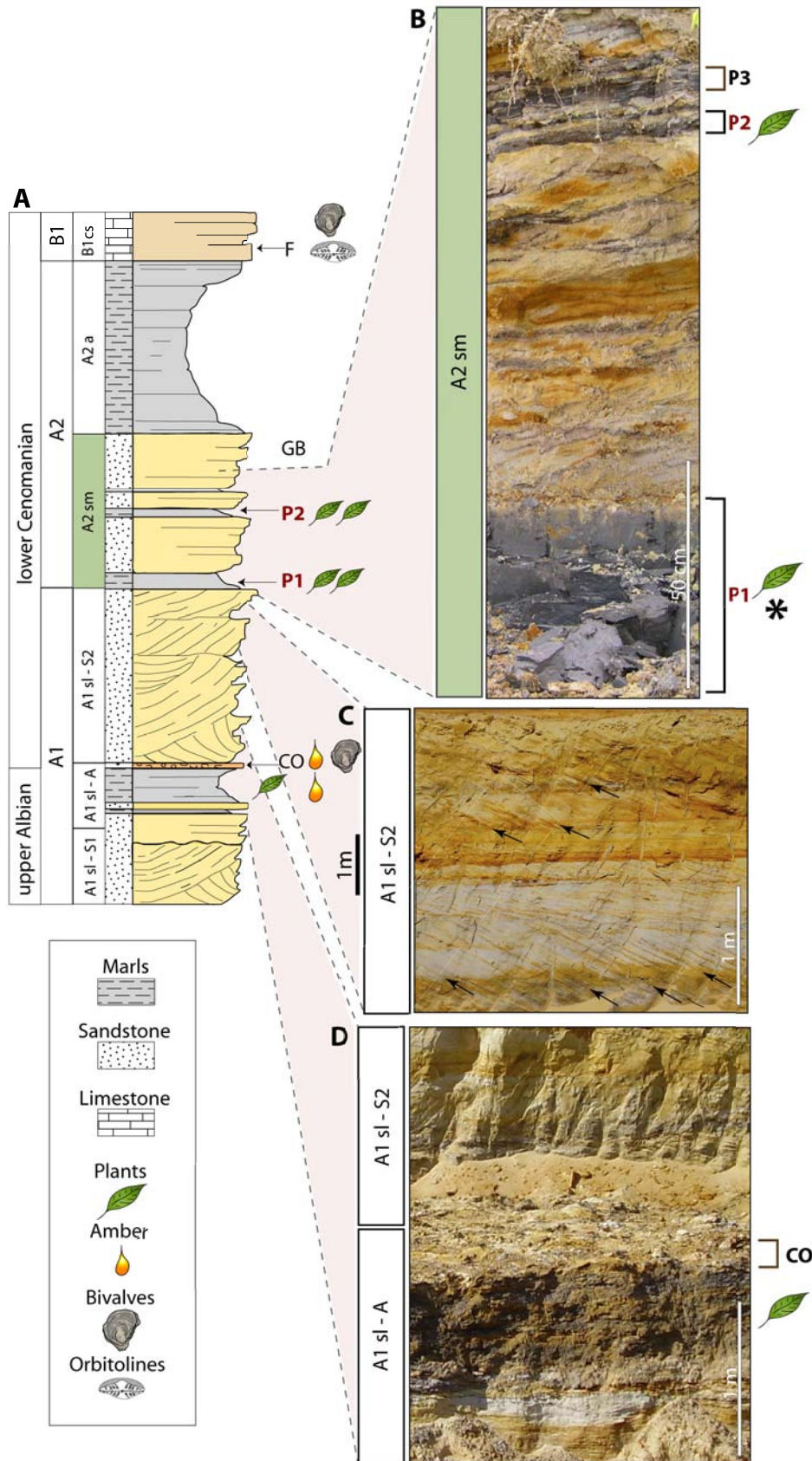
ACCEPTED MANUSCRIPT

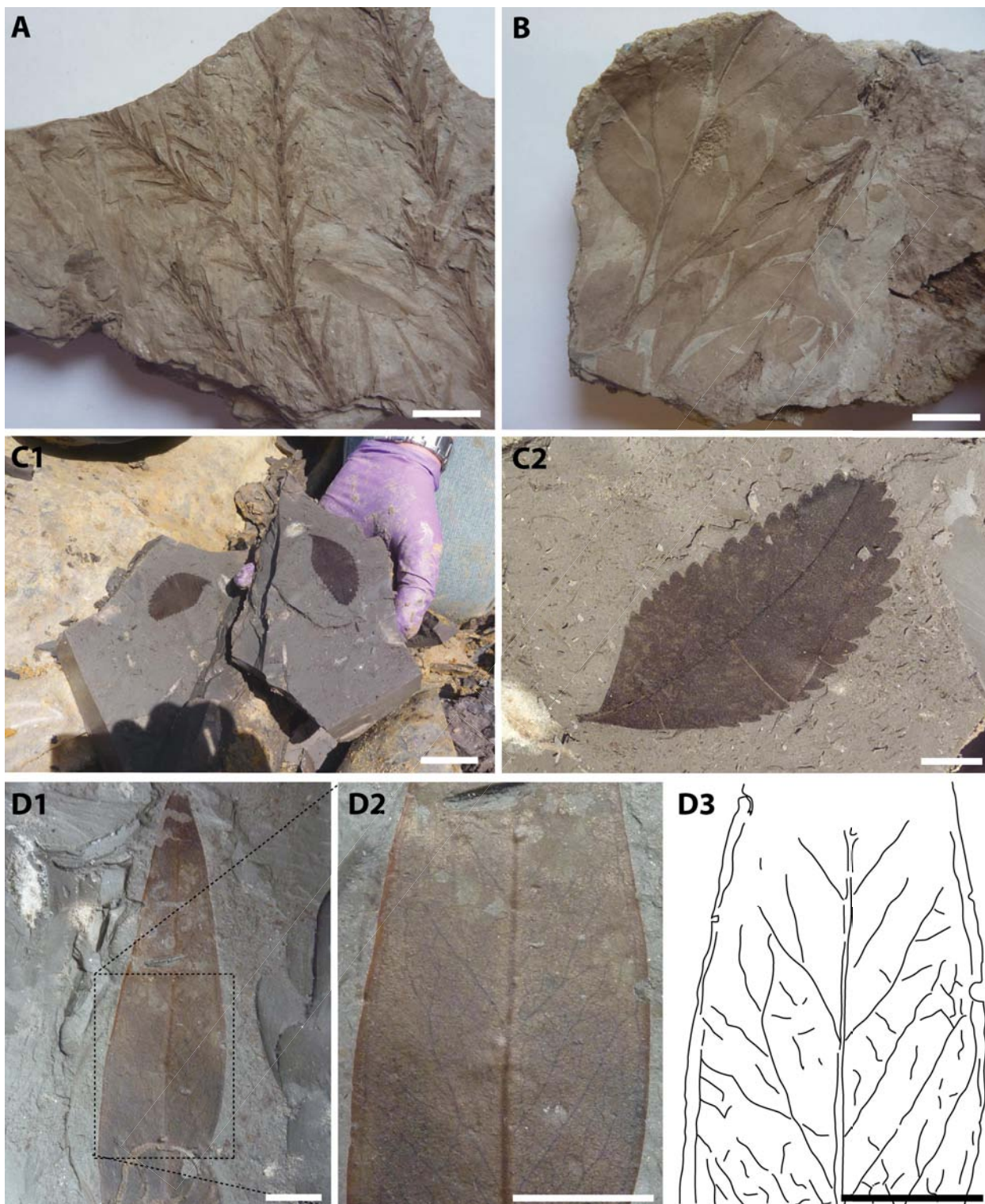
ACCEPTED MANUSCRIPT

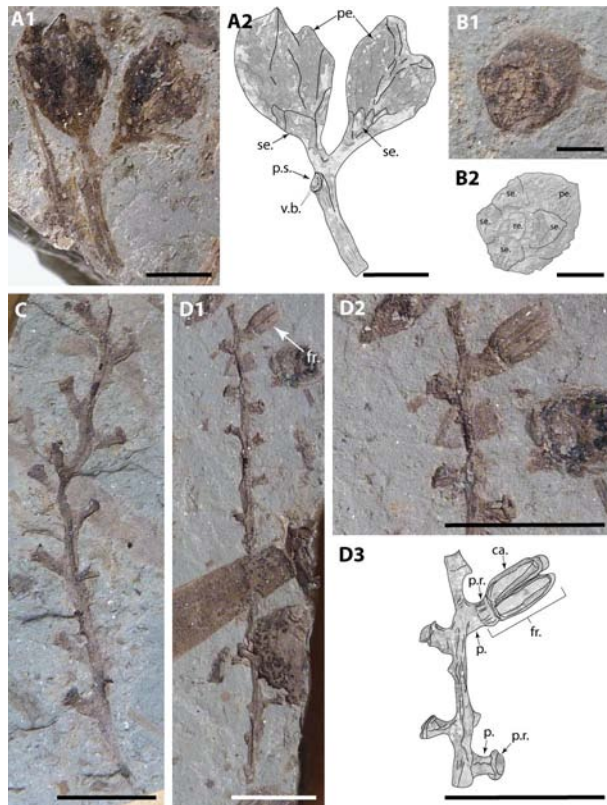


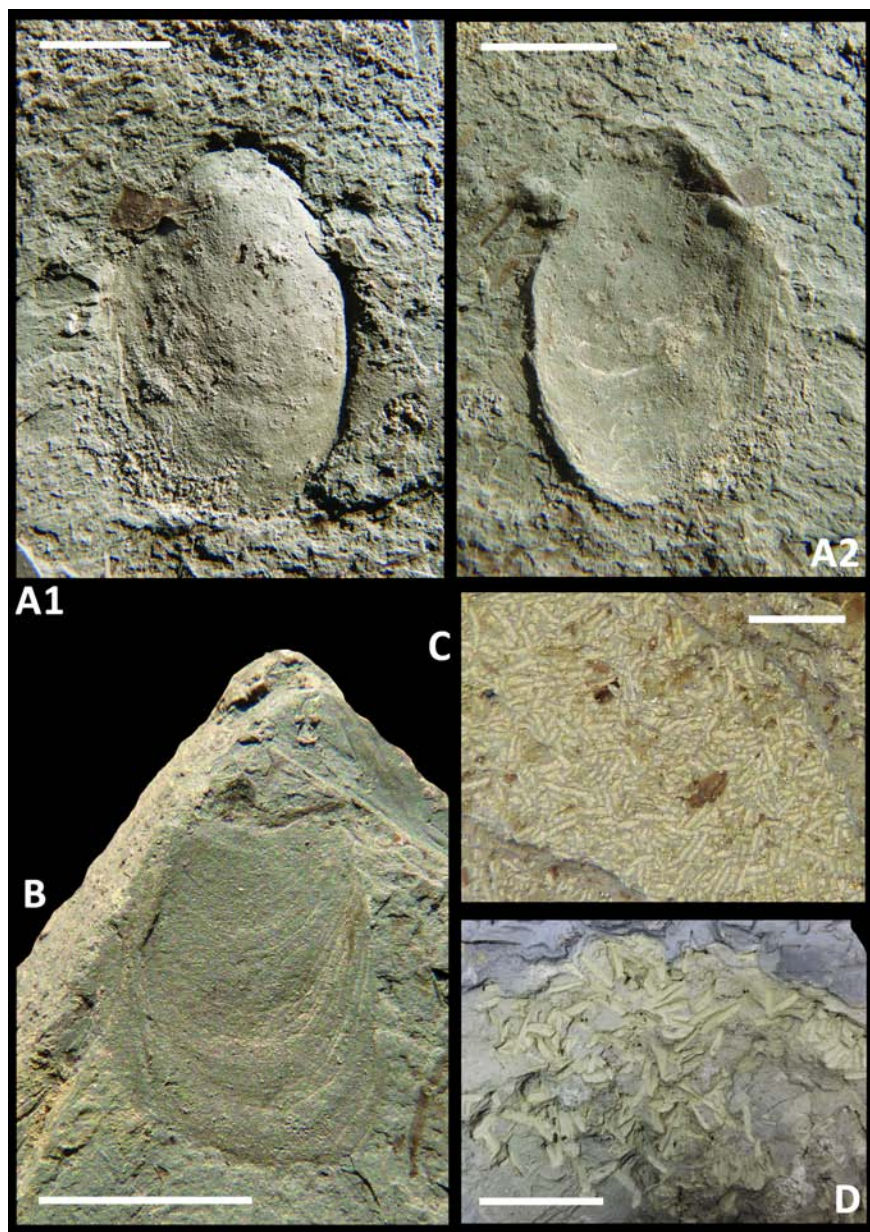
ACCEPTED MANUSCRIPT

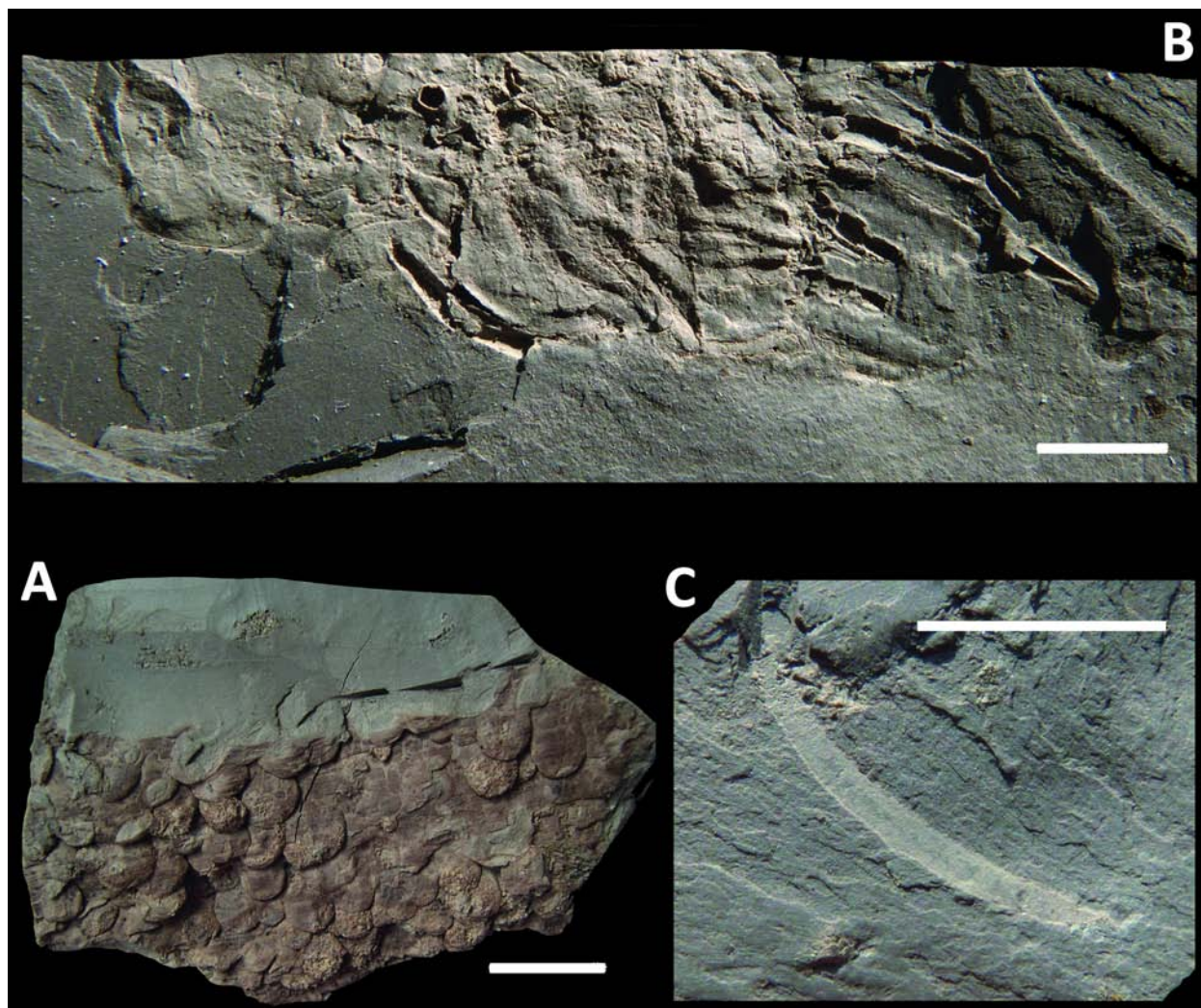




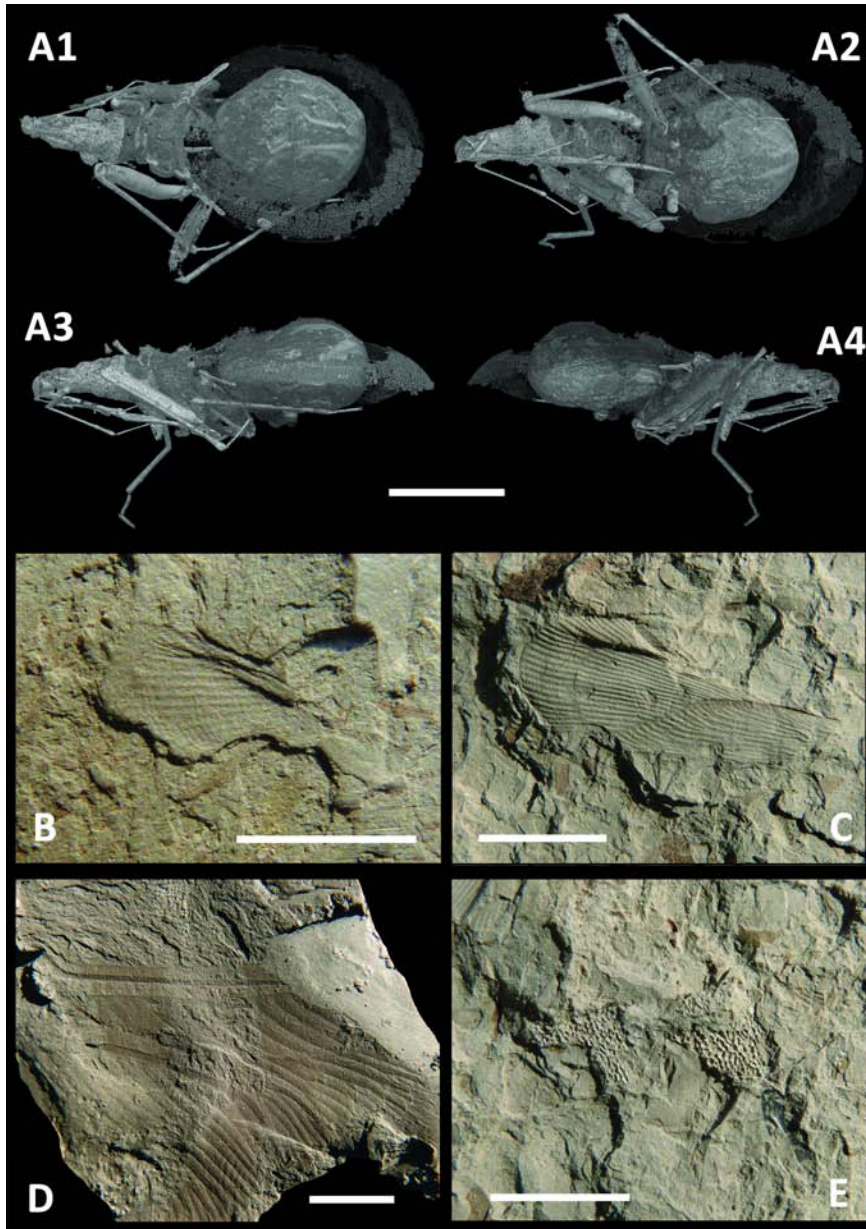








ACCEPTED MANUSCRIPT





- 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.

ACCEPTED MANUSCRIPT