



The Hauterivian–Barremian lignitic bone bed of Angeac (Charente, south-west France): stratigraphical, palaeobiological and palaeogeographical implications

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ARTICLE INFO

Article history:

Received 26 September 2011

Accepted in revised form 19 January 2012

Available online 12 April 2012

Keywords:

Lignite

Dinosaur

Palaeobotany

Palynology

Early Cretaceous

Charentes

France

ABSTRACT

This paper provides the sedimentological, palaeontological and biostratigraphical characteristics of a newly discovered lignite-bearing sedimentary succession in western France. The lignitic bed, which is reminiscent of some Wealden facies in southern England, is located in Angeac in the Charentes region. The plant remains occur as three-dimensionally preserved mesofossils (cuticles, charred ferns and seeds, cones and twigs) and larger pieces of wood. The deposits contain variable amounts of such material and at one horizon in particular, an outstanding accumulation of dinosaur teeth and bones. Among the vertebrate remains are the longest sauropod femur (ca. 220 cm) yet found and bones representing an ornithomimosaur herd of at least eight individuals. The palynomorph content of the clay associated with the bones and lignitic material indicates a Hauterivian–Barremian age. The abundance in the fossil assemblage of freshwater unionoid bivalves, some preserved in life position, the presence of freshwater algae, and the scarcity of brackish or marine species indicate that the depositional environment was a swamp only very occasionally connected to the sea. The forest bordering the swamp was dominated by cheirolepidiaceae trees co-occurring with a diverse assemblage of ferns.

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1. Introduction

Lignitic facies are relatively common in the lower and mid Cretaceous deposits of the Charentes region (which includes the Charente and Charente-Maritime departments) in south-western France (Fig. 1). Fleuriau de Bellevue (1817) was the first to note and describe these deposits, taking as a reference the lower Cenomanian lignites of Aix Island (Fig. 1) in the Charente-Maritime

department. He drew the first stratigraphical section for the island, showing the Cretaceous lignites and their outcrop on the tidal flats, which he named the “forêt fossile” (“fossil forest”; Néraudeau et al., 2009). Brongniart (1823) used a short paper by Fleuriau de Bellevue (1823) on which to base his chapter “Lignite” in the “Dictionnaire des Sciences naturelles”. He recognized the so-called “Lignite de l'île d'Aix” (“Aix Island Lignite”) Formation in other parts of the Charentes region, such as in the Angoulême area, and attributed these lignites to the “Wealden” (Brongniart, 1829, p. 217). Then, Coquand (1857b, 1858a, p. 5, 1858b) defined his “Gardonian” strata in south-eastern France (Gard department) as a mid Cretaceous lignitic facies and considered the Aix Island Lignite Formation to be

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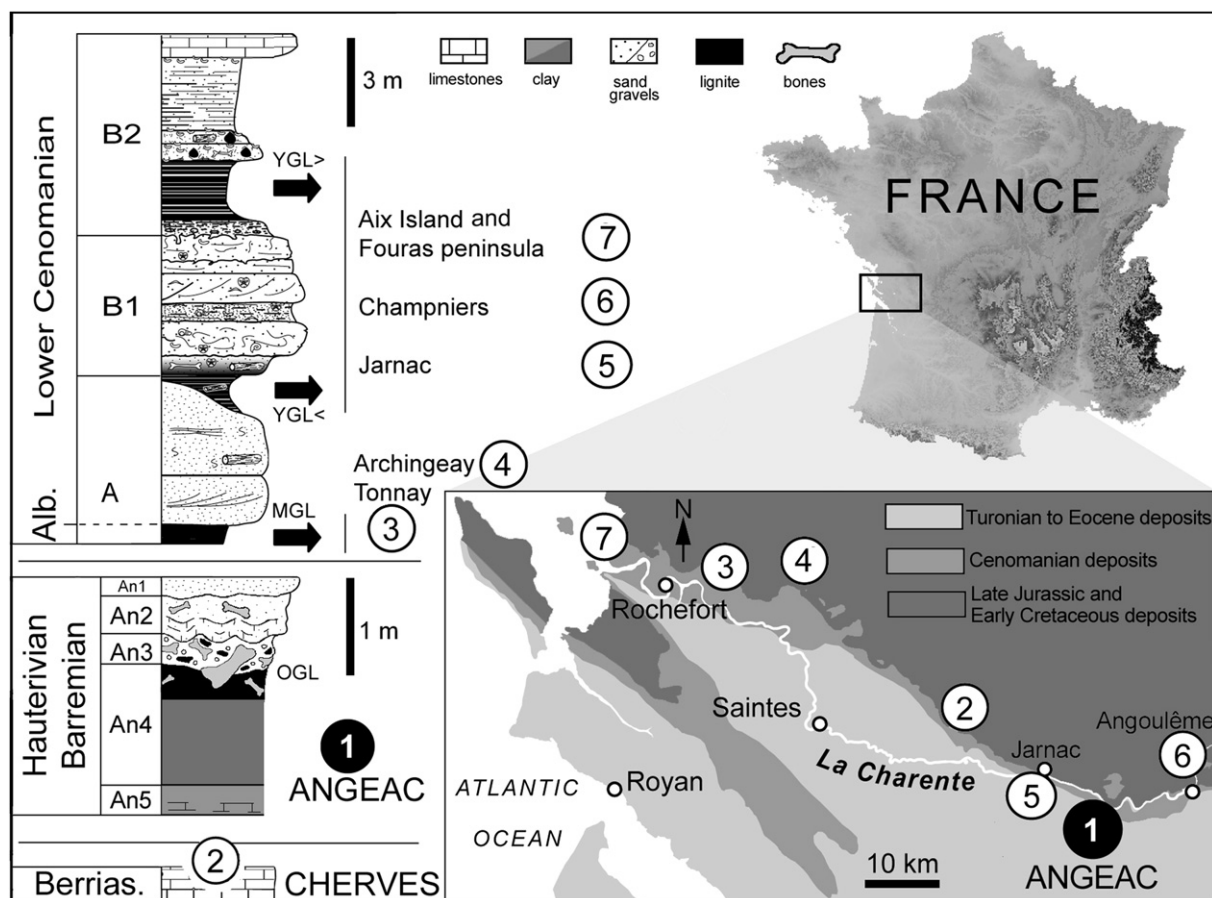


Fig. 1. Geographical and geological locations of the lignitic series encountered in the Charentes region of western France. Old “Gardonian” Lignites (OGL) of Hauterivian–Berremian age, from Angeac-Charente (1); Mid “Gardonian” Lignites (MGL) of latest Albian age, from Tonnay-Charente (3) and Archingeay (4); Young “Gardonian” Lignites (YGL) of Early Cenomanian age from Jarnac (5), Champniers (6), and Aix Island and Fouras Peninsula (7). In the Charentes region, the oldest Early Cretaceous deposits (non-lignitic), which are of Berriasian age, are known from Cherves-de-Cognac (2). These numbers (1–7) correspond to both the location of an outcrop on the map and its stratigraphical position in the regional Cretaceous series. The Angeac bone bed corresponds to the fossiliferous series from the top of unit An4 to the top of unit An2. The Albian–Cenomanian sedimentological units A, B1 and B2 and their geographical variations have been defined by Néraudeau et al. (2002, 2003, 2005). In the existing regional geological maps, the distinction between the Tithonian, Berriasian, Hauterivian–Berremian and Albian outcrops has not been recognized and differentiated from the “Purbeckian” and the non-marine earliest Cenomanian series.

its extension in the south-west. According to Coquand, the “Gardonian” facies was a lignitic facies typical of the mid Cretaceous (Coquand, 1857b). During the last ten years, several localities in the Charentes region have been identified where “Gardonian” lignites are exposed. Two stratigraphical occurrences in the Charente-Maritime department have been distinguished based on palynological and micropalaeontological data. The older of the two has been dated as latest Albian (Néraudeau et al., 2002; Dejax and Masure, 2005) while the younger is mid-Early Cenomanian in age (Néraudeau et al., 2003).

More recently, during the winter of 2009–2010, older lignitic deposits were discovered in the Charente department near Angoulême, at Angeac-Charente (Fig. 1), thanks to the vigilance of personnel of the Audouin Company, which owns and operates a quarry there. According to Coquand (1858a, b), all of the lignitic deposits in the Angeac area are typical of his “Gardonian” stage, contemporaneous with those of Aix Island and, therefore, linked to the Early Cenomanian transgression in this region (Moreau, 1993). Furthermore, he clearly distinguished (Coquand, 1858b, p. 423) the “Argile bleuâtre lignitifère et pyritifère du Gardonien” (blue lignitic and pyritous Gardonian clay) from the underlying “Argile bleuâtre ou grisâtre fouettée de rouge du Purbeckien” (blue to grey and sometimes reddish Purbeckian clay).

This paper provides the sedimentological, palaeontological and biostratigraphical characteristics of the Angeac lignitic deposits. It also

establishes their mid-Early Cretaceous age, older than the previously known “Gardonian” lignites and younger than the gypsiferous “Purbeckian” (Berriasian) clay, and limestones and evaporites of the geographically close Cherves-de-Cognac region (Fig. 1).

Notes. One institutional abbreviation is applied herein, namely ANG for the Angeac-Charente Collection, Musée d’Angoulême, Angoulême, France. Publications relating to the names of taxa are not listed in the references unless cited in another context.

2. Geological setting and sedimentological framework

The newly discovered lignitic deposits underlie Quaternary calcareous alluvial gravels laid down by the Charente River. These are exploited by the Audouin Company at Angeac-Charente, between Cognac and Angoulême (Fig. 1). For a dozen years, the alluvium has been yielding siliceous artefacts and mammoth remains. However, in 2008, a giant vertebra (30 cm in diameter) was recognized as being too large to come from a mammoth skeleton. It was passed on to personnel at the Angoulême Museum. They then contacted palaeontologists who quickly identified it as belonging to a sauropod. At that time, the geological provenance of the vertebra, which had been reworked into Quaternary alluvium, was unknown to the palaeontologists concerned.

In February 2010, some new sauropod bones were discovered in the Quaternary deposits: six vertebrae, three metapodials and a partial femur. Consequently, in collaboration with the Audoin Company, the decision was taken to initiate two excavations in the alluvium using a digger to estimate the thickness of the Quaternary deposits and, if possible, to reach the Mesozoic substratum. The operation was successful, despite flooding of the floor of the quarry by more than 1 m of water, and in the first excavation, ANG1-02-2010, more reworked sauropod bones (a broken ulna and a femur, and large bone pebbles) were recovered. Mesozoic yellow and grey limestones, and clay rich in dinosaur bones and plant remains were also exposed. These fossiliferous strata served to demonstrate that “Gardonian” lignites containing dinosaur remains are present at Angeac under the Quaternary alluvial deposits with reworked bones.

This finding amounted to the “rediscovery” of the “Gardonian” lignites of Coquand, which he had observed a few kilometres from Angeac at Saint-Brice, Bourg-Charente and Châteauneuf (Coquand, 1857a; Bourgueil and Moreau, 1967). He had noted the presence of “une vertèbre d’un reptile de grande taille” (a vertebra of a reptile of large size) in these deposits (Coquand, 1857a, p. 65), but the precise stratigraphical occurrence and age of both the lignites and bone remained unknown until now.

Subsequent widening by manual excavation of the first Angeac exposure created by the mechanical digger and removal of the water by pumping made it possible to determine the stratigraphy of his “Gardonian” deposits for the first time. This is as follows from the top downwards: sedimentological units An1–An5 (Fig. 1).

An1 (0.10–0.20 m, laterally variable in thickness and sometimes missing). Fine white to greyish sand rich in fish teeth and scales; the sand fills hollows in the eroded surface of the underlying bed and is more or less eroded at its top by waters of the Charente River and its bedload; rare oxidized bones occur at this level, but they comprise bone pebbles and the tops of bones, the lower parts of which are preserved in underlying units. Fig. 2. Diffractograms of the clay fraction (<2 µm) of the Hauterivian–Barremian level An1 from Angeac, on air-dried (top curve) and glycolated (mid height curve) orientated preparations, and then heated at 550°C (bottom curve): Sm, smectite; I, illite; K, kaolinite, Qz, Quartz; FK, K feldspar; Ca, calcite. The diffractograms obtained for sedimentological units An4, An3 and An2 are closely similar.

An2 (0.20–0.40 m). Beige to yellow and grey calcareous deposits with irregular stratification and both lateral and vertical transitions between marls and limestones; these sediments are rich in randomly distributed and orientated vertebrate remains; in places An2 appears to be a succession of “bowls” thrust into the underlying unit. These structures could represent footprints or be the result of trampling, but further excavation is necessary if this interpretation is to be confirmed.

An3 (0.20–0.40 m). Calcareous conglomerate with a blue-grey to beige grainstone matrix and whitish limestone clasts embedded in it; crocodile teeth are relatively abundant in association with small wood and plant cuticle fragments; ostracods, charophyte gyrogonites and insect (termite) coprolites are very abundant; bones of different sizes (a few cm to more than 1 m) also occur in this unit including sometimes the tops of very large bones, the lower parts of which are embedded in the underlying unit An4.

An4 (0.50–1.00 m). Blue-grey lignitic clay extremely rich in wood and plant cuticle fragments (of mm and cm size) and containing large, well-preserved dinosaur bones and sections of trunks or branches of trees; the upper part of the unit (the highest few centimetres) becomes rich in calcareous gravels, with the result that when not cemented and hard it is locally difficult to differentiate it from the base of An3.

An5 (more than 0.70 m; base not visible). Green clay devoid of any megafossils, but in places includes sub-angular blocks or lenses of grey-green limestone, possibly locally reworked, the source outcrop being nearby.

What is referred to as “the bone bed” in this paper is the whole fossiliferous series, namely sedimentological units An1–4. Several large bones cut across the stratification and are, therefore, present in two or three of the units, the differences between which are mainly based on sediment granulometry and colour.

A second mechanical excavation, ANG2-02-2010, 50 m distant from the first, also penetrated a densely lignitic lens especially rich in plant cuticles and containing a few bones. This demonstrated that the areal extent of the bone bed amounted to at least several hundred square metres and contains laterally variable fossil plant accumulations. However, owing to these variations it is impossible to determine (based on the excavations carried out to date) whether the lens corresponds to unit An4 or unit An3 of the first excavation, both being rich in plant debris.

The observations made during the two excavations encouraged more ambitious fieldwork in the summers of 2010 and 2011. Hence, during August and early September of 2010, two palaeontological investigations were undertaken: manual excavation (ANG1-08-2010) to extend laterally the trench created by the mechanical digger to reveal a surface of about 30 m², and three new mechanical excavations at various orientations to, and distances from, the first (ANG1-02-2010) to check the stratigraphy in different parts of the quarry. Located only 20 m distant from ANG1-02-2010, the excavation ANG3-08-2010 encountered different sedimentological units; An1–4 are absent, having been removed by erosion, but under the green clay An5, irregularly stratified grey limestones (unit An6) and a red clay devoid of fossils (unit An7) were found. More distant from ANG1-02-2010 than ANG2-02-2010 and ANG3-08-2010, the two further excavations did not allow clear observation of the Mesozoic stratigraphy, because of an increase in thickness of the alluvium. However, at the end of November 2010, quarrymen at the site discovered yet more sauropod bones reworked into the Quaternary alluvium several hundred metres from the mechanical excavations.

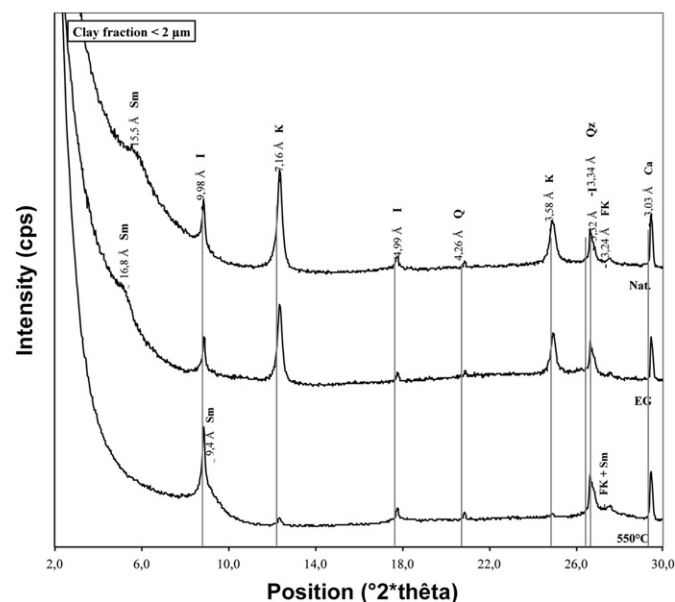
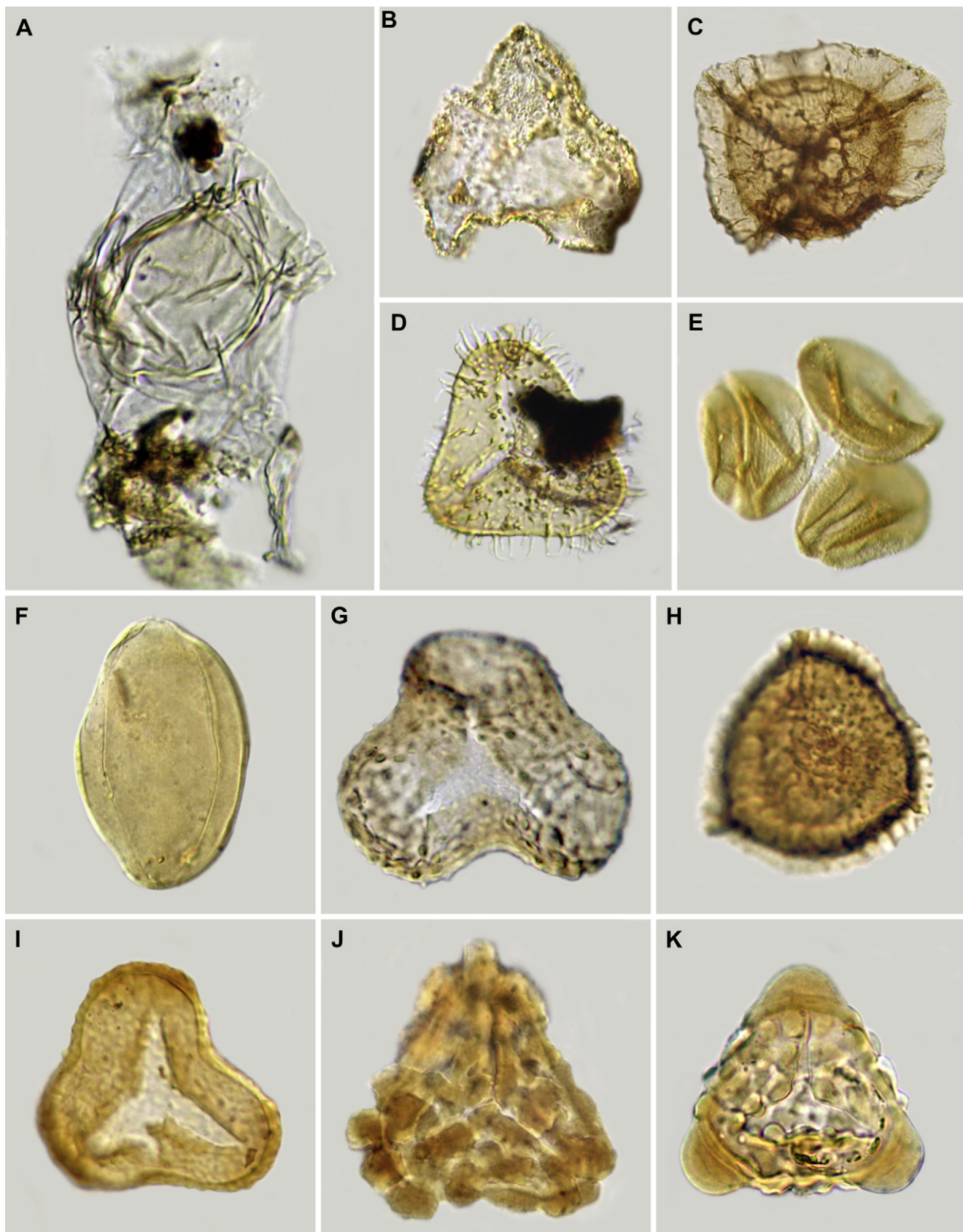


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3. Clay components and palaeoenvironmental implications

Clay phases (fractions <2 µm) were assessed by X-ray diffraction (XRD) on orientated preparations in air-dried (AD) and ethylene glycol saturation states (EG). Particular emphasis was placed on the characterization of the mica-illite, smectite, kaolinite and illite/smectite mixed layer minerals (I/S), which are good indicators of palaeoenvironmental and diagenetic conditions. X-ray diffraction (XRD) and clay mineral patterns were then recorded using a Panalytical Xpert Pro diffractometer with CuK radiation (40 kV, 40 mA) and equipped with a stepping-motor drive on the goniometer. The diffracted-beam was collected by an X'celerator detector.

The mineralogy of bulk-rock was determined from powders and recorded from 2.5 to 65 °2θ. Clay mineral characterizations were carried out on air-dried and glycolated orientated preparations (on <2 µm fraction and from 4 to 30 °2θ), and powders (<2 µm fraction) for main hkl reflections of illite and I/S (from 19 to 65 °2θ).

The clay mineral assemblage of the whole section is homogeneous and monotonous with respect to the mica-illite, kaolinite, smectite and mixed layer illite/smectite minerals (Fig. 2). Thus, the distribution of clay minerals in the section seems not to be dependent upon the facies. The data (e.g., presence of smectites) show that the lithological column has been only very weakly altered by diagenesis. As a result, the clay mineral assemblage reflects the original environmental conditions: (1) the preservation of this clay assemblage explains and confirms the exceptional preservation of most of the vertebrate and plant material, fossilized near its in-life habitat and/or place of death and only weakly modified by diagenesis; (2) the assemblage, and especially the abundance of kaolinite, reflects deposition in subtropical to tropical conditions (Chamley, 1989; Meunier, 2003); (3) the monotony and homogeneity of the assemblages in units An1–4 indicate that the different facies accumulated under the same conditions of diagenesis, climate and probably water quality, with the detrital minerals being derived from the same source.

4. Age of the sediments beneath the Quaternary alluvium

4.1. Problems and approach to age determination

There is evidence of significant reworking of some fossils into the Angeac Mesozoic deposits, which on the basis of exposures elsewhere in the Charente region, were considered likely to be Cretaceous in age. The conglomerate An3 is rather rich in derived marine organisms, especially eroded fragments of bryozoans, but a few spines and test fragments of pseudodiadematid echinoids have also been found. They are probably reworked from Late Jurassic (Kimmeridgian) marine deposits, which crop out a few kilometres from Angeac (Gabilly et al., 1997) and are also present in calcareous clasts incorporated in An3. Reworked bryozoan fragments also occur in the overlying units and are especially abundant in the white sand of An1.

The identification of obviously derived marine organisms suggests that other fossil groups, or some of the species of other groups, could also be reworked. It is especially difficult to differentiate between in situ and reworked taxa of brackish and freshwater microfossils such as ostracods, dinocysts and charophyte gyrogonites. This renders identification of good biostratigraphic markers

problematic. It is possible to have confidence only in records of the younger components, which are less likely to have been reworked.

In order to determine the age of the Mesozoic strata comprising the Angeac section, samples from the five sedimentological units exposed during the first mechanical excavation (ANG1-02-2010) were subjected to micropalaeontological and palynological analyses. In the event, the palynological data proved to be the most biostratigraphically informative. Other micropalaeontological data (obtained for foraminifera, ostracods and charophytes) and the occurrence of ornithomimosaur remains mostly provide supporting evidence for the palynological age determination or are at least consistent with it.

4.2. Palynological analysis

The palynological matter was extracted from the rocks by standard methods (see Dejax and Masure, 2005), the samples being subjected to digestion in 30% HCl followed by 70% HF at room temperature to remove the mineral content. The palynomorph assemblages were mounted on glass microscope slides in glycerine jelly and examined under a transmitted light microscope.

An5 proved to be entirely devoid not only of megafossils, as noted above, but also of palynomorphs and other microfossils. An4 yielded relatively impoverished palynological assemblages. However, triradial spores that are sculptured with verrucae are rather common. Among these are species of *Concavissimisporites* (Fig. 3G), *Converrucosisporites*, *Impardecispora* and *Leptolepidites*, *Trilobosporites* (Fig. 3I–K) and *Verrucosisporites*. These tend to be especially common in deposits of Berriasian–Valanginian age (e.g., Dörhöfer, 1977). The presence of *Aequitriradites spinulosus* (Fig. 3H) is also significant in this respect. Other taxa include species of the spore genera *Cyathidites* and *Retitrites* and gymnospermous *Callialasporites*, but surprisingly few bisaccate pollen grains. *Classopollis* grains (Fig. 3E) are, however, comparatively abundant. No dinoflagellate cysts or angiosperm pollen were recorded.

The presence in the samples from this unit of degraded *Cicatricosisporites*, a spore genus that is usually common in Lower Cretaceous non-marine deposits (e.g., in the Wealden succession of southern England; Hughes and Croxton, 1973; Batten, 1996), and of two specimens of the gymnosperm pollen grain *Chasmatosporites*, usually recovered from Jurassic deposits, could indicate the presence of some reworked palynomorphs. These observations tie in with the abundance of reworked Jurassic limestones and marls, especially in the An3–An4 transition and the An3 conglomerate. The assemblages from both of these units are marked by the maximum abundance of *Classopollis* pollen grains and the presence of *Januasporites* sp. (Fig. 3C).

An3 and especially An2 contain many verrucate spores of varying morphology and also common *Pilosporites trichopapillosus* (Thiergart, 1949) Delcourt and Sprumont, 1955 (Fig. 3D), but *Classopollis* pollen grains are uncommon. Algal remains consist mainly of freshwater indicators, such as *Ovoidites parvus* (Fig. 3F) and *Lecaniella* (Zygnemataceae). An2 yielded rare fresh- to brackish-water and marine dinoflagellate cysts: respectively *Lobionella hirsuta* Batten and Lister, 1988 (Fig. 3B) and *Odontochitina imparilis* (Duxbury, 1980) Jain and Khawaja-Ateequzaman, 1984 (one specimen; Fig. 3A). The LAD (last appearance datum, as opposed to FAD, first appearance datum: see below) of *O. imparilis* is in Early Barremian deposits (Duxbury, 1980). We agree with

Fig. 3. Palynomorphs from the Hauterivian–Barremian of Angeac. A, *Odontochitina imparilis* (Duxbury, 1980) Jain and Khawaja-Ateequzaman, 1984, length 152 µm, unit An2, slide 1. B, *Lobionella hirsuta* Batten and Lister, 1988, length 60 µm, unit An2, slide 1. C, *Januasporites* sp., specimen more conspicuously trilete than is usual for the genus, diameter 72 µm, unit An3–4. D, *Pilosporites trichopapillosus* (Thiergart, 1949) Delcourt and Sprumont, 1955, diameter 80 µm, unit An2, slide 1. E, *Classopollis* sp., diameter 40 µm, unit An4, slide 1. F, *Ovoidites parvus* (Cookson and Dettmann, 1959) Nakoman, 1966, zygnematacean spore, length 64 µm, unit An2, slide 1. G, *Concavissimisporites variverrucatus* (Couper, 1958) Brenner, 1963, diameter 60 µm, unit An2, slide 1. H, *Aequitriradites spinulosus* (Cookson and Dettmann, 1958) Cookson and Dettmann, 1961, diameter 42 µm, unit An2, slide 1. I, *Trilobosporites* sp. cf. *T. weylandii* Döring, 1965, diameter 48 µm, unit An2, slide 1. J, *Trilobosporites* sp. cf. *T. sphaerulatus* Phillips and Felix, 1971, diameter 58 µm, unit An2, slide 2. K, *Trilobosporites canadensis* Pocock, 1962, diameter 50 µm, unit An2, slide 2.

Duxbury that the species *imparilis* may represent an intermediate stage in the evolution of the genus *Odontochitina* from *Muderongia*.

Overall the productive sedimentological units An2–4 yielded palynological assemblages that are reminiscent of those of English Wealden facies. The presence of some reworked Jurassic palynomorphs is not surprising in view of other evidence to this effect. The few biostratigraphic indicators in the assemblages suggest that deposition took place during the Hauterivian–Barremian period.

5. Implications of age determination for a regional stratigraphic framework

Dating the lignites at Angeac as Hauterivian–Barremian means that a third Lower Cretaceous stratigraphic level with lignites in the Charentes region, and more generally in western France, is now recognized. Basal Cretaceous strata have previously been identified about 25 km from Angeac at Cherves-de-Cognac (Fig. 1; Colin et al., 2004; El Albani et al., 2004) where fresh- to brackish-water limestones and evaporites of Berriasian age have yielded thousands of vertebrate micro- and mesofossil remains (Mazin et al., 2006, 2008; Pouech, 2008; Billon-Bruyat et al., 2010). The uppermost Lower Cretaceous has been described from several parts of Charente-Maritime, about 70–100 km from Angeac, but mainly from two locations (Fig. 1): Archingeay (Néraudeau et al., 2002) and Tonnay-Charente (Néraudeau et al., 2005). Lignitic deposits there have been dated on the basis of palynology as latest Albian (Néraudeau et al., 2002; Dejax and Masure, 2005).

All Lower Cretaceous successions of the Charentes region suggest a fresh- to brackish-water depositional environment, but they differ in their fossil content. The Berriasian and Hauterivian–Barremian strata are rich in vertebrate remains, but the uppermost Albian deposits lack them. Both the Hauterivian–Barremian and uppermost Albian successions contain very rich plant accumulations locally, but amber has only been found in the latter. It is notable that in the same region just a few kilometres from Angeac, at Champniers and Jarnac (Fig. 1), lowermost Cenomanian deposits are rich in plant fossils, amber (Perrichot et al., 2007; Perrichot and Néraudeau, 2009) and vertebrate remains (Vullo, 2007). Hence, the differing Lower and mid Cretaceous successions of the Charentes region provide evidence of continental ecosystems, occasionally affected briefly by marine influence on the environment of deposition, from the Berriasian to the Early Cenomanian, a period of some 40 myr.

6. Fossil content

In addition to the palynomorphs noted above, the fossil assemblage recovered from Angeac comprises a fairly diverse assemblage of plants and vertebrates occurring in abundance at some horizons, and low diversity assemblages of charophyte algae and invertebrates.

6.1. Palaeobotany

Charophyte algae. Numerous but poorly preserved charophyte gyrogonites, some reworked, have been found in the conglomerate An3 and the yellow marls of An2, by washing (with water) and sieving of the sediments at 400 µm. They correspond both to Characeae (*Mesochara* sp., *Sphaerochara* aff. *verticillata* Peck, 1939) and Porocharaceae (*Porochara* sp.). An2 also contains Clavatoraceae, mainly *Nodosoclavator bradleyi* Harris, 1939, and a few specimens of *Clavator grovesii* Harris, 1939. This charophyte assemblage is typical of the Lower Cretaceous (Martín-Closas and Grambast-Fessard, 1986; Martín-Closas and Schudack, 1996; El Albani et al., 2004).

Cuticles and mesofossil remains. The dense plant accumulation exposed in the second mechanical excavation (ANG2-02-2010) is

mainly composed of cuticles. These were separated by maceration in H₂O₂, sieved with tap water using 1 mm, 500 µm and 100 µm mesh sieves, dried and sorted under a binocular microscope (see Gomez et al., 2008). By far the most abundant of the meso- and megafossil remains are isolated leaves and leafy twigs (Fig. 4C–E). In both cases the leaves have a very short free part that is mostly closely pressed against the stem, whereas the leaf cushion can be up to three-times longer. The leaves are borne in an opposite-decussate arrangement in whorls of three along the axis. Mesozoic shoots with such phyllotaxy and preserved as cuticle belong to the genus *Watsoniocladius* Srinivasan, 1995 of the extinct conifer family Cheirolepidiaceae.

The cuticles are very well-preserved. The abaxial cuticle shows distinct rows of stomata converging towards the leaf apex. The stomata have a raised rim around the stomatal pit and are protected by papillae borne by the subsidiary cells. From a systematic point of view, it is noteworthy that this conifer is very abundant in An3 and An4, which also contain dispersed *Classopollis* pollen grains in abundance, as noted above. The cuticle type species is *Watsoniocladius valdensis* (Seward, 1895) Srinivasan, 1995 from the Purbeck Limestone Group of southern England, where it is associated with the wood *Protocupressinoxylon purbeckensis* Francis (Francis, 1983; Watson, 1988; Watson and Alvin, 1996). Such wood has recently been recovered from the Kimmeridgian of Asturias in Spain and in Switzerland (Philippe et al., 2010). Although *Watsoniocladius* representatives range from the lowermost Jurassic to the uppermost Lower Cretaceous, it is noteworthy that hitherto it has only been found in pre-Aptian strata in Western Europe (Srinivasan, 1995; Watson and Alvin, 1996). Sorting under a stereomicroscope has permitted the retrieval of additional smaller mesofossil plant remains. These include charred circinate pinnae of ferns (Fig. 4A, B), conifer cones (Fig. 4G, H) and scales (Fig. 4F), and seeds (Fig. 4I–L).

Wood. In the first mechanical excavation (ANG1-02-2010), units An3 and An4 have mainly yielded wood fragments preserved as lignite. These are generally small (cm-size) but several larger pieces, reaching 50 cm and more in maximum dimension, have been collected. The large pieces are glassy and lack visible organic structures; they are impossible to identify. However, scanning electron microscope (SEM) examination of six cm-sized samples of secondary xylem revealed in radial view an araucarian pitting of the tracheid radial wall, with long uniseriate alignments (Fig. 5A). Locally, a few tracheids show alternate biseriate pits. Cross-fields are composed of numerous (6–12) cupressoid oculipores in araucarioid arrangement (Fig. 5B). These characters allow identification of the genus *Agathoxylon* Hartig, 1848 (Philippe and Bamford, 2008; Philippe, 2011). In western Europe, this genus has been recorded from both Jurassic and Cretaceous deposits (Philippe et al., 2010), and elsewhere in the Charentes region it has been found in Tithonian, Berriasian, Albian and Cenomanian strata (Néraudeau et al., 2002, 2003; El Albani et al., 2004).

The position in conifer systematics of the fossil wood genera *Agathoxylon* and *Protocupressinoxylon* is debatable. The characters of *Agathoxylon* compare well with the wood of modern Araucariaceae. The wood of representatives of the Cheirolepidiaceae, from the limited evidence available, is variable, with characters that fit those of the fossil genera *Agathoxylon*, *Brachyoxylon*, *Protocupressinoxylon* and *Protaxodioxylon*. Hence, the fossil wood and plant cuticles from Angeac could well belong to the same biological species. Whatever the case, the lack of amber in the rich accumulation of coniferous remains is rather surprising.

6.2. Invertebrate fossils

Micro-invertebrate remains, mostly ostracods and termite coprolites, are locally abundant, but the former are of low diversity

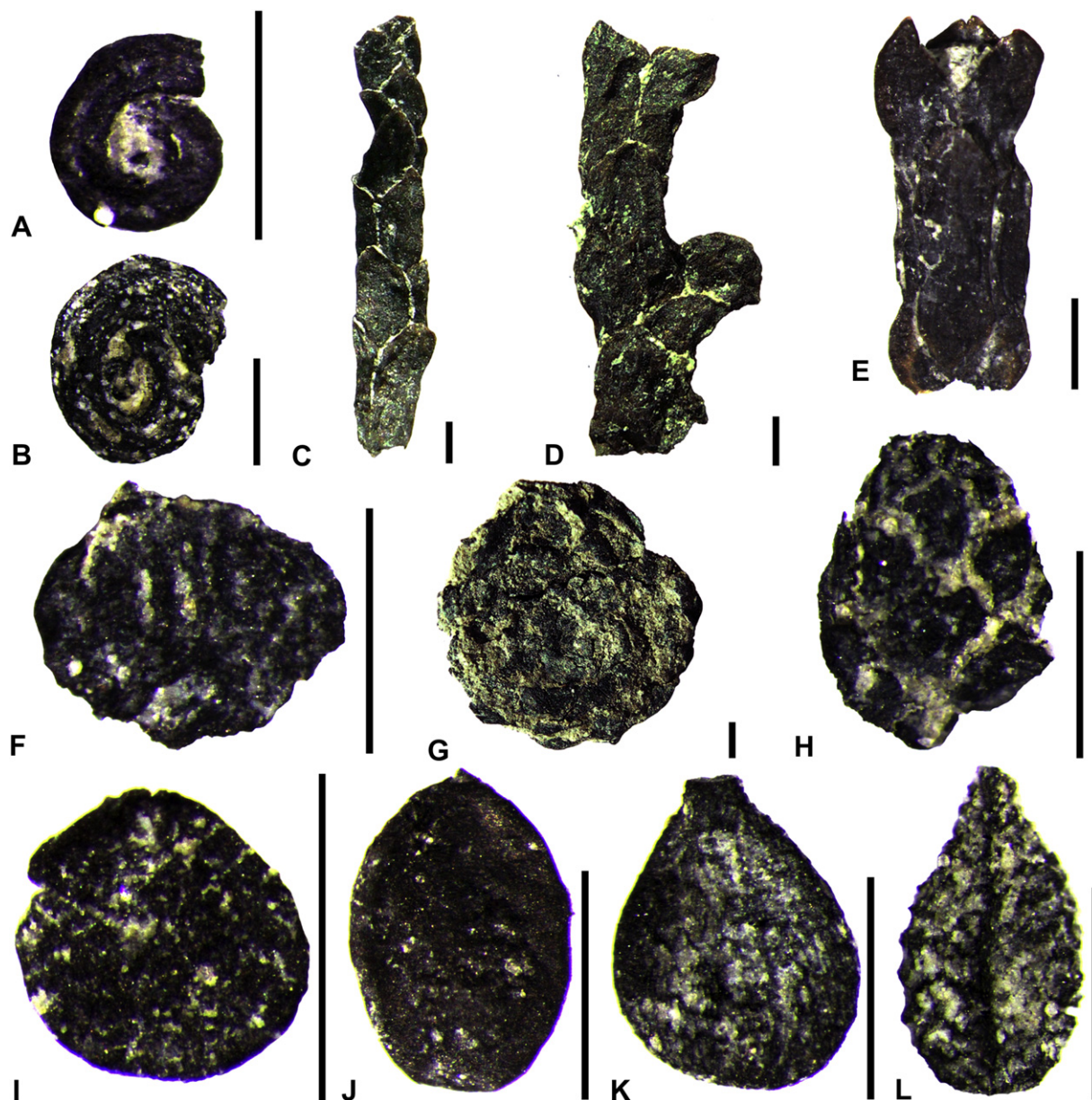


Fig. 4. Mesofossil plant remains from the Hauterivian–Barremian of Angeac. A, B, distal portion of circinate fern pinnae; ANG 10-582 and ANG 10-583 respectively. C–E, conifer twigs of *Watsoniocladius*. C, D, leaves in opposite-decussate phyllotaxis; ANG 10-584 and ANG 10-585 respectively. E, leaves in whorl of three; ANG 10-586. F, conifer cone scale; ANG 10-587. G, H, conifer cones; ANG 10-588 and ANG 10-589 respectively. I–L, seeds; ANG 10-590 to ANG 10-593. Scale bars represent 1 mm.

and sometimes possibly reworked from older deposits. In addition, rare foraminifera have been recovered. A broken and eroded specimen of *Trocholina* cf. *odukpaniensis* Dessauvage, 1968 was found in unit An1 exposed in the first excavation (ANG1-02-2010). Uncommon from the Berriasian to the Barremian, the species is most frequently encountered in Hauterivian and Barremian strata (Arnaud-Vanneau et al., 1989). Another broken foraminiferan identified as *Ammocycloloculina* sp. came from undifferentiated An3–An4 units exposed in the second excavation (ANG2-02-2010). The genus has a Lower Cretaceous stratigraphic range.

In the conglomerate An3 and its transition to the underlying clay An4 in excavation ANG1-02-2010, ostracods are quite common. The dominant form is the freshwater genus *Cypridea* Bosquet, 1852 (Horne and Colin, 2005), essentially represented by one species, *Cypridea* gr. *tuberculata* Sowerby, 1836. This rather long-ranging form in the English Wealden Supergroup has its highest occurrence in the

Cypridea pumila Subzone (*Theriosynoecum fittoni* Zone) as defined by Horne (1995) after the work of Anderson (1985), which is generally assumed to be of Hauterivian–early Barremian age (Horne, 1995, 2011). A single specimen of *Cypridea laevigata* Dunker, 1846 has been identified. This species is generally limited to the Berriasian and Valanginian (Schudack and Schudack, 2009) although recently *Cypridea* gr. *laevigata* has been reported from younger sediments (Early Albian) of Tunisia (Trabelsi et al., 2011). Two other forms of *Cypridea* have been found at the same horizon, but these are identified in open nomenclature (*Cypridea* sp. 1 and sp. 2) because they cannot be determined to species. Other species are long ranging late Tithonian–Barremian forms: these include *Damonella pygmaea* Anderson, 1941, *Damonella ellipsoidea* Wolburg, 1962, *Darwinula oblonga* Roemer, 1839, *Alicenula leguminella* Forbes, 1855, *Mantelliana* sp. and *Fabanella boloniensis* Jones, 1885. The presence of the last of these is important, because the genus is euryhaline, occurring

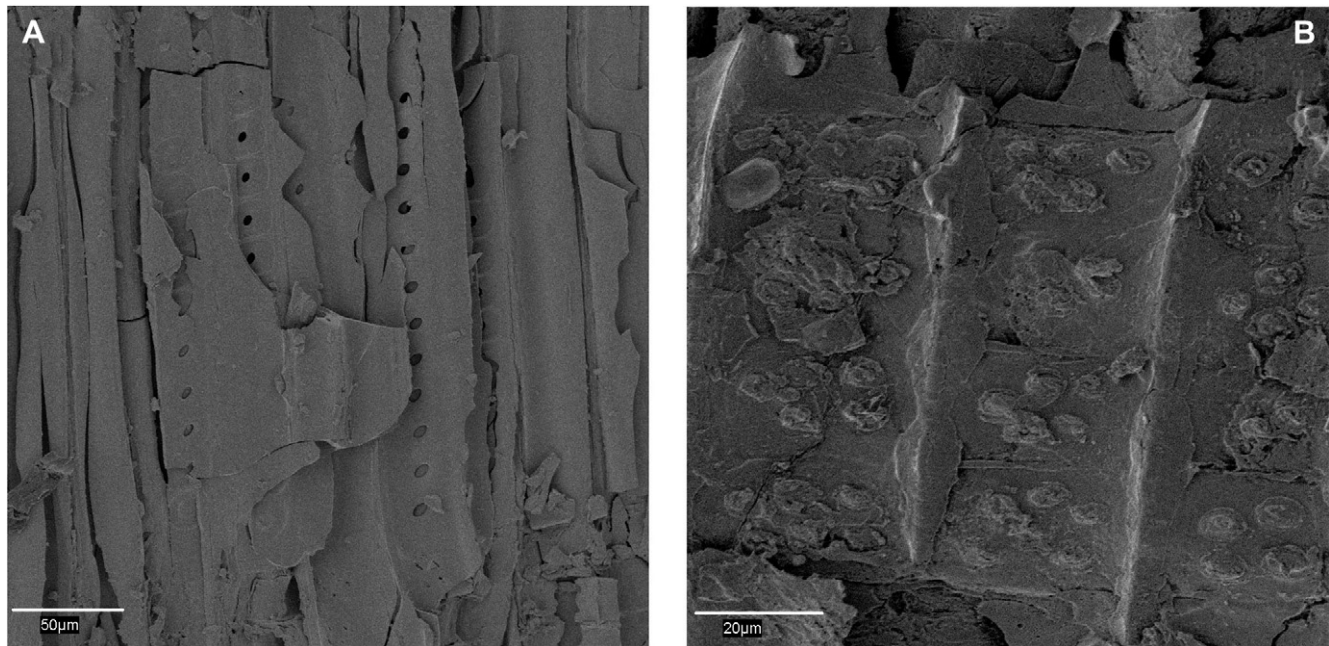


Fig. 5. Fossil wood from the Hauterivian–Barremian of Angeac. A, sample ANG MP1847; radial view; uniseriate radial pitting, areolae variously marked, locally obliterated by wall vitrification. B, sample ANG MP1858; radial view; part of a wood ray with araucarian cross-fields, with 4–6 cupressoid oculipores.

in freshwater sediments and those representing deposition in waters of slightly raised salinity (Colin et al., 1990). A single specimen of *Theriosynoecum forbesii* Jones, 1885, usually restricted to the late Tithonian–Valanginian, and a small number of *Eoparacypsis* sp. have also been found. *Cypridea* gr. *tuberculata* has been recorded in An2 where it occurs with rare *Cypridea* sp. 1, and in An1 where it occurs in isolation.

It is apparent from Horne's (1995) synthesis of Purbeck–Wealden ostracod stratigraphy in southern England that the FAD and LAD of ostracod species are generally imprecise. This is a result of the lack of marine index taxa in the fresh- to brackish-water deposits studied. It is also possible that elements of the Angeac ostracod assemblages are derived from underlying "Purbeck-type" deposits: small limestone and marl pebbles also possibly from these are abundant in the conglomerate An3 and in the overlying units An2 and An1.

In the second mechanical excavation ANG2-02-2010, the lignitic clay (corresponding to An3 or An4) has yielded the same diversity of ostracods as unit An3 and its transition to An4 in ANG1-02-2010: mainly *Cypridea* gr. *tuberculata* associated with *Darwinula oblonga* and *Fabanella boloniensis*.

In excavation ANG1-02-2010, the conglomerate An3 is also rich in coprolites representing the termite ichnotaxon *Microcarpolithes hexagonalis* Vangerow, 1954 (Colin et al., 2011). These micro-ichnofossils are quite frequent in various lignite deposits of the mid Cretaceous of Charentes. Indeed, they are always associated with *Agathoxylon* wood and amber in the Late Albian and Early Cenomanian lignites of this region. Undetermined termite coprolites are very common in the plant-debris beds of the Wessex Formation (Wealden Group, Barremian) of the Isle of Wight, southern England, where they occur in association with lignitic remains of the conifer *Pseudofrenelopsis parceramosa* (Sweetman and Insole, 2010), but they may also be encountered elsewhere in the Wealden succession (Batten, 2011), especially in the Weald Clay Group (Wealden Supergroup) in south-east England.

Two kinds of macro-invertebrate fossils have been encountered in the Angeac deposits: freshwater bivalves, with abundant large specimens, and moulds of gastropods, generally small, poorly

preserved and difficult to identify. About 100 bivalves have been found but only 80 more or less complete specimens could be collected. Almost all are large, from 70 to 90 mm long and 35 to 40 mm wide respectively. A few, which are assumed to represent juvenile individuals, are much smaller: these measure about 2–3 cm in maximum dimension. All are unionoids, morphologically close to those found in Early Cretaceous freshwater deposits of Spain (Delvene and Araujo, 2009), but with more elongated shells (Fig. 6). Almost all (90%) are isolated valves; only a few with articulated valves occur in life position in their burrows. Most of the bivalves have been found in units An2 and An3; the few with articulated valves come from the top of An2.

About ten moulds of gastropods have been observed, but only five could be collected. The poor preservation makes precise determination difficult, but the low, relatively globular shell with five to six whorls is closely similar to that of freshwater viviparids.



Fig. 6. Unionoid bivalve from the Hauterivian–Barremian of Angeac, sedimentological unit An2. Scale bar represents 2 cm.

6.3. Vertebrates

The vertebrate assemblage so far recovered comes almost entirely from the first mechanical excavation, ANG1-02-2010, and the surrounding manual excavation. Units An1–4, which constitute the bone bed, have yielded more than 1300 bones and teeth, most being located at the interface of An3 and An4, and in unit An2. Dinosaur remains are by far the most abundant. A first account of this vertebrate assemblage is given below and compared to the fauna of other European Early Cretaceous, especially Barremian, localities.

Vertebrate micro-remains have been collected by washing (with water) samples from the different sedimentological units and sieving at 40 µm. Micro-fragments of tetrapod bones and fish scales are relatively abundant (especially in units An3 and An2), but small teeth are relatively rare by comparison with the composition of other Early Cretaceous vertebrate deposits (e.g., Cherves-de-Cognac; Pouech, 2008), except in the fine sand of unit An1.

An incomplete tooth and a worn, fragmentary dorsal fin-spine of an indeterminate hybodont shark have been recovered from An3 (Fig. 7A). The latter is ornamented by a few strong, well-spaced longitudinal ridges. In Early Cretaceous deposits of Western Europe, these euryhaline sharks are a ubiquitous component of the fish fauna of the English Wealden succession and of similar non-marine sediments elsewhere (Patterson, 1966; Bermúdez-Rochas, 2009).

Fish remains are mostly represented by numerous scales and teeth of Ionoscopiformes and Semionotiformes (e.g., *Lepidotes* sp.) in every sedimentary unit from the top of An4 to An1 (Fig. 7J). An1 contains the highest diversity of fish remains. Most are ionoscopiform teeth, with a few teeth of Semionotiformes (Semionotidae),

Pycnodontiformes and Amiformes (Caturidae) associated with many indeterminate scales and bone fragments.

Turtles are represented by numerous isolated, fragmentary shell plates belonging to perhaps as many as three taxa on the basis of the outer surface ornamentation. Pleurosternids are common (Fig. 7D), with the outer surface covered in fine pitting and the plate margins bearing fine linear striations perpendicular to the margins, similar to *Pleurosternon* from the Purbeck Limestone Group of southern England (Owen, 1853; Milner, 2004). A small number of fragments represent solemydids. These are covered with discrete raised tubercles and pustules (Fig. 7C), in which they differ from the vermiculated ridges present in *Solemys* (de Lapparent de Broin and Murelaga, 1999), but are similar to some solemydid shell fragments (*Helochelydra*-type) from the Lower Cretaceous of the Isle of Wight (Joyce et al., 2011, text-fig. 3C), and the Cenomanian of Charentes (Vullo et al., 2010, fig. 6.1). A possible third taxon is represented by a fragment devoid of any ornamentation.

The presence of Plesiosauroidea in the Angeac assemblage is attested by a single epipodial limb bone (Fig. 7B). This specimen is broader than long and shows one proximal and two distal facets. The anterior and posterior margins are both concave. Such an element, most likely a tibia (but possibly a radius), may be referred to an indeterminate medium-sized pliosauroid. A few remains of this group have been recovered from the non-marine Wealden deposits of north-west Europe, with only a single valid taxon recognized so far, the pliosauroid *Leptocleidus superstes* Andrews, 1922 (Kear and Barrett, 2011).

Numerous crocodilian teeth have been found in the Angeac deposits. Most of the large specimens (more than 1 cm) are attributable to goniopholidids (Fig. 7E, F) and come mainly from

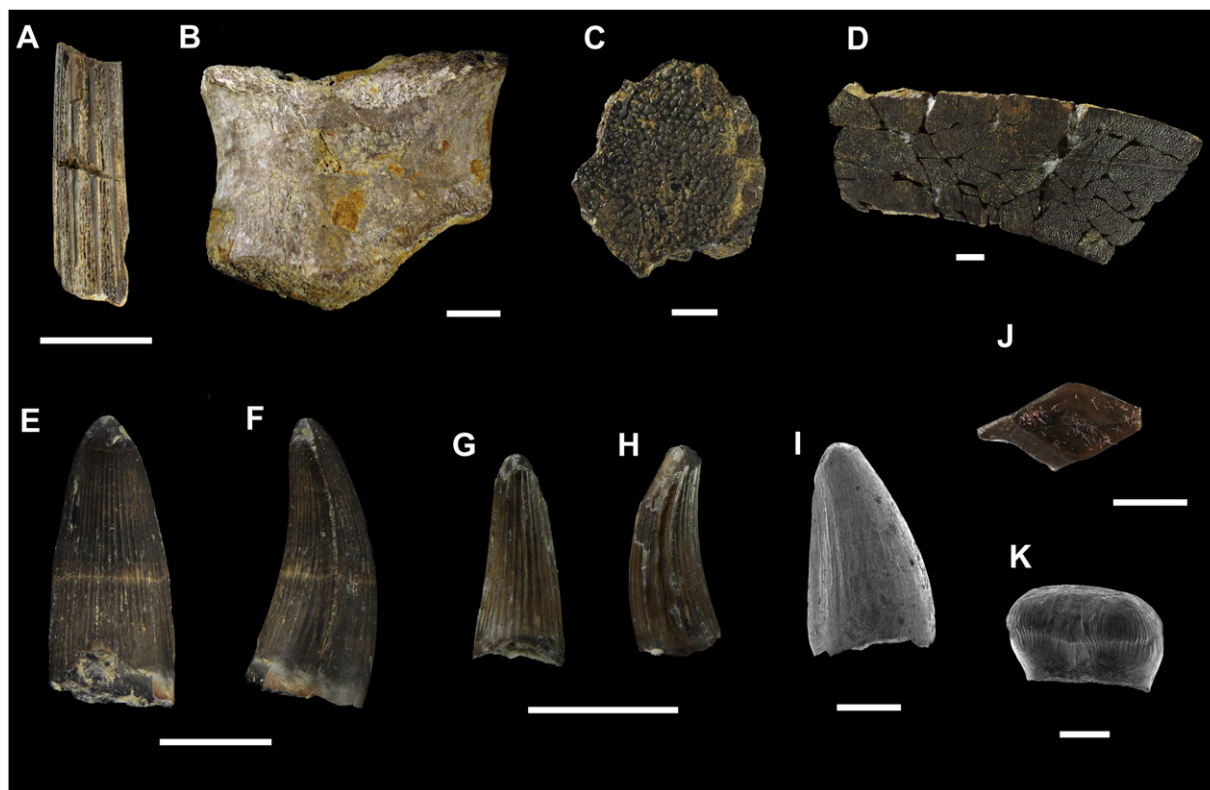


Fig. 7. Non-dinosaur vertebrate remains from the Hauterivian–Barremian of Angeac: A, hybodont dorsal fin spine; ANG 10-126. B, pliosauroid left tibia; ANG 10-581. C, peripheral plate of a solemydid turtle; ANG 10-409. D, pleural plate of a pleurosternid turtle; ANG 10-71. E, F, tooth of goniopholidid crocodile in lingual (E) and distal or mesial (F) views; ANG 10-263. G, H, tooth of pholidosaurid crocodile in lingual (G) and distal or mesial (H) views; ANG 10-265. I, tooth of atoposaurid crocodile in lingual view; ANG 10-267. J, scale of semionotid fish. K, tooth of bernissartiid crocodile; ANG 10-268. Scale bars represent 1 cm in A–F, 5 mm in G, H, J, 1 mm in I, K.

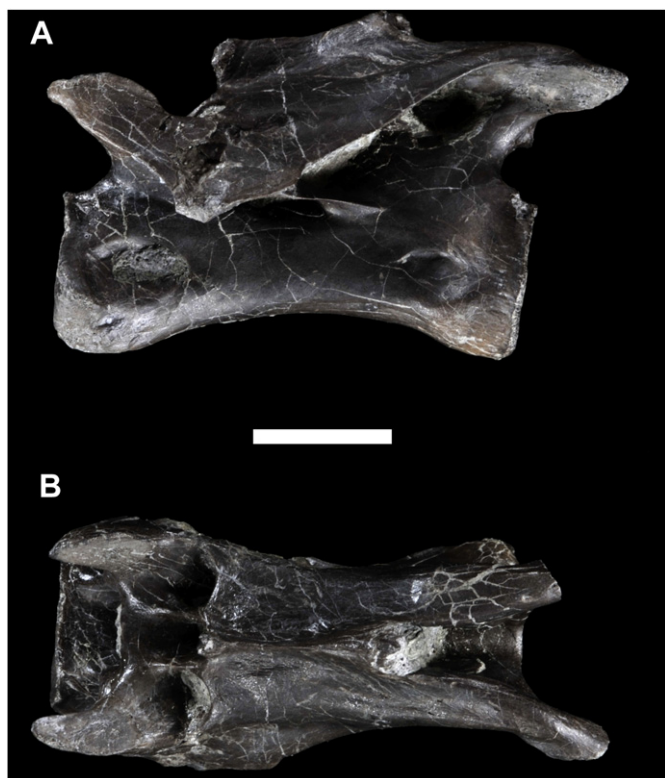


Fig. 8. Ornithomimosaur cervical vertebra (ANG 10-175) from the Hauterivian–Barremian of Angeac in A, left lateral and B, dorsal views. Scale bar represents 2 cm.

units An3 (including the An3–An4 transition) and An2. Only one has been found in unit An1 and none in An4. Smaller crocodilian teeth have been found in every sedimentary unit from An1 to An4: those representing Bernissartiidae from An1 to An3 (Fig. 7K), Atoposauridae from An1 and An3 (*Theriosuchus* sp. in An1, indet. atoposaurid in An3; Fig. 7I) and Pholidosauridae from An2 and An3 (including the An3–An4 transition; Fig. 7G, H).

The Angeac reptile assemblage is dominated by dinosaurs. Five taxa have been recovered so far. The vast majority of bones belong to a single theropod taxon related to ornithomimosaurs (Fig. 8). To date, more than 600 well-preserved but disarticulated elements including cranial material have been unearthed from a surface of about 30 m². A complete description of this new dinosaur will be

provided in due course following further excavations. However, based on the number and size of the recovered tibiae and femora, at least nine juvenile to adult individuals of this possibly herbivorous theropod are present within the excavated area of the Angeac bone bed. This suggests either a catastrophic mass mortality of a group of ornithomimosaurs or taphonomic effects; according to the uniform preservation of the bones (Varricchio et al., 2008) and the lack of abrasion, the former seems more likely. Hence, the ornithomimosaur bones are currently considered to have been preserved in situ or to have been transported over only a very short distance.

A second theropod is represented by teeth (Fig. 9E, F), which are indistinguishable from those of *Neovenator* from the Barremian of the Isle of Wight (Hutt et al., 1996; Brusatte et al., 2008), but distinct from those of *Erectopus* from the Albian of Meuse, France (Allain, 2005). The blade-like teeth are strongly recurved and have an asymmetrical cross-section. They bear enamel wrinkles that extend, as bands, across the labial and lingual surfaces of the tooth. The serrated distal carina extends from the tip to the base of the crown, while the mesial carina extends from the tip to approximately one-third of the distance to the base. In this respect the Angeac teeth differ from those of *Erectopus* in which both carina bear denticles extending to the base of the crown. The denticle size difference index (DSDI), calculated following Rauhut and Werner (1995), is 0.93 and 0.92 for ANG 10-51 (Fig. 9E) and ANG 10-262 (Fig. 9F) respectively, and lies within the range for *Neovenator* (Sweetman, 2004).

Sauropods are known from teeth (Fig. 10A–F), several limb bones (e.g., Fig. 11) and very large caudal vertebrae; it is not clear whether this material, which was recovered from several parts of the quarry (reworked in recent alluvium and in situ in Cretaceous strata) represents a single taxon. The teeth are reminiscent of *Turiasaurus riodevensis* Royo-Torres et al., 2006, a Tithonian–Berriasian taxon from the Villar del Arzobispo Formation of Teruel, Spain. However, such heart-shaped, spatulate teeth are known from various Jurassic and Early Cretaceous localities in Europe (e.g., see the teeth of *Neosodon* illustrated by Buffetaut and Martin, 1993). It should be noted that *Turiasaurus* is supposed to have strongly opisthocoelous caudal vertebrae (assuming that the single caudal vertebra referred to it by Royo-Torres et al., 2006 does belong to this animal). The caudal vertebrae from Angeac are procoelous (anterior caudals) or amphiplatyan (middle caudals) and thus differ markedly from those of *Turiasaurus*. They share many characters with another partially known Spanish sauropod, namely the Early Aptian *Tastavinsaurus sanzi* (Canudo et al., 2008), also found at Teruel, the teeth of which are still unknown. The most

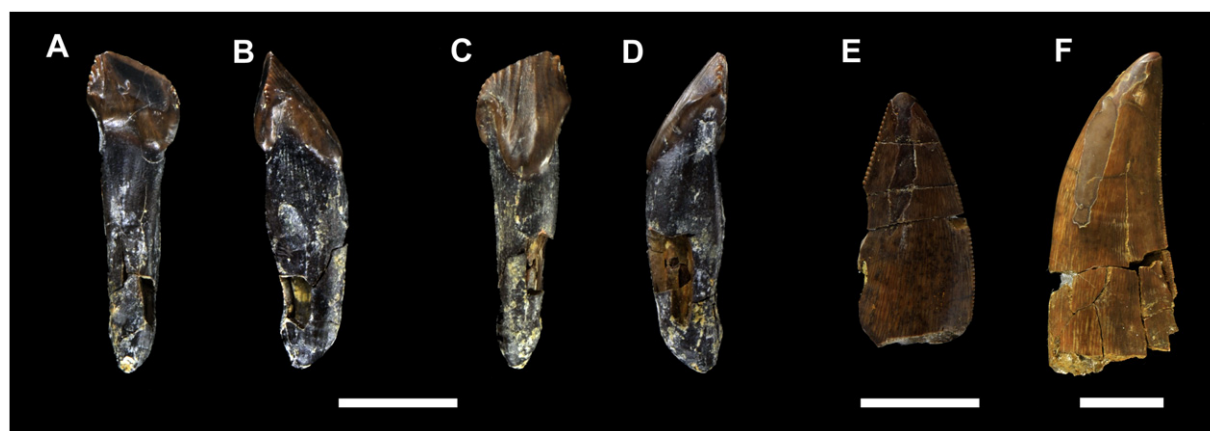


Fig. 9. Hypsilophodontid and theropod teeth from the Hauterivian–Barremian of Angeac. A–D, right maxillary tooth of *Hypsilophodon* sp. (ANG 10-153) in A, lingual, B, mesial, C, labial and D, distal views. E, F, allosauroid teeth in labial view; ANG 10-51 and ANG 10-262 respectively. Scale bars represent 1 cm.

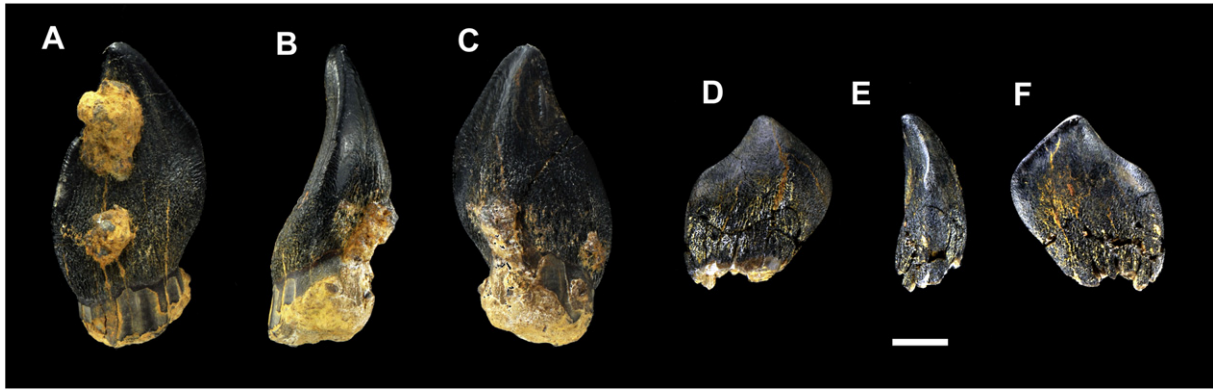


Fig. 10. Sauropod teeth from the Hauterivian–Barremian of Angeac: A–C, tooth ANG 10-10 in A, lingual, B, mesial and C, labial views. D–F, tooth ANG 10-27 in D, labial, E, distal and F, lingual views. Scale bar represents 1 cm.

spectacular discovery at Angeac is unquestionably that of a 220-cm-long sauropod femur, the longest yet recorded to our knowledge (Fig. 11).

Ornithopods are represented by two well-preserved, isolated teeth from unit An3. The first belongs to a small form (mesiodistal length of crown, 8 mm). This tooth has a long, mesiodistally compressed root and a crown that originally must have been more or less diamond-shaped, but is truncated by a large, labiolingually and mesiodistally oblique wear facet (Fig. 9A–D). The labial surface of the tooth shows a distinct cingulum, from which several

apicobasally orientated ridges emerge. Additional shorter ridges are present apically. In the unworn mesial and distal regions the ridges end in distinct denticles, which are partly obliterated by the wear facet in the central part of the crown. Lingual crown ornamentation also consists of ridges, but the lingual surface of the crown is largely destroyed by the extensive wear facet. This tooth resembles in every respect the maxillary teeth of *Hypsilophodon foxii* Huxley, 1869, from the Wealden Group of the Isle of Wight (Huxley, 1869; Hulke, 1882; Galton, 1974). The wear pattern is similar to that of *Hypsilophodon* illustrated by Nopcsa (1905) and shows that the tooth is from a right maxilla. This tooth is larger than most *Hypsilophodon* teeth described from England, which may be explained by the fact that most of the English *Hypsilophodon* specimens are apparently juveniles or sub-adults (Naish and Martill, 2001 and references therein). *Hypsilophodon* is known from the Barremian of England (Naish and Martill, 2001; Norman, 2011) and from the Barremian–Aptian of various parts of Spain (see review in Ruiz-Omeñaca and Canudo, 2003).

A much larger ornithopod is represented by a tooth typical of an iguanodontid, and perhaps by a poorly preserved and distorted vertebral centrum. The 20-cm-long centrum is weakly amphicoelous and may be that of an anterior caudal.

7. Stratigraphical, palaeoenvironmental and palaeogeographical implications

Stratigraphically, the lignitic deposits of Angeac represent the first evidence in France of deposits of Hauterivian–Barremian age that may be compared to those of the English Wealden Supergroup. They correspond to the older lignite bed of the “Gardonian” lignites identified regionally by Coquand (1857a, 1858a, b). Therefore, it is now possible to distinguish three lignitic series in western France (Fig. 1): (1) Old Gardonian lignites of Hauterivian–Barremian age; (2) Mid Gardonian lignites of late Albian age; and (3) Young Gardonian lignites of early Cenomanian age.

The Angeac lignites were deposited in an environment that clearly differed from those of the Albian and Cenomanian successions. They accumulated mainly in freshwater: connections to the sea were at most intermittent and brief (brackish taxa occur in units An1–3, but most may be reworked). By contrast, the Albian and Cenomanian lignites were more likely to have been deposited in estuarine brackish and marine environments (Néraudeau et al., 2002, 2003, 2005, 2009). Consequently, the plant assemblages differ. They consist mainly of cheirolepidiaceae conifers at Angeac, but those of the Albian–Cenomanian lignites are more diverse, with both araucariaceous and cheirolepidiaceae conifers as well as



Fig. 11. Right sauropod femur ANG 10-400 found in the Hauterivian–Barremian lignites of Angeac during the summer of 2010 (posterior view); length is about 220 cm.

angiosperms present. The differing conifer genera (*Watsoniocladius* vs. *Frenelopsis* and *Glenrosa*) are correlated with a lack of amber droplets in the Angeac lignites and an abundance of fossil resin in the Albian and Cenomanian lignites. It is too early to determine whether the lack of angiosperms at Angeac truly reflects their absence or is simply an indication of their scarcity at this very early stage in their evolution.

Finally, the lignitic deposits of Angeac are characterized by a great abundance of vertebrate macro-remains (dinosaurs, turtles, crocodiles) whereas the Cenomanian lignitic deposit contains mainly teeth and a few fragments of dinosaur and turtle bones (Néraudeau et al., 2003, 2009) and late Albian lignites are devoid of them. It seems that in Charentes only the lignitic deposits associated with carbonate sediments have preserved bones and/or teeth, as at Angeac and in the early Cenomanian deposits of Aix Island and Fouras, irrespective of the salinity of the depositional environment (mainly freshwater at Angeac, shallow marine at Fouras). Late Albian fluvial sands containing lignites are strongly oxidized (red with ferruginous concretions). As a result, if carbonates and vertebrate remains had been deposited, they would have been destroyed subsequently during diagenesis. The diagenetic destruction of shells and bones in the late Albian lignites is supported by the lack of calcareous and phosphatic micro- and macrofossils: ostracods are absent; foraminifers are very scarce and known from only a few organic-walled linings (Dejax and Masure, 2005); and although molluscs are locally present (mainly oysters), they are always pyritized (Néraudeau et al., 2002; Videt and Platel, 2005).

The Angeac dinosaur assemblage shares affinities with coeval Spanish and English faunas suggesting that trans-Tethyan faunal interchanges took place during the Early Cretaceous. The presence of a few brackish to marine taxa in the Angeac lignites shows that the coast and the western boundary of the Massif Central island was farther to the east than previously supposed in palaeogeographical reconstructions of the Early Cretaceous (e.g., Smith et al., 1995).

Only one ornithomimosaur (*Pelecanimimus polyodon* from the late Barremian Las Hoyas fossil site in Spain) has previously been recorded in Europe (Pérez-Moreno et al., 1994). Ornithomimosaurs are known from Early Cretaceous strata in China (Ji et al., 2003; Makovicky et al., 2010), Mongolia (Barsbold and Perle, 1984) and Thailand (Buffetaut et al., 2009), and are widespread in Late Cretaceous deposits in both Asia and North America. Thus, the discovery of this taxon at Angeac may prove crucial to understanding the origin and diversification of this group of herbivorous theropods.

8. Conclusions

The plant and vertebrate assemblages of Angeac are the first to be described from the Hauterivian–Barremian of France and provide abundant and varied data on the fauna and flora of a freshwater/terrestrial ecosystem coeval with those existing in Britain and other parts of north-west Europe, and in Iberia to the south.

The occurrence of three major plant accumulations in western France, representing deposition in the Hauterivian–Barremian, the late Albian and the early Cenomanian, is potentially an outstanding source of data for understanding the evolution of Early to mid Cretaceous European forest ecosystems. The abundance of continental vertebrate remains in both the Hauterivian–Barremian and early Cenomanian deposits will improve documentation of the evolution, diversity and community structure of different groups, especially dinosaurs.

The variety of plant and dinosaur remains found at Angeac on a surface of about 30 m² and within a stratigraphic thickness of only 1.5 m suggests that the site will yield further significant discoveries in the future. The presence of reworked bones in the

Quaternary gravels indicates that the fossiliferous beds may extend to more than 10,000 m².

Acknowledgements

The discovery and study of the Angeac lignites and bone bed would have been impossible without the agreement and the technical help of the Audoin Company. We are indebted to Jean-Marie, Philippe and Vincent Audoin for their useful collaboration. We are also grateful to Jean-Pierre Paillot of the Audoin Company, who works in the Angeac quarry and discovered the first sauropod bones in the Quaternary alluvium and then helped the scientific team technically on several occasions. We are indebted to Dominique Augier and Renaud Vacant who have prepared much of the material collected and contributed to the field programme, and to Philippe Loubry and Lilian Cazes for the photographs of the vertebrate remains. We thank S. Sweetman and an anonymous reviewer for comments on the manuscript. Finally, we have much appreciated the help of numerous students and amateur palaeontologists who have participated in the excavations for a few days or several weeks. This article is a contribution to the ANR project AMBRACE n° BLAN07-1-184190, to the INSU project NOVAMBRE and the OSUR scientific programs.

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