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**ABSTRACT**

This contribution describes the continental micro- and macrovertebrate fauna of Angeac-Charente (Berriasian, Early Cretaceous). The rich and diversified fauna includes at least 38 different vertebrate taxa from all major clades, and is represented by more than 50 000 specimens. The Angeac-Charente locality includes the most diverse earliest Cretaceous mixed continental bonebed and the only Lagerstätte known to date in the World, and it provides a good picture of a Purbeckian paleocommunity. It includes remarkable taxa such as a new ornithomimosaur, a large turiasaur, an helochelydrid turtle and numerous mammals. The vertebrate fauna of Angeac-Charente has beyond all a Purberckian character. Many exclusively European genera and species belong to families with an essentially Laurasian paleogeographic distribution. Some taxa nevertheless suggest dispersal events between Africa and Europe at the Jurassic/Cretaceous transition. The successive Charentese faunas of Chassiron (Tithonian), Cherves-de-Cognac (Berriasian) and Angeac-Charente improve our poor knowledge of the evolution of continental vertebrate faunas at the Jurassic/Cretaceous transition. Rather than reflecting an important faunal turnover between the Tithonian and the Berriasian, they record environmental changes related to the sea-level regression that characterizes the end of the Jurassic.

**KEY WORDS**

Vertebrata,  
Dinosauria,  
Mammalia,  
Amphibia,  
Reptilia,  
Early Cretaceous,  
Jurassic/Cretaceous  
boundary,  
Berriasian,  
France,  
Lagerstätte,  
Faunal list.

## RÉSUMÉ

*Paléobiodiversité des vertébrés du Lagerstätte du Crétacé inférieur (Berriasien) d'Angeac-Charente (sud-ouest de la France), implications pour le renouvellement faunique continental à la limite J/K.*

La faune de vertébrés continentaux, représentée à la fois par des macro- et des microrestes, du Berriasien d'Angeac-Charente est décrite ici. Cette faune riche et diversifiée comprend au moins 38 taxons différents de vertébrés provenant de tous les grands clades et est constituée de plus de 50 000 spécimens. Le gisement d'Angeac-Charente est le plus diversifié des bonebeds mixtes et le seul Lagerstätte continental du Crétacé connu à ce jour dans le monde. Il donne une bonne image de la paléocommunauté purbeckienne. Cette dernière comprend des taxons remarquables tels qu'un nouvel ornithomimosaur, un grand turiasaur, une tortue hélochelydride et de nombreux mammifères. La faune d'Angeac-Charente présente avant tout un cachet purbeckien. De nombreux genres et espèces exclusivement européens appartiennent à des familles dont la répartition paléogéographique est essentiellement laurasiatique. Certains taxons suggèrent néanmoins des événements de dispersion entre l'Afrique et l'Europe à la transition Jurassique/Crétacé. Les faunes charentaises des gisements de Chassiron (Tithonien), de Cherves-de-Cognac (Berriasien) et d'Angeac-Charente améliorent nos connaissances sur l'évolution des faunes continentales à la transition Jurassique-Crétacé. Plutôt que de refléter un important renouvellement faunistique entre le Tithonien et le Berriasien, elles enregistrent les changements environnementaux liés à la régression globale qui caractérise la fin du Jurassique.

## MOTS CLÉS

Vertebrata,  
Dinosauria,  
Mammalia,  
Amphibia,  
Reptilia,  
Crétacé inférieur,  
limite Jurassique-  
Crétacé,  
Berriasien,  
France,  
Lagerstätte,  
liste faunique.

## INTRODUCTION

The Purbeckian facies the type section of which is found in the Isle of Purbeck, Dorset, UK, was initially recognized by the French naturalist Alexandre Brongniart (1829). This term applied to the sediments accumulated in very shallow environments, often of the lagoon or lake type, which spanned the transition between the Late Jurassic and the earliest Cretaceous in southern England. These deposits are related to the significant global sea-level regression that characterizes the Jurassic/Cretaceous (J/K) boundary (Hallam 2001). The Purbeckian beds in southern England have also long been known for their fossils (Owen 1853, 1871; Milner & Batten 2002). Since that time, several “Purbeckian” sections and fossil localities have been reported from outside England in western Europe (*e.g.* Strasser 1986; De Cisneros & Vera 1993; Arp & Mennerich 2008). In the past two decades, three new productive “Purbeckian” fossil localities have been discovered in Charente and Charente-Maritime departments in western France: Chassiron, Cherves-de-Cognac and Angeac-Charente (Fig. 1).

Chassiron, the westernmost and oldest of these localities is located at the extreme northern point of Oléron Island (Fig. 1). It has yielded abundant and diverse fossil remains of plants and animals from an early Tithonian littoral ecosystem that comprises a mix of terrestrial, freshwater and marine taxa, including at least 31 vertebrate taxa (Schneider *et al.* 2012; Vullo *et al.* 2014). The gypsum quarry of Champblanc is located near Cherves-de-Cognac, 5 km north of Cognac. It records Tithonian and Berriasian deposits from a coastal lagoon to a continental lake (Colin *et al.* 2004; El Albani *et al.* 2004). The alternation of levels of gypsum, claystones, marlstones and limestones has yielded microremains of a diverse vertebrate assemblage, as well as

numerous macroremains of fish, turtles and crocodyliforms (Pouech 2008; Pouech *et al.* 2015; Louchart & Pouech 2017). The easternmost and youngest of these localities, Angeac-Charente, located equidistant from Cognac to the west and Angoulême to the east, yielded its first fossils in 2008 (Allain *et al.* 2017). The preliminary results, based on the material collected during the first two excavation campaigns in 2010 and 2011, have made it possible to highlight the taxonomic diversity of the site (Néraudeau *et al.* 2012). Further studies, based on the same material, have clarified the age of the deposit showing it to be late Berriasian (Benoit *et al.* 2017; Polette *et al.* 2018), and emphasized the originality of this continental fauna (Allain *et al.* 2014). Taphonomic and sedimentological studies conducted during the first ten years of excavations have shown that the Angeac-Charente locality represents a “snapshot” of an Early Cretaceous continental swampy ecosystem, and that the richness, diversity and preservation of the fossils qualify the site as a fossil Lagerstätte (Rozada *et al.* 2014; Gônet *et al.* 2019; Rozada 2019; Rozada *et al.* 2021).

The main aims of this study are to describe in outline and figure the complete vertebrate fauna of Angeac-Charente, including the microfauna collected over the past ten years, and to examine the diversity and paleoenvironmental characteristics of this fossil assemblage. Our goal is also to compare this fauna with those known, during the restricted interval that spans the Tithonian and the Berriasian in western France and England and, to a lesser extent, in the Iberian Peninsula and Northern Africa. In the context of the poorly known J/K continental faunal transition (Tenant *et al.* 2017; Campos-Soto *et al.* 2019; Lasseron *et al.* 2020), the latter comparisons are useful to test whether continental vertebrate assemblages record any extinction events, at least at a continental scale.

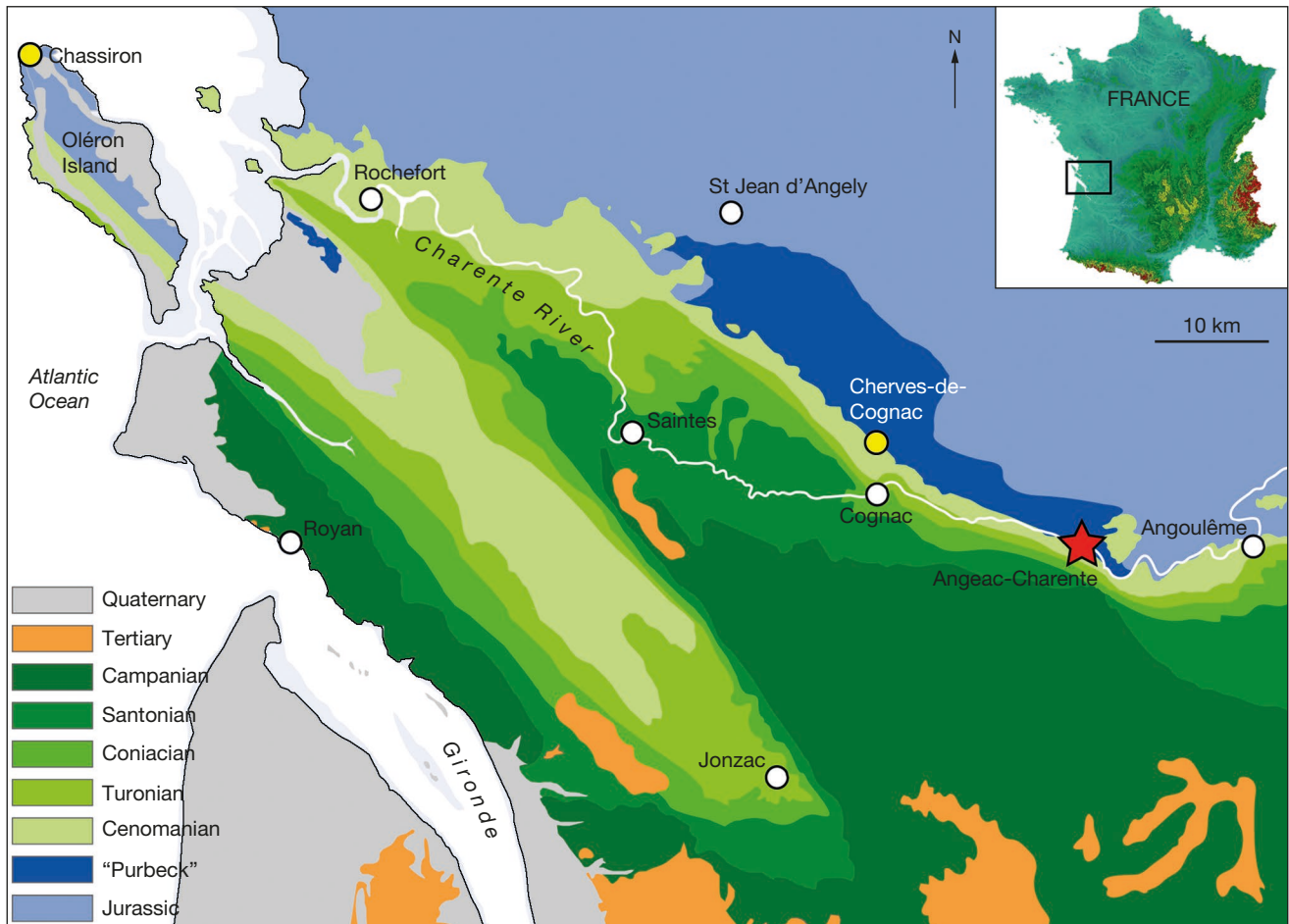


FIG. 1. — Geographical distribution of the three continental fossil localities documenting the Late Jurassic to Early Cretaceous transition in Western France: Chassiron (Tithonian, Department of Charente-Maritime), Cherves-de-Cognac (Berriasian, Department of Charente) and Angeac-Charente (Berriasian, Department of Charente).

## MATERIAL AND METHODS

### INSTITUTIONAL ABBREVIATIONS

- ANG Angeac-Charente Collection, Musée d'Angoulême, Angoulême, France;  
 DORCM Dorset County Museum, Dorchester, United Kingdom;  
 FMNHN Field Museum of Natural History, Chicago, United States.

### FIELDWORK

The first dinosaur bones were discovered at Angeac-Charente as early as 2008, in a quarry operated by the Audoin & Fils Company. By exploiting the sands and gravels left during the Pleistocene by the Charente River, which now flows 2 km northeast of the site, the quarry worker Jean-Pierre Paillot discovered a vertebra, a metatarsal and some fragments of large sauropod bones (Néraudeau *et al.* 2012; Allain *et al.* 2017). Following the discovery of new bones by quarrymen in January and February 2010, a first excavation campaign involving about 15 people from the Musée d'Angoulême, the Rennes University and the Muséum national d'Histoire naturelle was carried out between late August and early Sep-

tember 2010 (Fig. 2A). The excavation area of 20 m<sup>2</sup> yielded 599 fossils of vertebrates, invertebrates and plants, including a 2.2 m long sauropod femur (Néraudeau *et al.* 2012: fig. 11). On the strength of these results, from the following year, and thanks to the support of the local authorities and the Audoin Company, larger scale excavations were set up. Thus, every year for one month since summer 2011, a team of around forty people has been manually excavating the fossiliferous clays of Angeac-Charente (Fig. 2). The paleontological excavations are divided into two main plots, a northwestern plot called CG, and a southwestern plot called R (Fig. 3; Rozada *et al.* 2021). “CG” means “Conseil Général” and refers to the fact that this part of the site is today the property of the Department of Charente, while “R” stands for “Rodet”, the family name of the owner of this part of the quarry. By the end of the 2019 campaign, more than 800 m<sup>2</sup> had been excavated on an average thickness of 1 m. More than 7500 macrofossils were collected, identified, mapped using theodolite and total station, and fully prepared. To these can be added around 67000 unidentified specimens (i.e. bone fragments), 3350 coprolites and tens of thousands of microremains (Rozada *et al.* 2021).



FIG. 2. — Views of the Angeac-Charente gravel quarry: **A**, CG1 plot at the end of the 2010 excavation campaign; **B**, CG1 and CG3 plots at the beginning of the 2013 excavation campaign; **C**, CG4, CG6, CG7 plots (on the left) and CG9 plot (on the right) during the 2018 excavation campaign.

#### MICROREMAINS

Nearly all the microremains presented in this study were collected in 2014 from within a large lens in Unit 3 clay of R1 plot (Fig. 3), composed of sand, soft white calcareous clasts, wood fragments and vertebrate remains, including a near-complete turtle shell (Gônet *et al.* 2019; Rozada *et al.* 2021). Several hundred kilograms of sediment from other plots have also been sampled but have yet to be fully sorted. All sediment samples were dried before treating by screen-washing. In the

field, the dissociation of clay was only performed with water. Screen-washing was made through four successive sieves of 4, 1.2, 0.8 and 0.5 mm mesh. In the laboratory of the Centre de Recherche en Paléontologie – Paris (CR2P), at the Muséum national d’Histoire naturelle, the lithoclastic and bioclastic sand sieved following this process was reconcentrated using formic acid for carbonate dissolution and sodium dithionite to remove iron-bearing mineral phases. The size fractions were then separated using sieves of 2, 1 and 0.5 mm mesh



FIG. 3. — Spatial distribution of identified vertebrate bodyfossil remains of Angeac-Charente recovered from 2013 to 2018: **A**, aerial view of the Angeac-Charente site with the location of the manual (R1-3 and CG1-8) excavation plots and some remarkable fossils (drone picture ©D. Abit, July 2017); **B**, diagram of the Angeac-Charente locality with the position of vertebrate body fossil remains according to taxon type. Each point represents the position of one specimen (3-D SIG data measured from 2013 to 2018 projected with ArcGIS Desktop 10.3.1.). SIG data from the CG1 plot (2010-2012) are lacking (in grey) (See Rozada *et al.* 2021).



and sorted under stereomicroscope by two of us (G. Bailly and R. Vacant). The vertebrate microremains were counted using the ‘Count Image Elements’ script, specifically developed by A. Gailliègue (pers. comm., April 2017) and based on the principle of picture segmentation (see Lasseron *et al.* 2020). SEM photomicrographs were made at the CR2P and at Rennes University.

#### REPOSITORY

All fossil specimens collected in Angeac-Charente were officially donated to the Musée d’Angoulême (Charente, France) by the owners of the different plots of land that made up the fossiliferous part of the quarry: the Audoin & Fils Company, Mrs Rodet and the Charente department. These fossils are deposited in the collections of the Musée d’Angoulême, under collection numbers with the following syntax: *ANGyy-nnnn*, *ANGyy-Rnnnn* or *ANG M-nnnn*, where “ANG” is an abbreviation of Angeac-Charente, “M” means microremain, “R” means Rodet, “yy” year of discovery and “nnnn” the specimen number.

#### SEDIMENTOLOGICAL FRAMEWORK AND TAPHONOMY

##### DEPOSITIONAL ENVIRONMENT

A detailed account of the general taphonomy and sedimentology of the Angeac-Charente Lagerstätte has already been published (Rozada *et al.* 2021). The site represents a “snapshot” into a Lower Cretaceous swampy environment and the sedimentological assemblage consists mainly of clay deposits. We provide here a synthetic sedimentary log of the Angeac-Charente bonebed (Fig. 4). The sandy clay (Unit 2), clay of decantation (Unit 3), and sand/conglomerate (Unit 4) deposits contain the bonebed and have the same paleontological content, but they correspond to different energy of deposition episodes (Fig. 4):

- Deposition Event 1 (DE 1): The system begins with the deposition of a high energy sandy clay (Unit 2), which erodes the underlying green clay (Unit 1) and brings into it many plant and vertebrate fossils.

- Deposition Event 2 (DE 2): The clay of decantation (Unit 3) is deposited over a longer time interval and under a stagnant water column. There is no discordance or break in sedimentation between Units 2 and 3. A few mudcracks may indicate occasional, localized and temporary exposure of the clay. This low energy deposit is occasionally interrupted by streams of variable energy, depositing lenses rich in coarser grains and fossils. Unit 3 has yielded most of the Angeac-Charente fossils.

- Deposition Event 3 (DE 3): A more or less clayey and silty sandbank that sometimes grades laterally into sandstone and conglomerate (Unit 4) was deposited at a higher energy level. It probably corresponds to a discrete flooding event from a nearby river. During the 2019 field campaign, interbedded lamination of silt and sand that may indicate deposits left by a river channel have been observed in this unit.

In parallel with these three depositional events, synsedimentary deformational structures formed in water-saturated sediments can be observed such as convolute lamination in clay, folded figures in sands and rebalance loads. These numerous sedimentological structures, allied with taphonomic “frozen scenes”, suggest a coeval and continuous deposition of all three units (Rozada *et al.* 2021). The homogeneous composition of the clay mineral assemblage of the whole lithostratigraphic section (Néraudeau *et al.* 2012) and the Rare Earth Elements and Yttrium profiles measured in sediment throughout the lithological section and on dinosaur fossil biogenic apatite samples (Rozada *et al.* 2021) also confirm that all the sediments and vertebrate remains were deposited under similar, coeval, poorly oxygenated burial and diagenetic conditions. These mineralogical and geochemical analyses also indicate that the Angeac-Charente organisms fossilized near their living habitat and/or place of death in a local depositional environment and demonstrate a limited time averaging of the fossil concentration.

Thus, the site represents a “snapshot” into an Early Cretaceous swampy ecosystem, very likely a floodplain connected to a nearby river. The Angeac-Charente bonebed accumulated on a poorly oxygenated freshwater floodplain dominated by cheirolepidiacean vegetation in a tropical to subtropical climate (Néraudeau *et al.* 2012; Polette *et al.* 2018; Rozada *et al.* 2021). The fossil richness, diversity and preservation permit designation of the site as a fossil Lagerstätte (Rozada *et al.* 2021).

##### SPATIAL DISTRIBUTION OF ANGEAC-CHARENTE VERTEBRATE MACROREMAINS

Rozada *et al.* (2021) provide the first data concerning the spatial distribution of vertebrate remains based on identified and unidentified macroremains collected between the 2010 and 2017 field campaigns. Herein, we supplement these data by mapping the position of identified vertebrate remains recovered between the 2013–2018 field campaigns (Fig. 3B).

Turtle remains are mainly represented by isolated, complete or fragmented shell plates and a few bones, and are quite homogeneously distributed throughout the whole site (Fig. 3B). The collected remains of *Pleurosternon bullockii* belong at least to twelve individuals of different sizes. The remains are generally well-preserved, with no evidence of weathering or erosion, although they are frequently fragmented. A very well-preserved and nearly complete turtle shell of *Pleurosternon bullockii* was collected in 2014, from a lens in R1 (Gönet *et al.* 2019; Fig. 3A). At several loci of the site, connected plates of *P. bullockii* were also collected. In 2017, numerous plates belonging to a nearly complete specimen have been found in loose articulation in the R3 plot (Fig. 3A). All these observations suggest that pleurosternid turtles were autochthonous.

Crocodyliforms are known from numerous isolated teeth (mostly shed due to continuous tooth replacement), osteoderms, and other bones including numerous skull bone fragments, randomly distributed throughout the whole site. Most of these remains belong to the generalist genus *Goniopholis* (see below). In 2018, numerous *Goniopholis* bones (skull, mandibles, vertebrae, limb, girdle bones and osteoderms) belonging

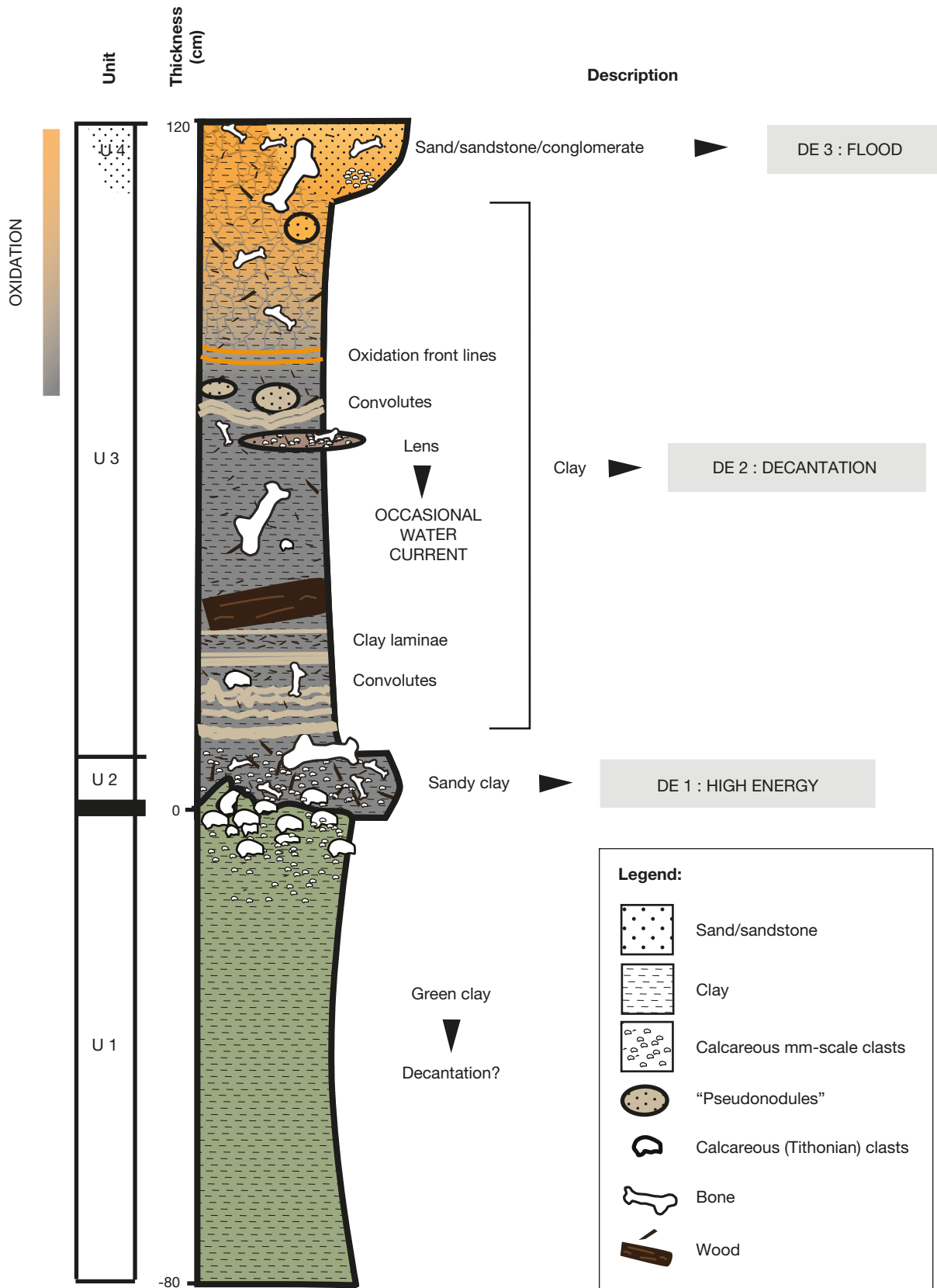


FIG. 4. — Angeac-Charente synthetic log based on the lithostratigraphic sections of R3, CG3 and CG9, of Rozada *et al.* (2021), and the main corresponding depositional events. The thickness is measured above and below the Unit 1/Unit 2 limit, which marks the base of the bonebed. Abbreviations: **DE**, Depositional Event; **U**, Unit.

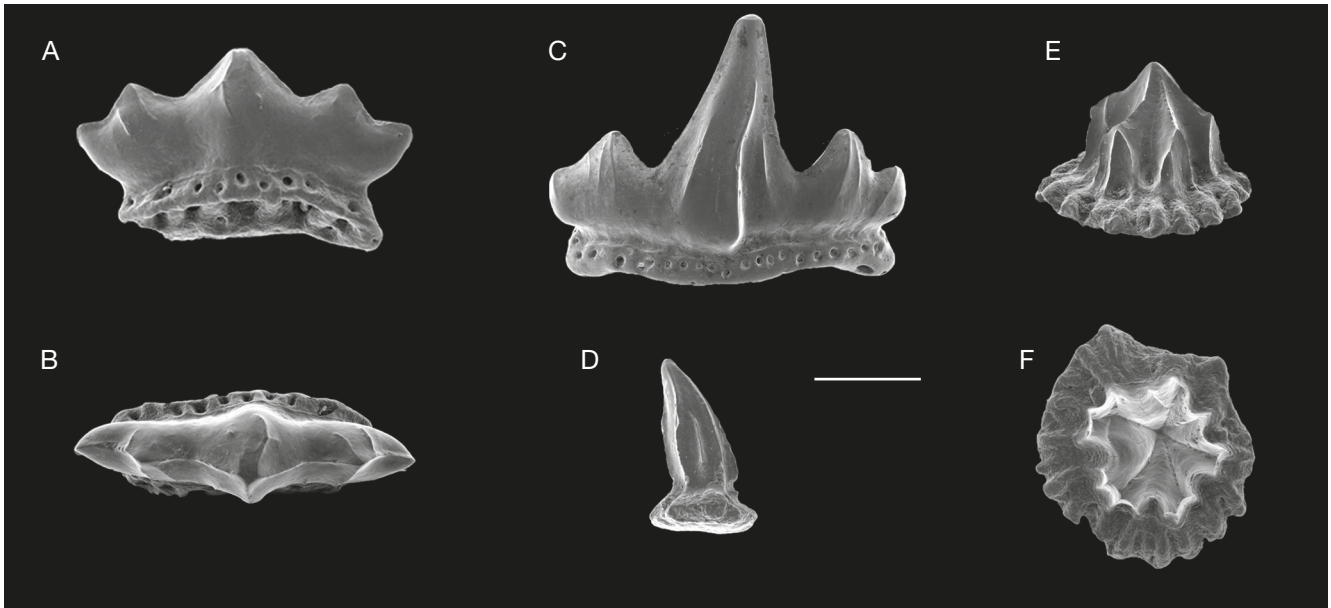


FIG. 5. — Scanning electron micrographs of hybodont shark teeth from Angeac-Charente: **A, B**, lateral tooth of *Parvodus celsucuspus* Rees, Cuny, Pouech & Mazin, 2013 (ANG M-107) in labial (**A**) and occlusal (**B**) views; **C**, anterior tooth of *Parvodus celsucuspus* (ANG M-17) in labial view; **D**, dermal denticle (ANG M-109) in lateral view; **E, F**, dermal denticle (ANG M-108) in lateral (**E**) and apical (**F**) views. Scale bar: C, 1 mm; A, B, D-F, 400  $\mu$ m.

to a single individual were found in loose articulation in the CG9 plot (Fig. 3A). Otherwise, the remains of Pholidosauridae, Bernissartiidae and Atoposauridae are rarer and mainly recovered from sieved microremains, and are therefore under represented on the map (Fig. 3B).

Ornithomimosaur remains are concentrated in the CG1-9 plots (85% of the ornithomimosaur bones) and become progressively rarer toward the SE and in the NW part of the site, in the CG9 plot (Fig. 3). This spatial distribution supports a mass mortality event involving a herd (Rozada *et al.* 2021).

So far, no postcranial remains of carnivorous dinosaurs have been discovered at Angeac-Charente. However, nearly 150 isolated teeth have been collected. They are randomly distributed and most of them have not been mapped.

Sauropod remains, represented by numerous teeth and bones from all parts of the skeleton, come from at least seven individuals with no apparent connection to each other. They are abundant in most areas, but become rarer toward the NW and the SE. Although they seem mainly concentrated in R1 plot, this is a false impression as bones are heavily fragmented, and each fragment has been mapped at some point. The R2 and CG10 plots have yielded the well-preserved hindquarters of a single individual, including the last dorsal vertebra, the sacrum, the two ischia, a few chevrons and ribs, and a complete femur (Figs 3A; 27).

Stegosaurs are represented by a few bones, mostly vertebrae and ribs and scarce appendicular and skull bones. Although they are present in all plots of the site, they are particularly concentrated in CG4. In this area, the bones show a homogeneous state of preservation, and probably belong to a single individual, which died near the site. Other ornithischian remains (camptosaurid ornithopods, hypsilophodontids, heterodontosaurids and ankylosaurs) are rare.

## SYSTEMATIC PALEONTOLOGY

VERTEBRATA Lamarck, 1801  
 PISCES Linnaeus, 1758  
 CHONDRICHTHYES Huxley, 1880  
 ELASMOBRANCHII Bonaparte, 1838  
 HYBODONTIFORMES Patterson, 1966  
 Family LONCHIDIIDAE Herman, 1977  
 Genus *Parvodus* Rees & Underwood, 2002

*Parvodus celsucuspus* Rees, Cuny, Pouech & Mazin, 2013  
 (Fig. 5)

### DESCRIPTION

This species is characterized by high-cusped anterior teeth, and is well represented at Angeac-Charente. The material includes numerous isolated teeth and dermal denticles (Fig. 5), as well as a few incomplete cephalic and dorsal fin spines (Néraudeau *et al.* 2012), that are identical to those of Cherves-de-Cognac (Rees *et al.* 2013).

OSTEICHTHYES Huxley, 1880  
 ACTINOPTERYGII Klein, 1885  
 PYCNODONTIFORMES Berg, 1937  
 Family MESTURIDAE Nursall, 1996  
 Genus *Microptycnodon* Hibbard & Graffham, 1945

cf. *Microptycnodon* sp.  
 (Fig. 6A-C)

### DESCRIPTION

Teeth attributed to Mesturidae, sub-circular to oval in occlusal view, are characterized by the presence of several

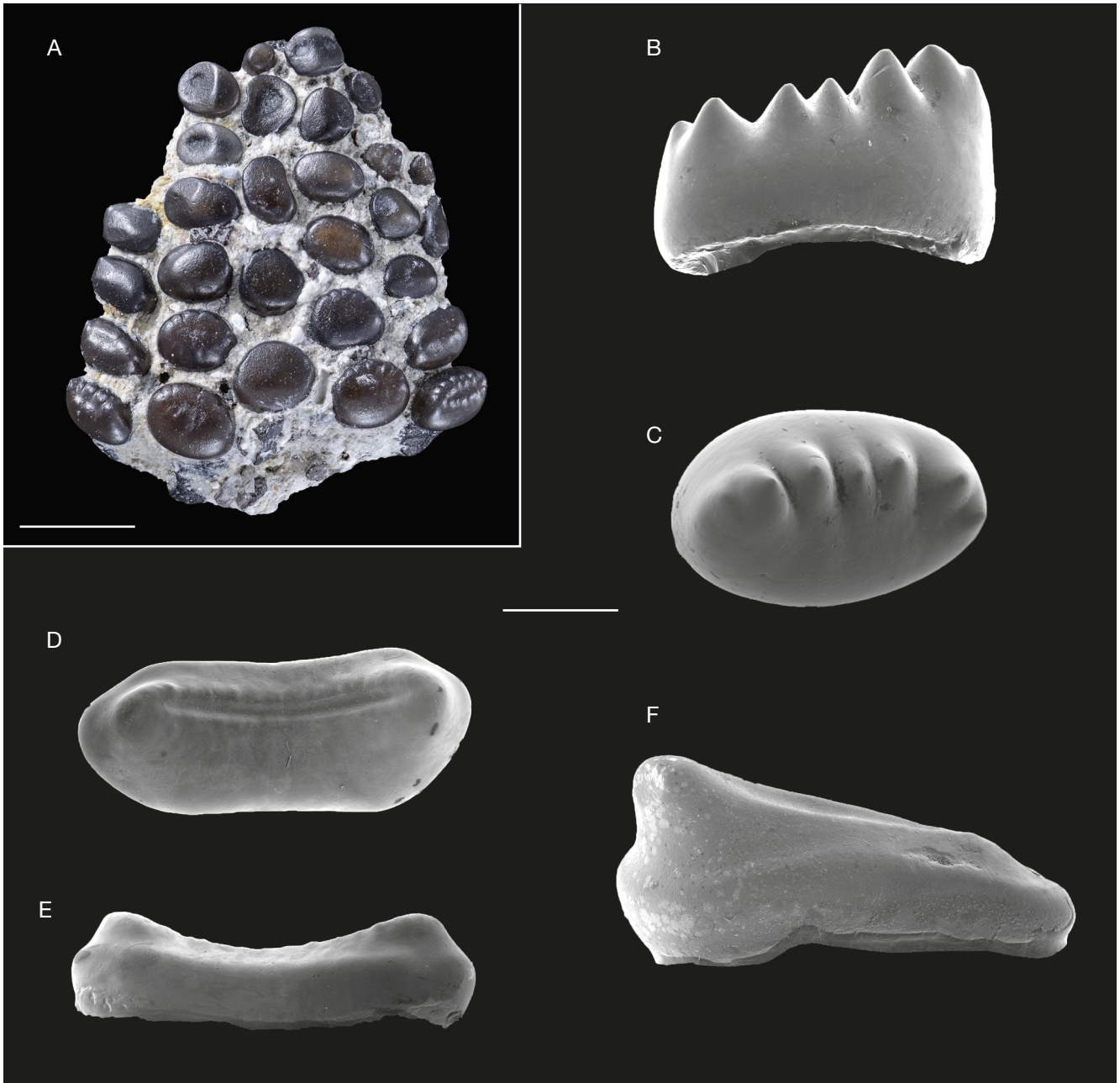


FIG. 6. — Actinopterygian remains from Angeac-Charente: **A**, vomerine dentition of cf. *Micropycnodon* sp. (ANG M-69) in occlusal view; **B**, **C**, detailed view of an isolated vomerine tooth of cf. *Micropycnodon* sp. (ANG M-28) in **(B)** anterior and **(C)** occlusal views; **D**, **E**, isolated tooth of Pycnodontidae indet. (ANG M-50) in occlusal **(D)** and lateral **(E)** views; **F**, isolated tooth of Pycnodontidae indet. (ANG M-59) in lateral view. Scale bars: A, 2.5 mm; B, C, F, 500  $\mu$ m; D, E, 1 mm.

small, sharp tubercles, arranged in rows or surrounding a shallow central depression (Fig. 6A-C). A nearly complete, relatively broad vomerine dentition shows six tooth rows (Fig. 6A). Crown morphology and tooth arrangement are similar to those of *Micropycnodon* (Dunkle & Hibbard 1946; Cronin & Shimada 2019). *Micropycnodon* is known from the Late Cretaceous of North America, but similar genera (possibly subjective junior synonyms) known from the Early Jurassic of Germany (*Grimmenodon*; Stumpf *et al.* 2017) and the Early Cretaceous of Texas (*Texasensis* pro *Callodus*; Thurmond 1974; Özdikmen 2009) suggest a long temporal range for this lineage. The form in Angeac-Charente also

occurs in the Purbeckian facies of Cherves-de-Cognac, and was described as “pycnodontiform tooth morphotype 10” by Pouech *et al.* (2015: fig. 8e-f).

#### Family PYCNODONTIDAE Agassiz, 1835

##### Pycnodontidae indet. (Fig. 6D-F)

#### DESCRIPTION

A second pycnodontiform taxon is represented by bean-shaped to suboval teeth with a transverse groove or depression

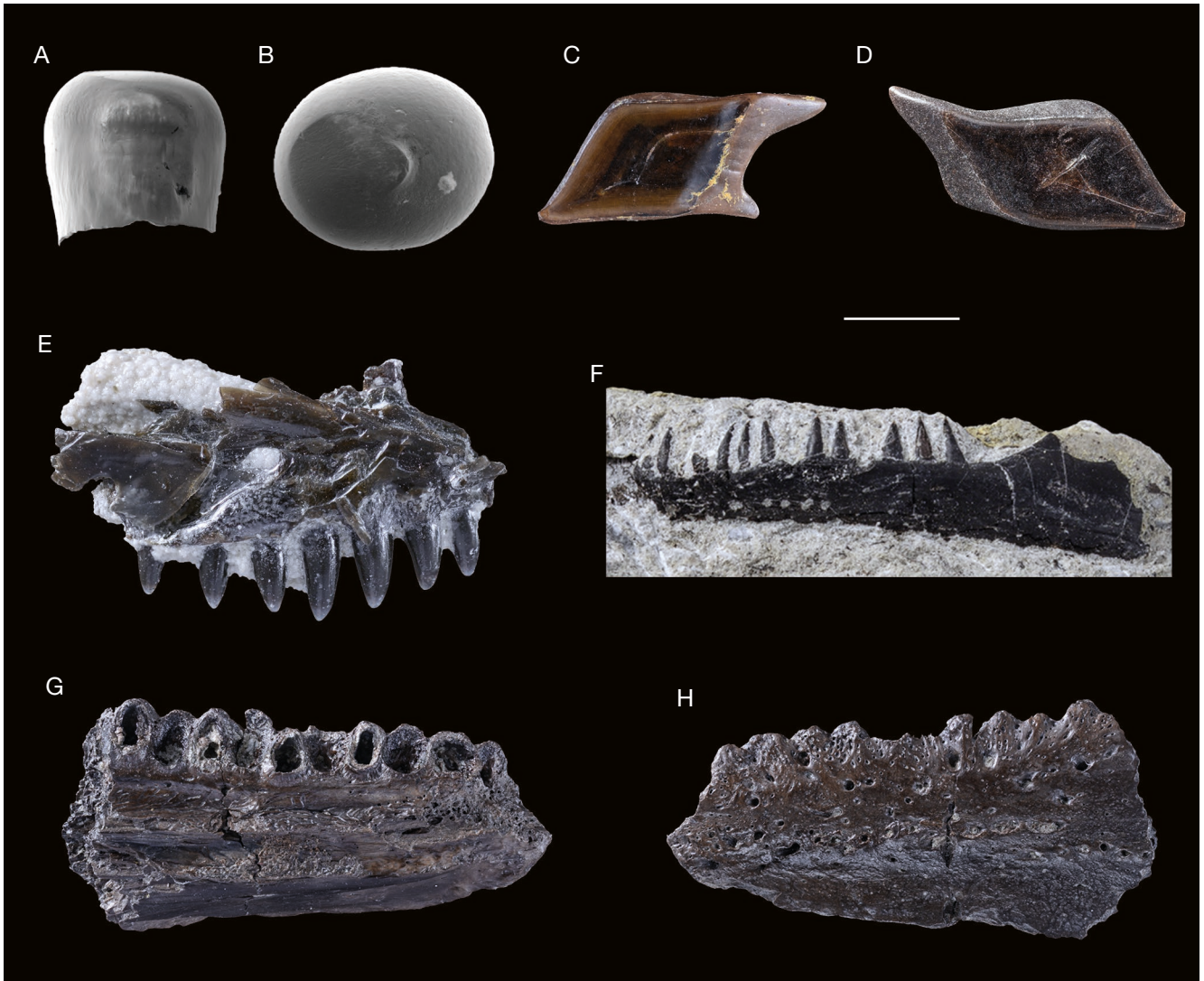


FIG. 7. — Actinopterygian remains from Angeac-Charente: **A, B**, isolated tooth of *Ginglymodi* indet. (ANG M-30) in anterior/posterior (**A**) and occlusal (**B**) views; **C**, *Ginglymodi* indet. scale (ANG M-68); **D**, *Ginglymodi* indet. scale (ANG M-67); **E**, upper jaw fragment of *Amiiformes* indet. (ANG M-62) in lingual view; **F**, left dentary of *Amiiformes* indet. (ANG M-117) in labial view; **G, H**, fragmentary left dentary of *Amiiformes* (ANG 15-4062) in lingual (**G**) and labial (**H**) views. Scale bar represents: A, B, 1 mm; C, 4 mm; D, 2 mm; E, 2.5 mm; F, 10 mm; G, H, 5 mm.

and one or two lateral tubercles (Fig. 6D-F). This taxon is also present in the Purbeckian facies of Cherves-de-Cognac, and has been described as “tooth morphotype 7” by Pouech *et al.* (2015: fig. 8b). A very similar and likely congeneric form has also been described from the Wealden facies of southern England as *Coelodus* sp. (Sweetman *et al.* 2014) then assigned to *Ocloedus* sp. (Sweetman 2016). However, the English material includes nearly complete vomerine dentitions with three tooth rows (Sweetman *et al.* 2014: fig. 10e), indicating that this unnamed species does not belong to either *Coelodus* or *Ocloedus*, which both have five vomerine tooth rows (Poyato-Ariza & Wenz 2002). Numerous ventral keel scales showing contacting spines of anteroposteriorly increasing size, can be assigned to Pycnodontidae (see Poyato-Ariza & Wenz 2002; Sweetman *et al.* 2014).

HOLOSTEI Müller, 1844 (*sensu* Grande 2010)  
 GINGLYMODI Cope, 1872  
 (*sensu* López-Arbarello & Sferco 2018)

*Ginglymodi* indet. (Fig. 7A-D)

DESCRIPTION

Material from Angeac-Charente mainly includes isolated teeth and ganoid scales (Fig. 7A-D). Most teeth show a typical sub-hemispheric, unornamented crown. A small tip is sometimes developed at the apex of the crown. Scales are relatively thick and rhomboid in shape. An anteroventral process can be present in addition to the anterodorsal process. The posterior margin is not serrated. Based on the available material, one or two ginglymodian taxa may be present, with possibly a callipurbeckiid (*Semionotiformes*) and/or a lepidotid (*Lepisosteiformes*) (*sensu* López-Arbarello & Sferco 2018).

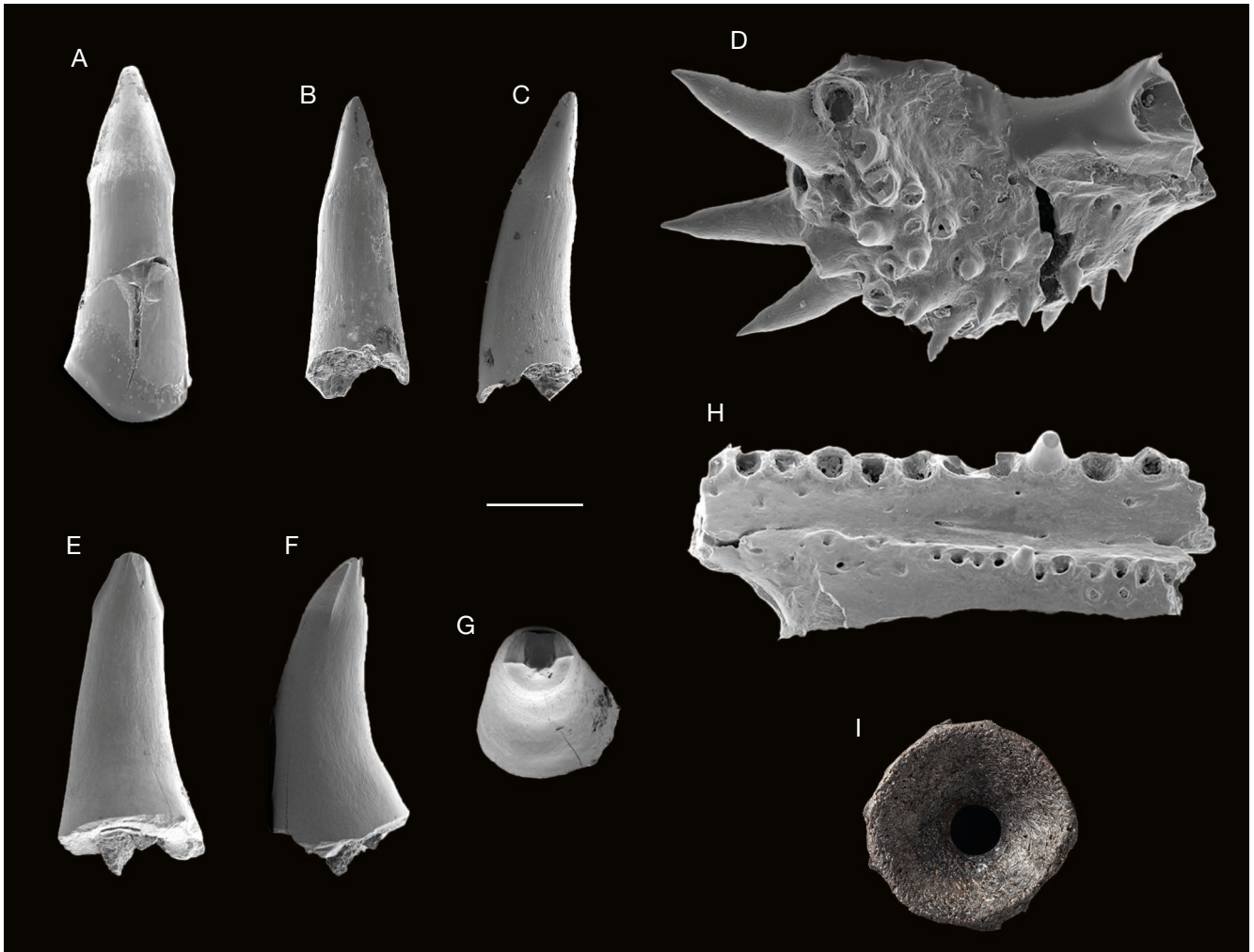


FIG. 8. — Actinopterygian remains from the Berriasian of Angeac-Charente: **A**, isolated tooth of Amiiformes indet. (ANG M-39); **B**, **C**, isolated tooth of Amiiformes indet. (ANG M-110); **D**, dentulous vomerine element of Amiiformes indet. (ANG M-56); **E-G**, isolated tooth of Ionoscopiformes indet. (ANG M-111); **H**, jaw fragment of Actinopterygii indet. (ANG M-38) in lingual view; **I**, vertebra of Actinopterygii indet. (ANG M-069). Scale bar: A-C, E-H, 500 µm; D, 250 µm; I, 2 mm.

HALECOMORPHI Cope, 1872  
AMIIFORMES Hay, 1929  
(*sensu* Grande & Bemis 1998)

Amiiformes indet.  
(Figs 7E-H; 8A-D)

DESCRIPTION

Amiiform fish are represented in the assemblage by isolated teeth, jaw remains (Fig. 7E-H) and vertebrae. Most of the labiolingually compressed teeth show a typical triangular crown apex and bear two well-developed carinae (Fig. 8A-C). Such teeth were previously referred to *Caturus* sp. (Sweetman *et al.* 2014; Vullo *et al.* 2014; Pouech *et al.* 2015), although this dental morphology is also present in more derived members of Amiiformes (i.e., Amiidae). Some tooth associations are interpreted as vomerine dentitions (Fig. 8D). These elements bear teeth of various sizes, subconical and devoid of carinae, as those found in many Amiiformes (Grande & Bemis 1998). It is worth noting that this tooth morphology corresponds

to that usually assigned to the aspidorhynchid *Belonostomus* (e.g., Sweetman *et al.* 2014; Pouech *et al.* 2015). However, the rounded morphology of the vomerine tooth plates from Angeac-Charente and the fact that they are paired elements preclude assignment to *Belonostomus* (in which the vomer is unpaired); therefore, all isolated small teeth with a conical crown devoid of carinae are here referred to Amiiformes indet.

IONOSCOPIFORMES  
*sensu* Grande & Bemis (1998)

Ionoscopiformes indet.  
(Fig. 8E-G)

DESCRIPTION

Small, curved teeth with a pointed apex bearing two short, blunt carinae are assigned to an indeterminate ionoscopiform (Fig. 8E-G). Small ganoid scales characterized by a finely serrated posterior margin may also belong to this group. Such a

material is similar to that described from the Purbeckian beds of Chassiron (Vullo *et al.* 2014). As some recent studies suggest that Ionoscopiformes is not a monophyletic clade (Ebert 2018; López-Arbarello & Sferco 2018), the material from Angeac-Charente is assigned to Ionoscopiformes *sensu* Grande & Bemis (1998).

AMPHIBIA Linnaeus, 1758  
LISSAMPHIBIA Haeckel, 1866  
ALLOCAUDATA Fox & Naylor, 1982  
Family ALBANERPETONTIDAE Fox & Naylor, 1982

Albanerpetontidae indet.  
(Fig. 9)

#### DESCRIPTION

Albanerpetontids are represented in Angeac-Charente by numerous and diverse bones, including dentaries, premaxillae, maxillae, vertebrae and forelimb bones (Fig. 9A-K). All the material was recovered from screen washing residues. It is always disarticulated, and almost always fragmentary. Several diagnostic characters allow their assignment to the Albanerpetontidae, including: 1) intertonguing symphyseal joint between dentaries, in a mortise-and-tenon style (Fox & Naylor 1982; Milner 1988; McGowan & Evans 1995; McGowan 1996, 2002; Gardner 1999b, 2000; Gardner *et al.* 2003; Sweetman & Gardner 2013; Matsumoto & Evans 2018). In the Angeac-Charente specimens, there are two symphyseal prongs (Fig. 9A, B); 2) pleurodont, chisel-like and regularly arranged non-pedicellate teeth, labiolingually compressed and bearing three faint, mesiodistally aligned cusps (Fig. 9A-G; Fox & Naylor 1982; Gardner 1999a, b, 2000; McGowan & Evans 1995; Sweetman & Gardner 2013; Matsumoto & Evans 2018); and 3) foramina arranged in line on external face of dentary (Fig. 9F; Fox & Naylor 1982; Gardner 2000).

In Angeac-Charente albanerpetontids, the maxilla is unornamented labially, except for scattered external nutritive foramina that are characteristic of the group (Fig. 9D; Fox & Naylor 1982; Gardner 2000). In this respect, they differ from *Albanerpeton inexpectatum* from the Miocene of France (Gardner 1999a). As in other albanerpetontid for which trunk vertebrae have been described (Estes & Hoffstetter 1976; McGowan 1996, 2002; McGowan & Ensom 1997; Sweetman & Gardner 2013; Matsumoto & Evans 2018), those from the Angeac-Charente material (Fig. 9I-K) are amphicoelous, hourglass-shaped and bear a short unicipital transverse process. The centrum is narrowly constricted at its center (Fig. 9I, K) and the cotyles are circular in outline and have thickened rims (Fig. 9J). As in other albanerpetontid trunk vertebrae described elsewhere, the notochordal canal is anteroposteriorly continuous (Fig. 9J; Sweetman & Gardner 2013) and thus the vertebrae are fully notochordal.

Angeac-Charente specimens also show numerous features that have been described in other albanerpetontids and allow the distinction from other lissamphibians and lizards. The premaxilla (Fig. 9D, E) and maxilla (Fig. 9C) have a deep *pars dentalis* and the dentary (Fig. 9A, B, F, G) has a tall dental parapet, allowing

the attachment of highly pleurodont teeth (Gardner 2000). Upper jaws are also characterized by a prominent, shelf-like *pars palatinum* lingually (Fig. 9E; Gardner 2000). The maxilla has a low, posteriorly tapered *pars facialis* (Fig. 9C; Gardner 1999a, 2000). On the dentary, the Meckelian canal is closed anteriorly, and the subdental shelf is low, narrow and gutter-like anteriorly (Fig. 9A; Gardner 1999a, b, 2000). As in other known albanerpetontid species, the humeral condyle is spherical, fully ossified and larger than the adjacent radial epicondyle (Fig. 9H; Sweetman & Gardner 2013). Above this humeral ball is a triangular and well-defined cubital fossa, at the proximal extremity of which a small foramen can be seen (Fig. 9H), as also reported for *Albanerpeton inexpectatum* (Estes & Hoffstetter 1976) and *Wesserpeton evansae* (Sweetman & Gardner 2013).

The albanerpetontids from Angeac-Charente differ from *Anoualerpeton* and *Albanerpeton nexuosum*, but resemble other *Albanerpeton* species, *Celtedens* and *Wesserpeton* in having dentaries and maxillae with relatively straight occlusal margins, and teeth weakly heterodont in size (Sweetman & Gardner 2013). Unfortunately, the diagnostic characters necessary for identification at the generic level are lacking. Neither the maxilla nor the dentary is diagnostic for *Albanerpeton* and *Celtedens* (Gardner 2000), as their diagnoses are based on frontal characters (Gardner 1999a, b, 2000; McGowan & Evans 1995; McGowan 2002). We did not find any frontal bones in the Angeac-Charente material, and so we cannot attribute the albanerpetontid material to these genera with certainty. Within *Albanerpeton*, the premaxilla is the most taxonomically informative bone for species (Gardner 1999b, 2000), but the specimens found to date at Angeac-Charente are too incomplete to be relevant.

Thus, considering the characters mentioned above, we can attribute the Angeac-Charente specimens to the family Albanerpetontidae, but so far the material is too incomplete to allow a further attribution at the generic and specific level.

ANURA Fischer von Waldheim, 1813

Anura indet.  
(Fig. 10)

#### DESCRIPTION

Despite a swampy paleoenvironment that might be suitable for their occurrence and preservation, anurans are relatively scarce among the microvertebrate material from Angeac-Charente. In Angeac-Charente, anurans are represented by isolated, fragmentary bones, such as fused zeugopods (Fig. 10A, B) and urostyles (Fig. 10C, D)

Among fused zeugopods, some are sufficiently well preserved to allow their identification. For instance, the general shape and length (even if the proximal part is missing) of specimen ANG M-63 (Fig. 10A, B), as well as several other features, allow its identification as a tibiofibula (Thomas 1996): presence of a tibiofibular groove, deeper on the anterior face, between the fused zeugopod, and presence of a tibial crest on the anterior face (Fig. 10A). Among well-known Early Cretaceous anuran families are the Alytidae (= "Discoglossidae"), but within this

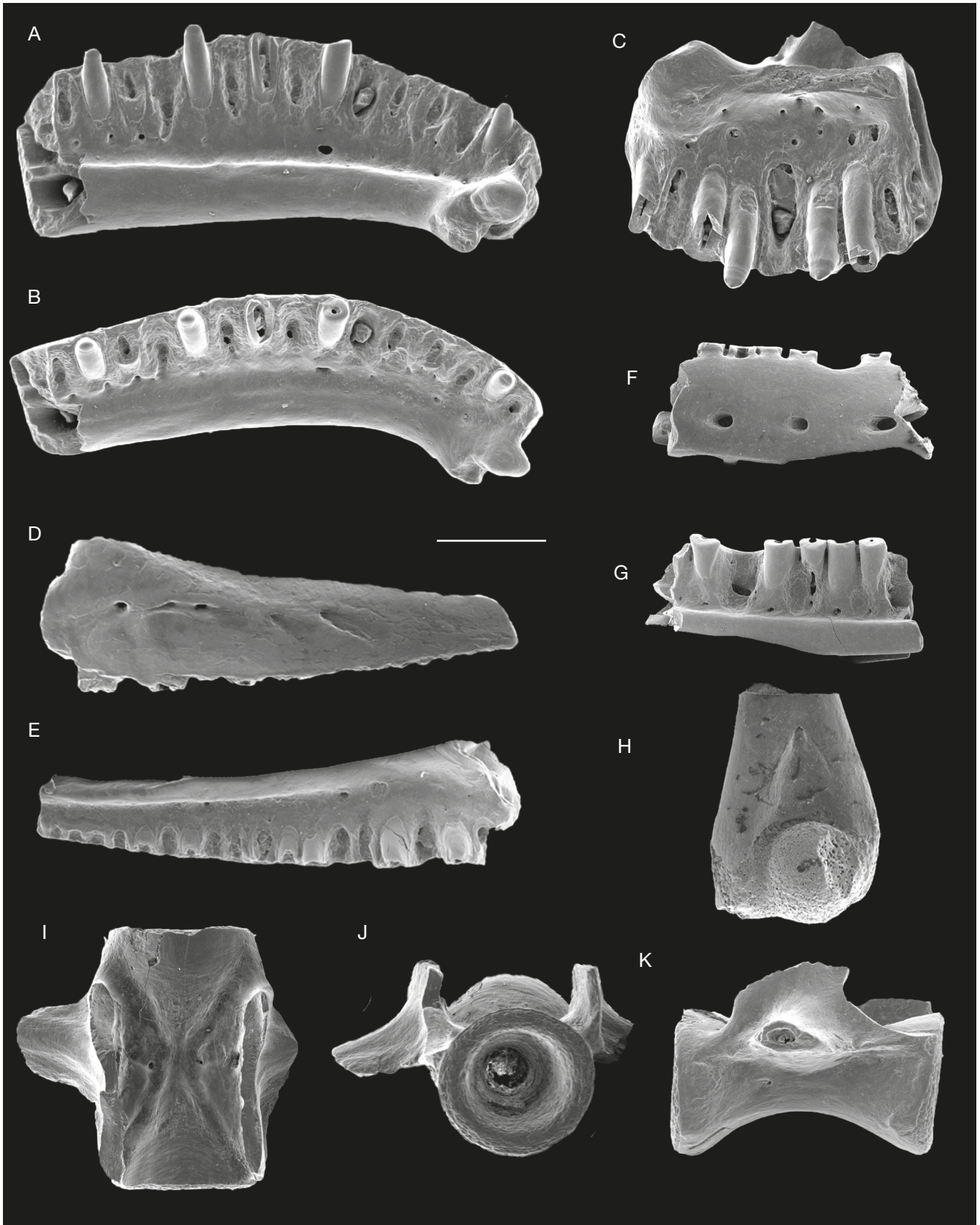


FIG. 9. — Albanerpetontid remains from Angeac-Charente: **A, B**, left dentary of Albanerpetontidae indet. (ANG M-101) in lingual (**A**) and dorsal (**B**) views; **C**, pre-maxillary of Albanerpetontidae indet. (ANG M-102) in ventrolingual view; **D, E**, left maxillary of Albanerpetontidae indet. (ANG M-51) in labial (**D**) and lingual (**E**) views; **F, G**, dentary fragment of Albanerpetontidae indet. (ANG M-35) in labial view showing foramina discussed in the text (**F**) and lingual (**G**) view; **H**, distal end of a left humerus of Albanerpetontidae indet. (ANG M-36) in ventral view; **I-K**, dorsal vertebra of Albanerpetontidae indet. (ANG M-103) in dorsal (**I**), anterior (**J**) and lateral (**K**) views. Scale bars: A-E, H-K, 400 µm; F, G, 1 mm.





FIG. 10. — Anuran remains from Angeac-Charente: **A, B**, right tibiofibular of Anura indet. (ANG M-63) in anterior (**A**) and posterior (**B**) views; **C, D**, urostyle of Anura indet. (ANG M-64) in dorsal (**C**) and ventral (**D**) views. Scale bar represents: **A, B**, 5 mm; **C, D**, 2 mm.

family, the tibia and fibula remain unfused (Roček 2000), unlike the Angeac-Charente specimen.

The specimen ANG M-64 (Fig. 10C, D) bears two broad and flattened articular facets anteriorly, and a small crest arises from its dorsal face. Four weakly marked ridges can be seen alongside this small crest, two on each side (Fig. 9C). This morphology identifies it as a urostyle. To date, incompleteness of the material limits comparisons with other Mesozoic anurans.

#### CAUDATA? Scopoli, 1777

Caudata? indet.  
(Fig. 11)

#### DESCRIPTION

Among the microvertebrates from Angeac-Charente, a specimen could be referred to Caudata. Indeed, the vertebra ANG M-71 (Fig. 11) is anteroposteriorly elongated, with a broad, almost circular cotyle (Fig. 11A) and with well-defined pre- and postzygapophyses. The posterior part of the centrum is abraded, but the vertebra is clearly procoelous. Two small subcentral foramina are present on the ventral face (Fig. 11F). The general shape, presence of transverse processes extending posterolaterally, and broad vertebral cotyle are reminiscent of Caudata (Rage *et al.* 1993). In Caudata, the trunk vertebrae are, however, commonly opisthocoelous or amphicoelous and the procoelous condition is rare (see Estes 1981; Rage *et al.* 1993; Alloul *et al.* 2018 for examples of procoelous caudates). On the contrary, the procoelous condition is common within Squamata, to which this vertebra could be alternatively referred. Moreover, anterior basapophyses, which are present in many caudate groups (Estes 1981), are not discernable, and the presence or absence of a notochordal pit, which is usually observed on caudate vertebrae (Alloul *et al.* 2018), cannot be inferred because of the abraded condyle. However, the left transverse

process (= rib-bearer), although broken, has an expanded head (Fig. 11C, E, F), indicating that it may be bilobed as in salamanders, and a ridge extending between the transverse process and the condyle seems to be present, as in Caudata (Alloul *et al.* 2018), but the preservation is too poor to reach a conclusion. Thus, this vertebra is tentatively referred to Caudata?, although an assignment to Squamata cannot be excluded.

#### TESTUDINATA Klein, 1760

#### PRELIMINARY STATEMENT

Turtles are well represented in Angeac-Charente, notably by numerous isolated shell plates and bones of the axial and appendicular skeletons, and more rarely by articulated shell material (see Table 1; Fig. 35A). Only a few pieces of skulls, including a maxillary and a mandible, have been recovered. Néraudeau *et al.* (2012) have previously reported the presence of three distinct turtle taxa in Angeac-Charente: a pleurosternid, a solemydid (now helochelydid), and a third taxon characterized by shell bones without surface ornamentation (Figs 12; 13). Since then, additional and more complete material confirms these preliminary conclusions (see below). The third taxon is now identified as a thalassochelydian.

#### PERICHELYDIA Joyce, 2017

Family HELOCHELYDRIDAE Nopcsa, 1928  
(*sensu* Joyce *et al.* 2016)

Helochelyridae indet.  
(Fig. 12A, B)

#### DESCRIPTION

In Angeac-Charente, helochelydrids are mostly represented by incomplete isolated shell elements covered by typical

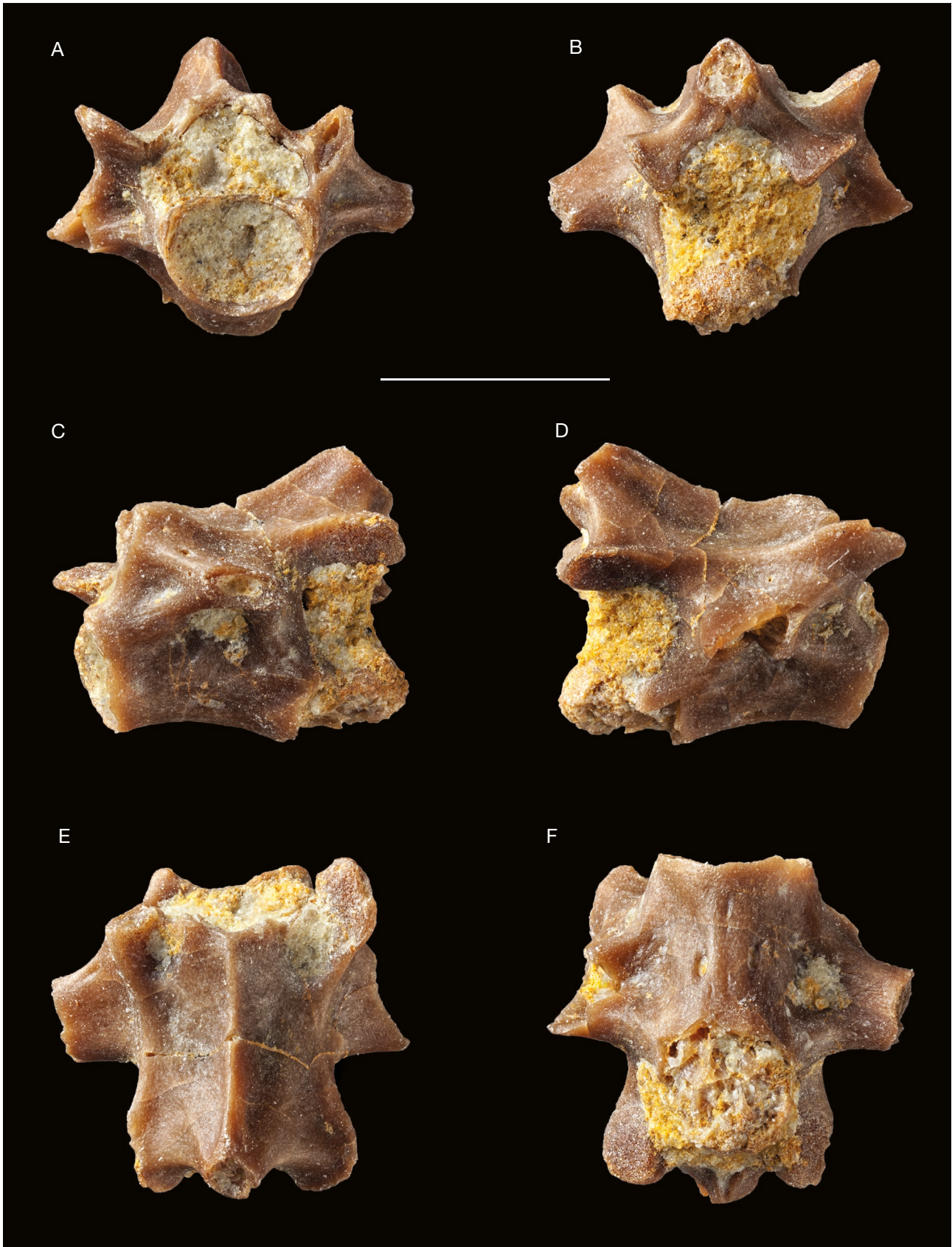


FIG. 11. — Vertebra of Caudata indet. from Angeac-Charente: **A-F**, (ANG M-71) in anterior (**A**), posterior (**B**), left lateral (**C**), right lateral (**D**), dorsal (**E**) and ventral (**F**) views. Scale bar: 2 mm.

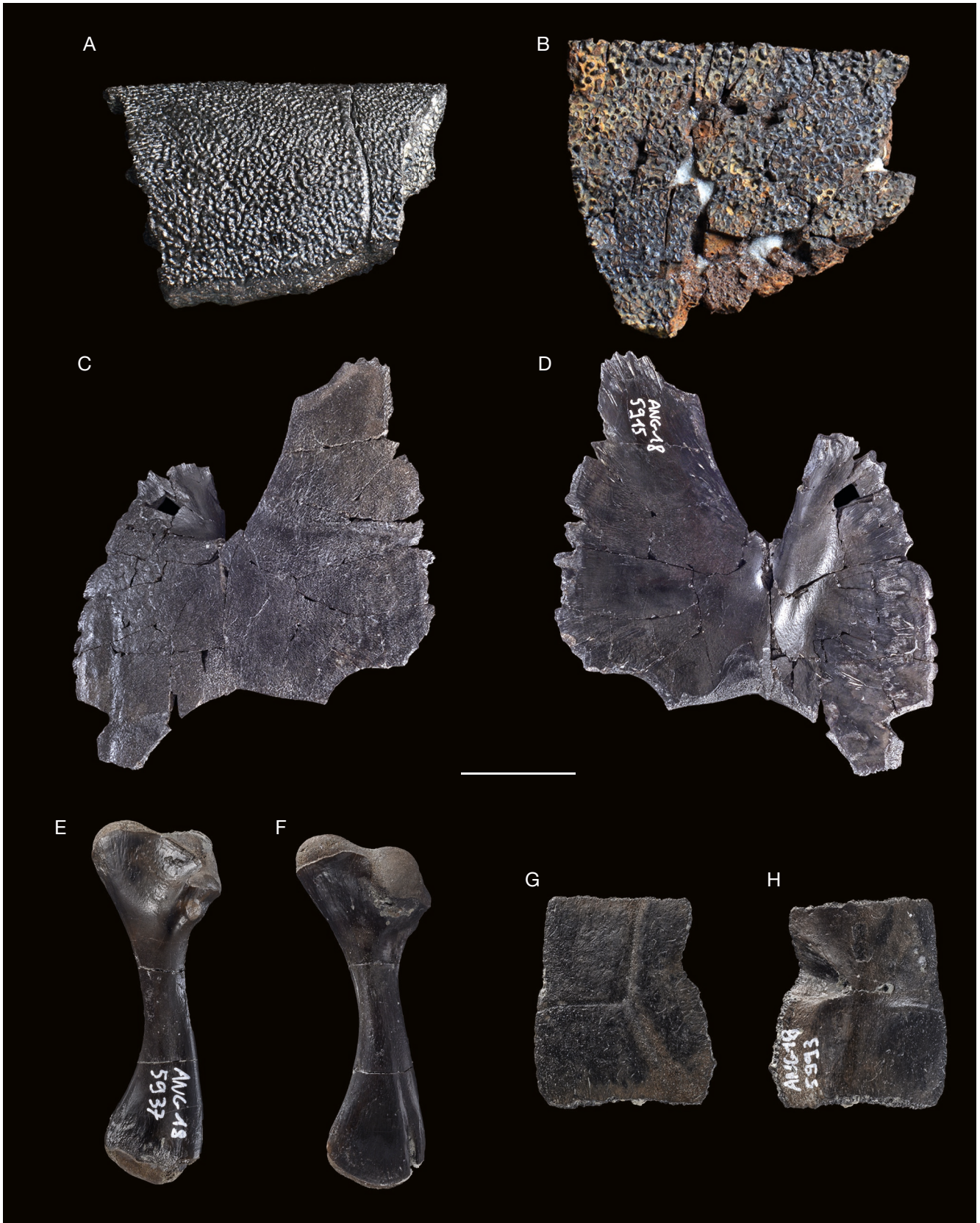


FIG. 12. — Helochelyrid and thalassochelydian turtle remains from Angeac-Charente: **A**, peripheral plate of Helochelyridae indet. in dorsal view; **B**, pleural plate of Helochelyridae indet. in dorsal view; **C**, **D**, right hyoplastron of *Hylaeochelys belli?* (Mantell, 1844) (ANG18-5915) in ventral (**C**) and dorsal (**D**) views; **E**, left humerus of *Hylaeochelys? belli?* (ANG18-5937) in ventral view; **F**, right humerus (ANG18-5938) in dorsal view; **G**, **H**, Peripheral of *Hylaeochelys? belli?* (ANG 18-5993) in dorsal (**G**) and ventral (**H**) views. Scale bar: A, 1 cm; E-H, 2 cm; B, 3 cm; C, D, 4 cm.

tubercles, pustules and crests (Fig. 12A, B) that diagnose this clade (Lapparent de Broin & Murelaga 1999; Joyce 2017). Probably based on the previous stratigraphical claim by Néraudeau *et al.* (2012) that Angeac-Charente was Hauterivian-Barremian in age, Joyce (2017) provisionally referred this material to *Helochelydra nopcsai*, a species otherwise diagnosed by a shell surface ornamentation consisting of distinct, easily dislocated tubercles. Our observations reveal, however, that the helochelydrid material from Angeac-Charente usually displays distinct tubercles that do not easily dislocate. This ornamentation is more similar to the morphotypes of “*Helochelydra*” *anglica* and “*Helochelydra*” *bakewelli* (Joyce 2017), respectively from the Purbeck Group (Berriasian) of Dorset and the Wealden (Valanginian) of Sussex, United Kingdom (Joyce *et al.* 2011). That being said, the systematics of Early Cretaceous helochelydrids remains highly confused. For that reason, the helochelydrid material from Angeac-Charente is herein conservatively referred to Helochelydridae indet.

The posterior part of a large carapace collected in 2018 and 2020 provides new information on the morphology of the helochelydrid from Angeac-Charente. However, the material is not fully prepared yet and will be described in more detail elsewhere. A raised midline keel on the posterior neurals is clearly observable, which is a character shared with other helochelydrids (Lydekker 1889; Lapparent de Broin & Murelaga 1999; Milner 2004; Vullo *et al.* 2010; Joyce *et al.* 2014; Joyce 2017; Pérez-García *et al.* 2020). The general morphology resembles that of other species in which this region is sufficiently known, such as “*Helochelydra*” *anglica*, *Naomichelys speciosa*, *Aragoichersis lignitesta*, and *Solemys vermiculata* (Lydekker 1889; Lapparent de Broin & Murelaga 1999; Milner 2004; Joyce *et al.* 2014; Joyce 2017; Pérez-García *et al.* 2020). Neurals V and VI are elongate and hexagonal. Neurals VII and VIII are probably fused. They are wide and hexagonal anteriorly and posteriorly, and narrower on the midline. There are three suprapyrgals, which are reminiscent of the condition in FMNH PR273, a nearly complete specimen referred to the North American species *Naomichelys speciosa*. However, the number of suprapyrgals is known to be rather variable in basal turtles. The morphology of the suprapyrgals and pygal differs from other known helochelydrids, but detailed comparisons are needed in order to assess the systematic value of these characters. The shell surface sculpturing is less prominent on the neurals and becomes more pronounced on the distal part of the costals and on the peripherals, suprapyrgals, and pygal.

Helochelydrids are considered by numerous authors to be terrestrial forms (Lapparent de Broin & Murelaga 1999; Joyce *et al.* 2011; Scheyer *et al.* 2015). They are known to have limbs and neck covered with osteoderms (Barrett *et al.* 2002; Joyce *et al.* 2014; Scheyer *et al.* 2015). Such osteoderms have also been found at Angeac-Charente. Known cranial material suggests a durophagous diet, although it is still unclear exactly which hard-shelled food elements these turtles fed on (Joyce *et al.* 2011, 2014).

PARACRYPTODIRA Gaffney, 1975  
(*sensu* Lyson & Joyce 2011)  
Family PLEUROSTERNIDAE Cope, 1868  
(*sensu* Lyson & Joyce 2011)  
Genus *Pleurosternon* Owen, 1853

*Pleurosternon bullockii* (Owen, 1842)  
(Fig. 13)

#### DESCRIPTION

Pleurosternids are the most abundant turtles in Angeac-Charente representing nearly 85% of the turtle material (Table 1). Most of the material consists of isolated shell plates characterized by an external surface covered by regular pits with fine linear striations perpendicular to the plate margins. This character combination is only shared with the Portuguese Late Jurassic (Kimmeridgian) *Selenemys lusitanica* and the British and French Late Jurassic-Early Cretaceous (Tithonian to Berriasian) *Pleurosternon bullockii* (Pérez-García & Ortega 2011). An almost complete shell collected in 2014 confirmed the attribution to the species *Pleurosternon bullockii* (Fig. 13; Gônet *et al.* 2019). The carapace is oval in outline and depressed with no nuchal emargination (Fig. 13A). The nuchal is trapezoidal, wider posteriorly than anteriorly. The cervical scute is absent. The vertebral scutes are wide and cover about half of the costals. Unlike British specimens, suprapygal 2 is a wide hexagonal element that presents several morphotypes in Angeac-Charente. The plastron has a pair of mesoplastra and a wide anal notch posteriorly (Fig. 13B). The large entoplastron is triangular anteriorly and rounded posteriorly. The posterior plastral lobe is longer than the anterior one. The near-complete shell and the remaining pleurosternid material in general will be described in detail elsewhere. The pleurosternid from Angeac-Charente differs from *Selenemys lusitanica* in characters including: nuchal width less than twice its maximum length; anterior nuchal edge constituting the anterior carapace rim; posterior margin of the first peripheral two times shorter than the anterior one; overlap of the first vertebral on the first pair of peripherals; first vertebral wider than the nuchal; first pair of marginals wider than long; and development of an anal notch.

*Pleurosternon bullockii* is known by numerous specimens from the Berriasian Purbeck Group of Dorset (United Kingdom), including complete shells, carapaces, plastra, elements of the appendicular skeleton, and one skull (Evans & Kemp 1975; Milner 2004; Sterli *et al.* 2010; Evers *et al.* 2020), but it is also identified in the Tithonian record of Dorset and the French locality of Wimille (Boulogne-sur-Mer) (Guerrero & Pérez-García 2020).

Pleurosternids are freshwater turtles, of which most of the remains have been collected from fluvial and lacustrine sedimentary deposits (Joyce & Anquetin 2019). This hypothesis is confirmed by the depressed shell shape, appendicular bone morphology, and feeding specializations. *Pleurosternon bullockii* presents an elongate skull with low labial margins which suggests a gape and suction feeding (Pritchard 1984; Foth *et al.* 2017; Joyce & Anquetin 2019). The abundance of pleurosternid material and the presence of different growth stages suggest that the Angeac-Charente paleoecosystem probably corresponds to the preferred habitat of this turtle.

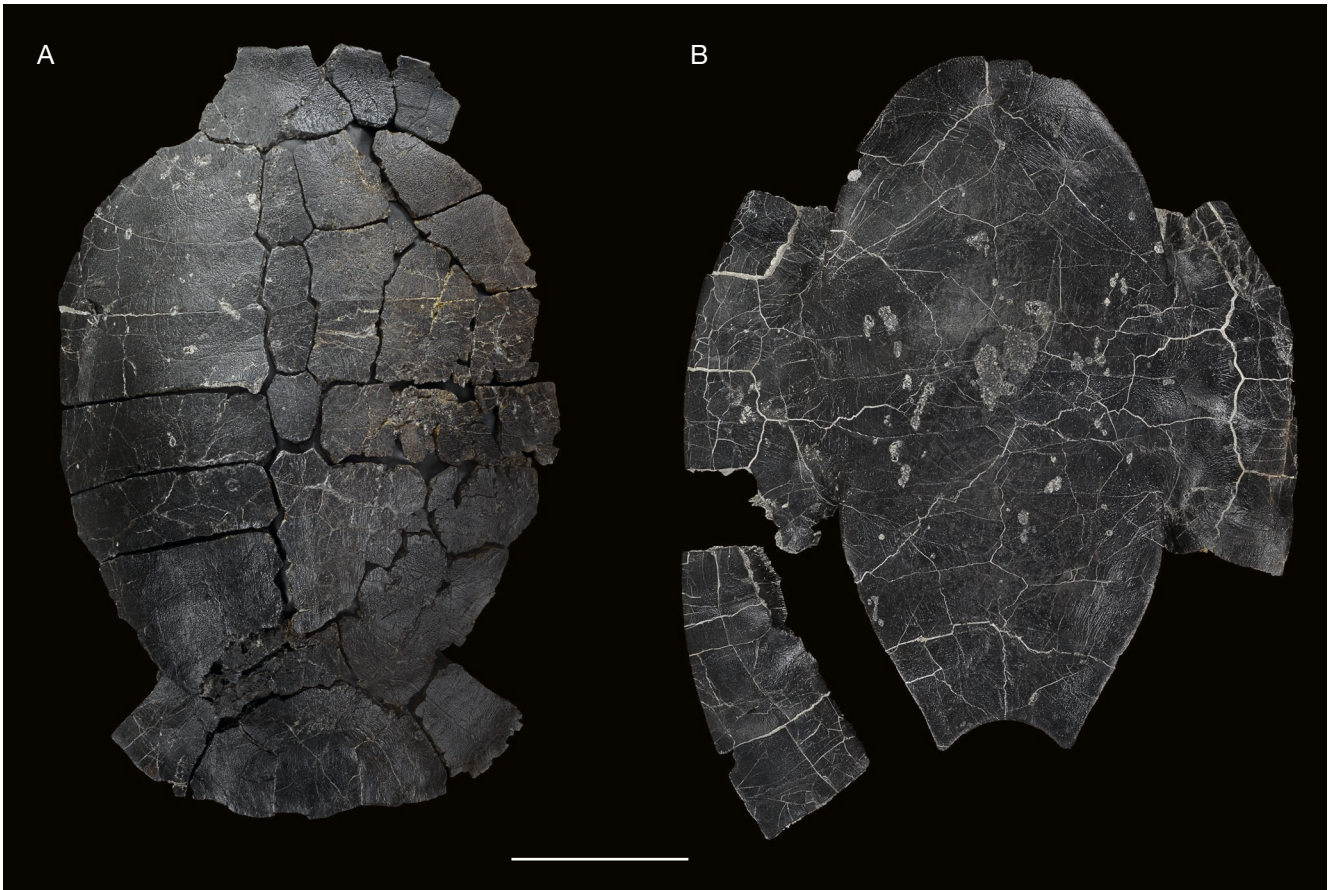


FIG. 13. — Pleurosternid turtle from the Berriasian of Angeac-Charente: **A**, carapace of *Pleurosternon bullockii* (Owen, 1842) (ANG14 R-454) in dorsal view; **B**, plastron and right peripheral plates 1 and 2 of *Pleurosternon bullockii* (ANG14 R-474 & ANG15 R-1082) in ventral view. Scale bar: 10 cm.

THALASSOCHELYDIA  
Anquetin, Püntener & Joyce, 2017  
Family indet.  
Genus *Hylaeochelys* Lydekker, 1889

*Hylaeochelys belli?* (Mantell, 1844)  
(Fig. 12C-H)

#### DESCRIPTION

The third turtle taxon is represented by many isolated plates and one incomplete specimen discovered in 2018, consisting of parts of the plastron, some peripherals and both humeri (Fig. 12C-H). The shell bone surface is nearly smooth with shallow grooves, which clearly distinguishes this taxon from the two others previously described. The shell bones are relatively thin. The vertebral scutes are very wide and cover more than half of the costals laterally. The neurals are narrow and elongated, especially in the mid-posterior part of the carapace. The plastron bears a central plastral fontanelle. The mesoplastron is absent. The humerus shape is unremarkable and similar to that recently described in Late Jurassic thalassocheilydians (e.g., Püntener *et al.* 2014, 2017). Based on the available characters, this form is possibly closely related to the Early Cretaceous (Purbeck and Wealden of the United Kingdom) thalassocheilydian *Hylaeochelys belli* (Lydekker 1889;

Hirayama *et al.* 2000; Pérez-García 2012; Pérez-García & Ortega 2014; Anquetin & André 2020).

*Hylaeochelys belli* is generally considered to be a freshwater turtle based on the sedimentary contexts of the localities in which it occurs (Milner *et al.* 2012; Pérez-García & Ortega 2014; Anquetin & André 2020). Most of the Angeac-Charente material represents juveniles or sub-adults, which may suggest that the swampy environment was a rookery for this turtle.

LEPIDOSAURMORPHA Benton, 1983  
LEPIDOSAURIA Haeckel, 1866  
RHYNCHOCEPHALIA Günther, 1867  
SPHENODONTIA Williston, 1925  
Family indet.  
Genus *Opisthias* Gilmore, 1909

cf. *Opisthias*  
(Fig. 14)

#### DESCRIPTION

ANG M-120 (Fig. 14) is a posterior dentary fragment bearing two preserved acrodont teeth in addition to seven broken teeth, there are six anteriorly and one posteriorly. Tooth crowns are



FIG. 14. — Rhynchocephalian right dentary fragment from Angeac-Charente: **A-C**, cf. *Opisthias* sp. (ANG M-120) in labial (**A**), lingual (**B**) and dorsal (**C**) views. Scale bar: 2.5 mm.

sub-pyramidal in shape, angulous anteriorly, more rounded posteriorly, and slightly inclined anteriorly throughout the dentition (Fig. 14A). As suggested by tooth bases, teeth are gradually increasing in size posteriorly. In occlusal view, the tooth row is straight (Fig. 14C). The coronoid process is broken at its base and the mandibular ramus is broken ventrally at the level of the Meckelian groove (Fig. 14B).

ANG M-120 is here tentatively referred to cf. *Opisthias* because of the tooth morphology and gradual heterodonty pattern which is similar to that observed in previously described *Opisthias* dentaries (Gilmore 1910; Evans & Fraser 1992). In lateral view, the dentary of *Homoeosaurus* shows wider tooth bases and crown apices that are less acute and not anteriorly inclined (Cocude-Michel 1963). *Tingitana* from the Tithonian-Berriasian of Morocco, has dentary teeth bearing a strong, inwardly concave, anterolingual crest between a large posterior cone and a small anterolingual one (Evans & Sigogneau-Russell 1997). It is worth noting that a sphenodontian from Cherves-de-Cognac, represented by a partial skeleton, was referred to *Homoeosaurus* by Buffetaut *et al.* 1989. A revision of this material, housed in a private collection, including a detailed comparison with the Angeac-Charente specimen would be useful to assess sphenodontian diversity in western Europe.

SQUAMATA Oppel, 1811  
 SCINCOMORPHA Camp, 1923  
 Family PARAMACELLODIDAE Estes, 1983  
 Genus *Paramacellodus* Hoffstetter, 1967

*Paramacellodus* sp.  
 (Fig. 15A-C)

DESCRIPTION

ANG M-20 (Fig. 15A-C) is a jaw fragment bearing two closely spaced teeth, with the anterior tooth slightly larger

than the posterior. Curvature of the teeth suggests that this fragment might come from a premaxilla or the anterior part of a dentary. Tooth implantation is pleurodont. Both tooth crowns are gently recurved and twisted so that the lingual face is slightly inclined posteriorly. The anterior marginal zone has a shoulder or *angulus mesialis*, following the terminology of Richter (1994). A similar shoulder, that would represent the *angulus distalis*, is absent in the distal marginal zone. The labial face is cambered and smooth whereas the lingual face is ornamented with longitudinal ridges, which are more numerous in the anterior tooth. The sharp and pointed tooth apex shows two small cusps (i.e., *cusps labialis* and *cusps lingualis*) closely adpressed and linked by a short carina (i.e., *carina intercuspidalis*). The ornamented central zone of the lingual face (i.e., *pars furcata*), delineated by long *striae dominantes*, is moderately wide. In lingual view, several foramina are present between the columnar roots of the teeth (Fig. 15A). The tooth crown shape (which is twisted with an acute apex and shows an *angulus mesialis*) and ornamentation combined with the presence of *cusps labialis* and *cusps lingualis* united by a short *carina intercuspidalis* is consistent with referral of ANG M-20 to *Paramacellodus* (Broschinski & Sigogneau-Russell 1996; Evans & Searle 2002). The other closely related genus *Parasaurillus* has more pointed crowns, no *angulus mesialis*, and longer lingual ridges (Evans & Searle 2002). Three species of *Paramacellodus* are known to date: *P. oweni* from the Late Jurassic of U.S.A and the Berriasian of England, *P. marocensis* from the Tithonian and/or Berriasian of Morocco, and *P. sinuosus* from the Barremian of Spain (Hoffstetter 1967; Richter 1994; Broschinski & Sigogneau-Russell 1996; Evans & Chure 1998; Evans & Searle 2002). A fourth species from the late Early Cretaceous (Aptian-Albian) of the United States, characterized by a well-developed cuspule on the anterior carina, was tentatively referred to *Paramacellodus* (cf. *P. keebleri*; Nydam & Cifelli 2002). Other occurrences tentatively referred to *Paramacellodus* have been reported from the Bathonian-Barremian of Europe, North America, Asia and Africa (Evans & Searle 2002). The Angeac-Charente form might belong to *P. oweni* or *P. marocensis*; however, pending the discovery of additional material, we refer it to *Paramacellodus* sp.

Numerous osteoderms (Fig. 15D-F) have been collected from Angeac-Charente. These elongated plate-like elements are subrectangular and show more or less numerous pits visible on their external surface. A low, longitudinal ridge can be present, either in the midline or displaced laterally. The unornamented imbrication shelf is variably developed. These isolated osteoderms are morphologically consistent with scincomorph osteoderms (e.g., Krause *et al.* 2003; Nydam *et al.* 2013), including those referred to paramacelodids (e.g., Hoffstetter 1967; Richter 1994; Broschinski & Sigogneau-Russell 1996; Nydam & Cifelli 2002; Sweetman & Evans 2011).

ARCHOSAURMORPHA von Huene, 1946  
 CHORISTODERA Cope, 1876

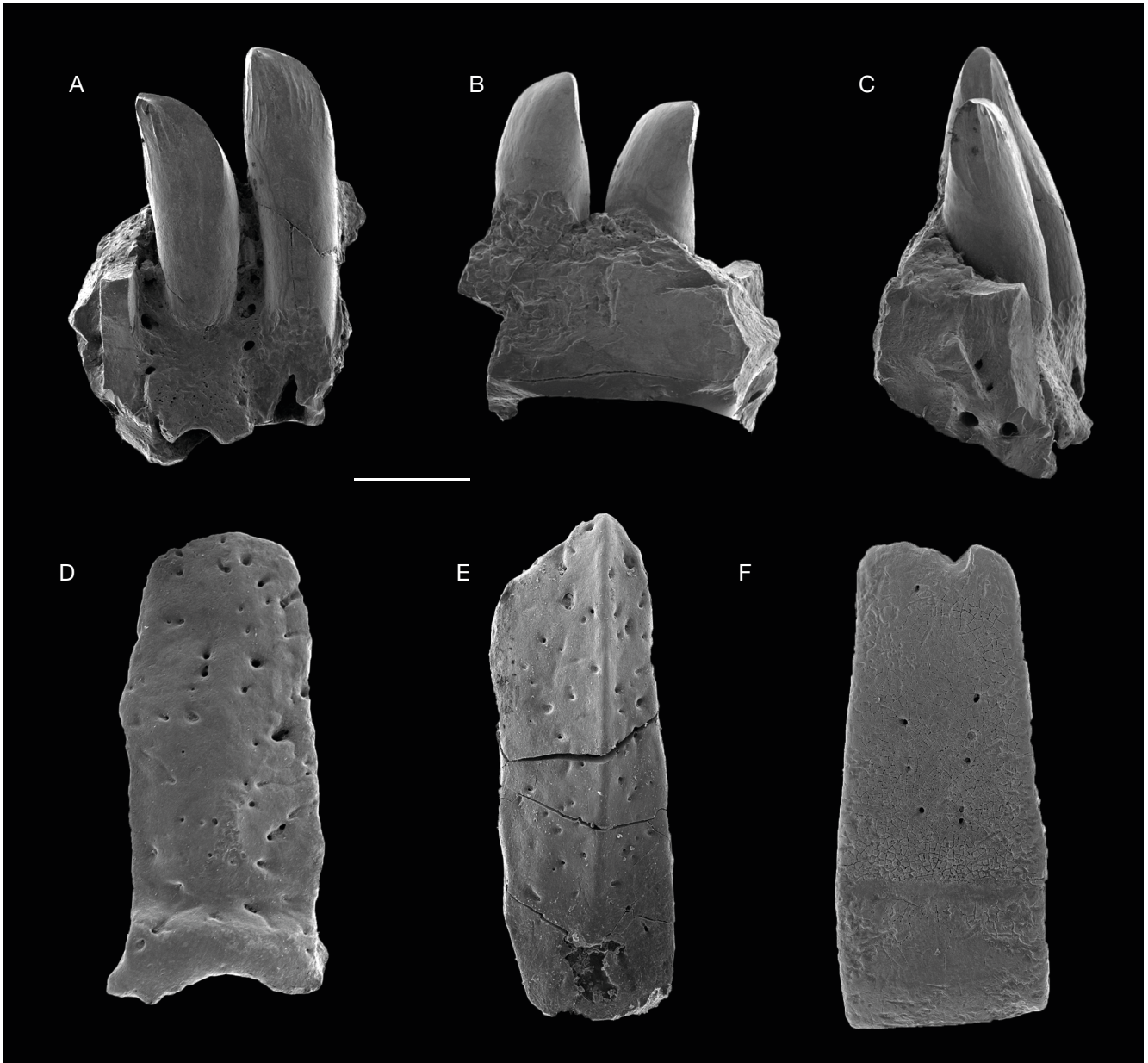


FIG. 15. — Scincomorph lizard remains from Angeac-Charente: **A-C**, fragment of left dentary of cf. *Paramacellodus* sp. (ANG M-20) in lingual (**A**), labial (**B**) and distal (**C**) views; **D-F**, osteoderms of *Scincomorpha* indet., ANG M-46 (**D**), ANG M-49 (**E**), ANG M-58 (**F**) in dorsal view. Scale bar: 500  $\mu$ m.

Family CTENIOGENYIDAE Seiffert, 1975  
Genus *Cteniogenys* Gilmore, 1928

cf. *Cteniogenys*  
(Fig. 16A-E)

DESCRIPTION

A characteristic robust vertebra (Fig. 16A-C), as well as a smaller vertebra that probably belongs to a juvenile individual (Fig. 16D, E), have been discovered among the microremains. Both centra are amphicoelous, with an opened neurocentral suture. Dorsally, a distinct longitudinal ridge is laterally bordered by longitudinal grooves on the floor of the neural canal (Fig. 16A). In ventral view, the lower half of the cen-

trum is pinched into a keel (Fig. 16D). The margins of the cotyle are thick (Fig. 16E). All these characters are reminiscent of choristoderan reptiles (Evans 1991; Averianov *et al.* 2006; Vullo *et al.* 2014; Haddoumi *et al.* 2016; Lasseron *et al.* 2020). ANG M-20 is nearly identical to the vertebra of *Cteniogenys* figured by Evans & Milner (1994: fig.18.5). Hence, it is here tentatively assigned to this genus, although this identification needs to be substantiated with additional material. These freshwater or amphibious diapsids are well known in Laurasia (Matsumoto *et al.* 2013), but have also been reported from the Jurassic-Cretaceous transition of North Africa (Lasseron *et al.* 2020). In the Lower Cretaceous of Asia, the diversity and abundance of choristoderans is particularly high in the faunal assemblages, in which crocodyliforms are

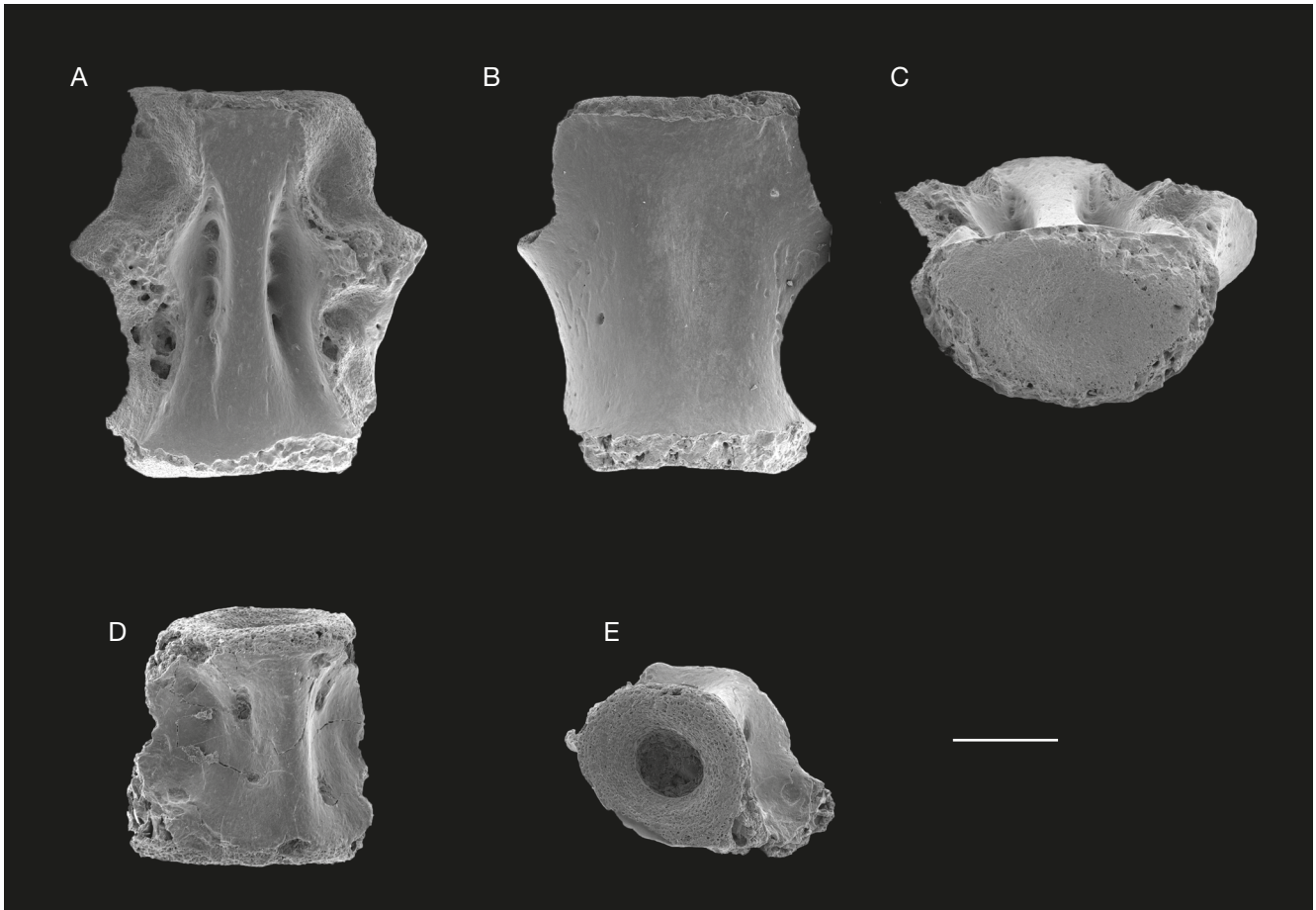


FIG. 16. — Choristoder remains from Angeac-Charente: **A-C**, anterior dorsal vertebra of cf. *Cteniogenys* sp. (ANG M-20) in dorsal (**A**), ventral (**B**) and posterior (**C**) views; **D, E**, juvenile dorsal vertebral centrum (ANG M-47) in ventral (**D**) and oblique anterior (**E**) views. Scale bar: A-C, 1 mm; D, E, 200  $\mu$ m.

scarce (Matsumoto *et al.* 2015; Skutschas & Vitenko 2017). Conversely, the abundance and diversity of crocodyliforms at Angeac-Charente may explain the scarcity of choristoderans.

ARCHOSAURIA Cope, 1870  
 CROCODYLOMORPHA Hay, 1930  
 MESOEUCROCODYLIA  
 Whetstone & Wybrow, 1983  
 NEOSUCHIA Benton and Clark, 1988  
 Family ATOPOSAURIDAE Gervais, 1871  
 Genus *Theriosuchus* Owen, 1879

*Theriosuchus* sp.  
 (Fig. 17A-D)

DESCRIPTION

Small isolated teeth are commonly recovered from residues obtained from bulk screening. Many of them (Fig. 17A-D) are leaf-shaped, labiolingually compressed, low-crowned and pseudoziphodont, a characteristic of the posterior dentition in the atoposaurid genus *Theriosuchus* (Schwarz & Salisbury 2005; Lauprasert *et al.* 2011; Martin *et al.* 2014b). Members of the genus *Theriosuchus* are small crocodyliforms with

total body lengths less than 1 m (Schwarz & Salisbury 2005). Besides teeth, two skull bones might belong to this genus: a right jugal (ANG 16-5179) and a fragmentary frontal (ANG 14-3692). The jugal is about 1 cm long and its ornamented lateral surface is thin and projects ventrally. The frontal preserves the interorbital area and displays an acute median keel on its dorsal surface. A finely sculpted osteoderm, longer than wide and possessing a shallow median keel (Fig. 19D), matches the morphology of dorsal osteoderms of the tail region in *Theriosuchus pusillus* (Owen 1879; Clark 1986).

COELOGNATHOSUCHIA  
 Martin, Lauprasert, Buffetaut, Liard & Suteethorn, 2014  
 NEOSUCHIA Benton & Clark, 1988  
 Family GONIOPHOLIDIDAE Cope, 1875  
 Genus *Goniopholis* Owen, 1841

*Goniopholis* sp.  
 (Fig. 18)

DESCRIPTION

In addition to fragmentary cranial remains and numerous isolated teeth, a nearly complete skull and mandibular elements



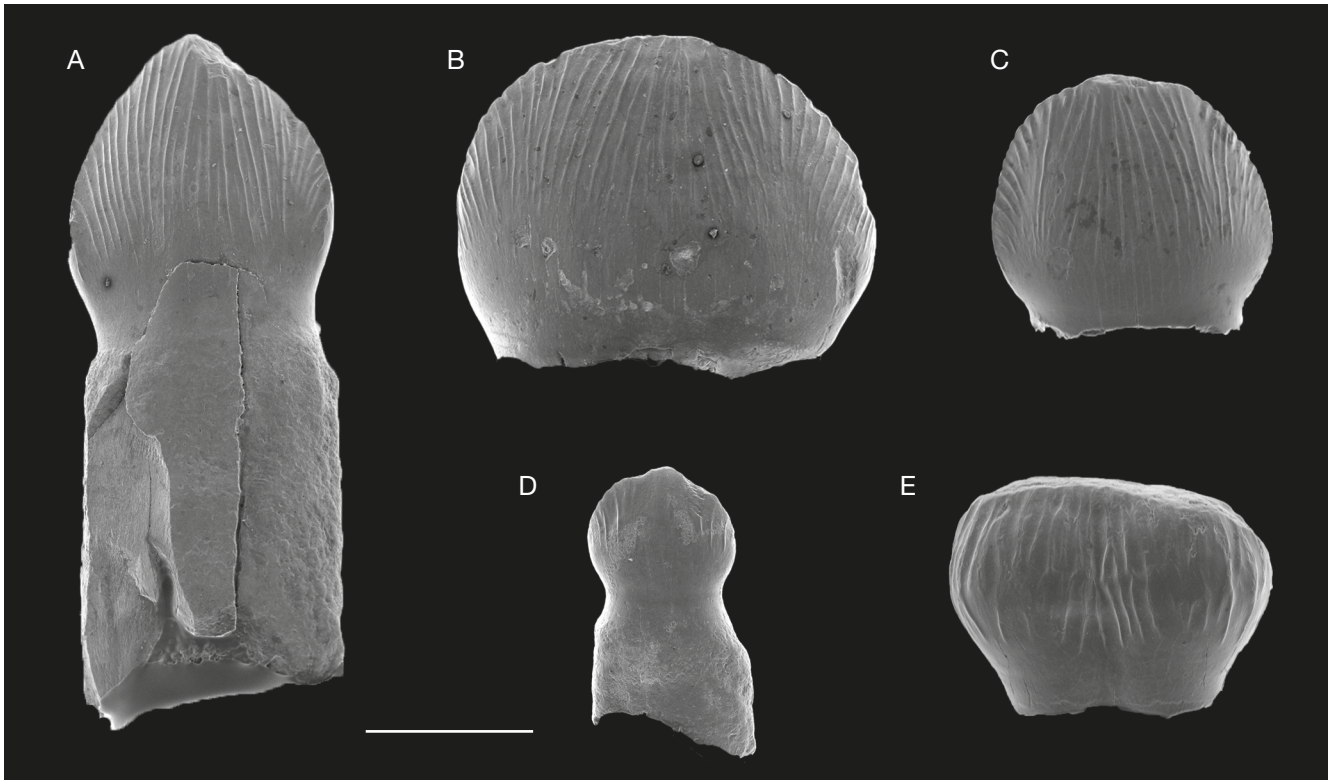


FIG. 17. — Crocodyliform teeth from Angeac-Charente: **A-D**, broadened teeth of *Theriosuchus* sp., ANG M-13 (**A**), ANG M-07 (**B**), ANG M-19 (**C**), ANG M-12 (**D**); **E**, tooth of Bernissartiidae indet. (ANG M-11). Scale bar: 1 mm.

(ANG18-5914, 5920, 5921 and 5925) of a single individual have been excavated and prepared in 2018 (Fig. 18). The skull is broken transversally in front of the orbits and the rostrum is split longitudinally along the nasals and premaxillae. The associated mandible preserves both dentaries. In comparison with other goniopholidids from Europe, this skull is notable for its exquisite preservation, being minimally compacted dorsoventrally.

Based on recent works (Salisbury *et al.* 1999; Schwarz 2002; Andrade *et al.* 2011; Buscalioni *et al.* 2013; Puértolas-Pascual *et al.* 2015; Martin *et al.* 2016a), several diagnostic characters used in combination permit assignment of this specimen to Goniopholididae, including: 1) a mesorostrine condition with a rostrum to skull ratio *c.* 0.65; 2) constricted outline of the upper jaw at the level of the premaxillary-maxillary suture; 3) double-caniniform maxillary teeth 4+5; 4) confluent dentary alveoli 3+4; 5) orbits smaller than supratemporal fenestrae and slightly smaller than frontal width at interorbital level; 6) skull table and dorsal surface of quadratojugal and jugal densely covered by large circular cupules; 7) internal choanae anteriorly bound by palatines; 8) semi-arched and widely expanded premaxillae with fifth alveolus more laterally placed than the rest of the premaxillary tooth row; and 9) absence of contact between ectopterygoid and posterior margin of maxillary tooth row.

The Angeac-Charente specimen (ANG18-5914, 5920, 5921 and 5925) also exhibits several characters that permit provisional assignment to the genus *Goniopholis*. Among these,

antorbital and interorbital ornamentation is informative. The presence of periorbital crests on the prefrontal and lacrimal are present in *Goniopholis* (Andrade & Hornung 2011) but absent in *Anteophthalmosuchus* and *Hulkepholis* (Salisbury & Naish 2011; Buscalioni *et al.* 2013; Martin *et al.* 2016a). The interorbital ridge is restricted to the frontal in *Hulkepholis* (Salisbury & Naish 2011; Buscalioni *et al.* 2013). In the Angeac-Charente specimen, the presence of both antorbital and interorbital crests is also a character shared with *Goniopholis*. A short postorbital spine is present in the Angeac-Charente specimen, a condition similar to other specimens of the genus *Goniopholis* (Salisbury *et al.* 1999; Schwarz 2002; Andrade *et al.* 2011) but unlike *Anteophthalmosuchus* in which this spine is longer, almost contacting the anterior margin of the orbits (Salisbury & Naish 2011; Martin *et al.* 2016a). The Angeac-Charente specimen is also similar in its maxillary tooth count (20) to *Goniopholis kiplingi* (Andrade *et al.* 2011) and with *Anteophthalmosuchus*, which possesses 19 alveoli (Martin *et al.* 2016a). The maxillary alveolar count has not been established for *Goniopholis simus* (Salisbury *et al.* 1999). However, this count is less than that of the goniopholidid *Hulkepholis willetti*, in which at least 24 maxillary alveoli are present (Salisbury & Naish 2011). Obvious differences in rostrum proportions are observed with *Vectisuchus* and *Hulkepholis*, which possess long and narrow rostra (Buffetaut & Hutt 1980; Salisbury & Naish 2011; Buscalioni *et al.* 2013). As in *Anteophthalmosuchus* and *Goniopholis*, the palpebral in the specimen from Angeac-Charente is small and not large and triangular as in

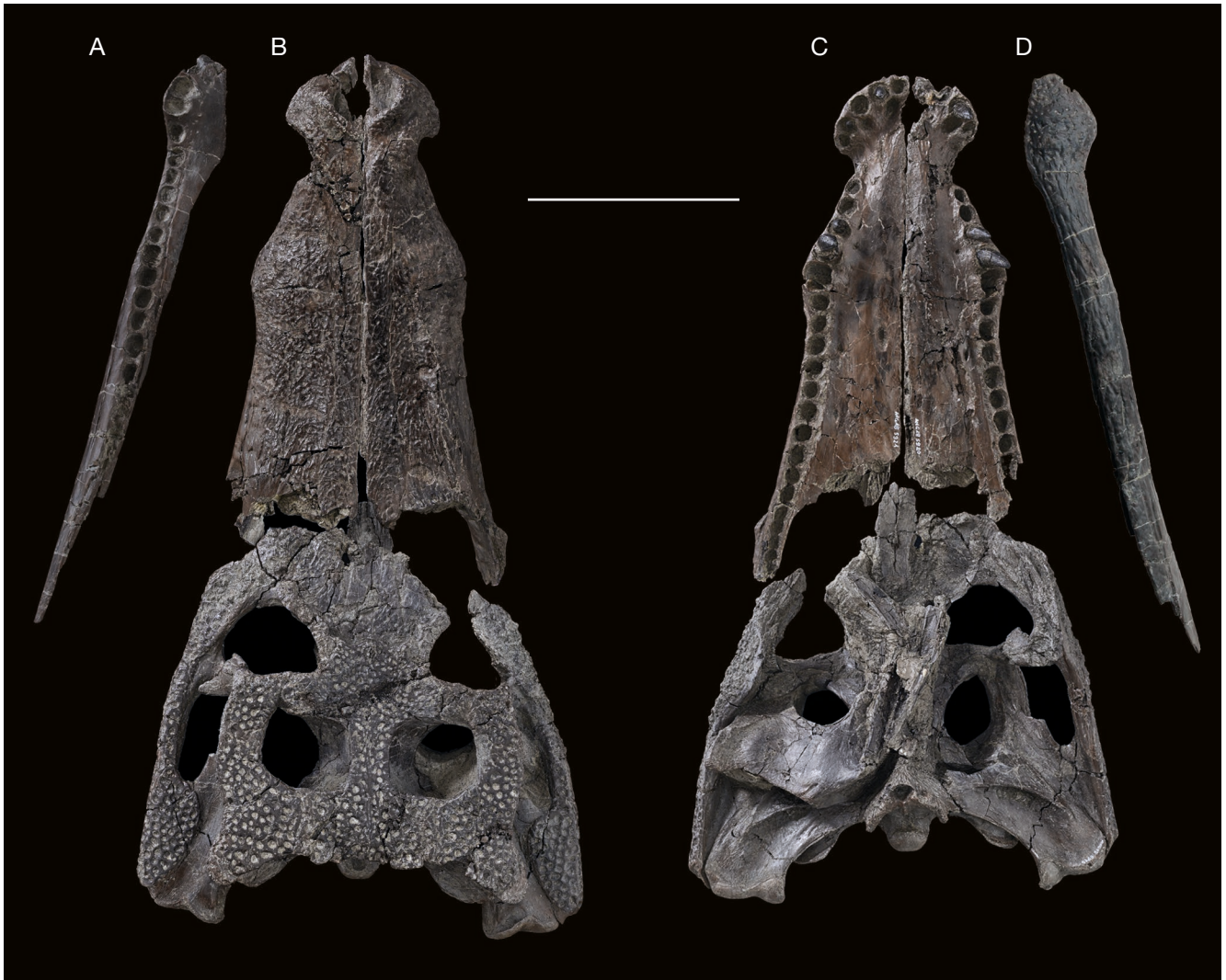


FIG. 18. — Goniopholidid crocodyliform Angeac-Charente: **A, D**, left dentary of *Goniopholis* sp. (ANG18-5925) in dorsal (**A**) and ventral (**D**) views; **B, C**, skull of *Goniopholis* sp. (ANG18-5914, ANG18-5920, ANG18-5921) in dorsal (**B**) and ventral (**C**) views. Scale bar: 10 cm.

*Hulkepholis* (Salisbury & Naish 2011; Buscalioni *et al.* 2013; Martin *et al.* 2016a). Comparison with *Nannosuchus* will not be discussed here as this taxon has been viewed either as a juvenile of *Goniopholis* (Salisbury 2002) or as a valid taxon (Andrade *et al.* 2011). Therefore, considering the characters mentioned above, we tentatively refer the Angeac-Charente specimens to *Goniopholis* sp.

A detailed description of the Angeac-Charente material will be provided elsewhere. In the meantime, a study of the numerous goniopholid specimens from Cherves-de-Cognac and assigned to *Goniopholis* (Raslan-Loubatié 2007) will provide a useful basis for discussing morphological variability within a goniopholidid population. Preliminary observations concerning the Angeac-Charente specimen do not reveal any obvious morphological differences between the goniopholidids at both localities but further study is required.

Family PHOLIDOSAURIDAE von Zittel & Eastman, 1902  
Genus *Pholidosaurus* Meyer, 1841

*Pholidosaurus* sp.  
(Fig. 19E-J)

DESCRIPTION

The genus *Pholidosaurus* is attested to at Angeac-Charente by the presence of numerous isolated teeth (Fig. 19E-J). These are characteristic being slender, curved and bearing numerous apicobasal ridges that converge near the apex. Identical teeth are known from the Tithonian of Chassiron (Vullo *et al.* 2014), and in *Pholidosaurus purbeckensis* recently described from the nearby locality of Cherves-de-Cognac (Martin *et al.* 2016b). A right anterior portion of a dentary (ANG14-2959) displaying an extensive splenial symphysis can also be assigned to *Pholidosaurus*.

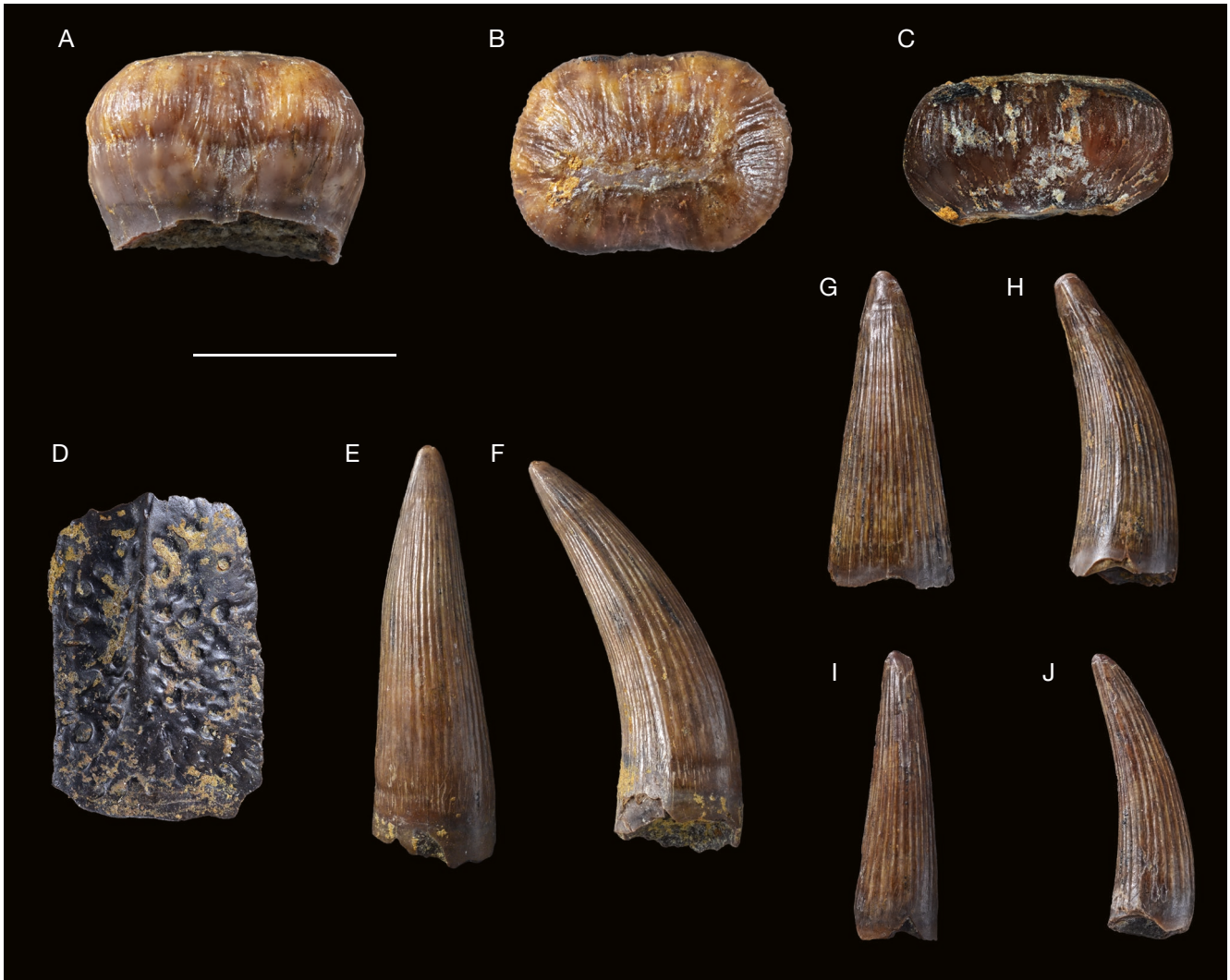


FIG. 19. — Crocodyliform remains from Angeac-Charente: **A, B**, tooth of *Bernissartiidae* indet. (ANG10-268) in lingual/labial (**A**) and occlusal (**B**) views; **C**, tooth of *Bernissartiidae* indet. (ANG10-76) in lingual/labial view; **D**, osteoderm of *Atoposauridae*? (ANG 10-167) in dorsal view; **E, F**, tooth of *Pholidosaurus* sp. (ANG11-960) in labial (**E**) and mesial/distal (**F**) views; **G, H**, tooth of *Pholidosaurus* sp. (ANG11-883) in labial (**G**) and mesial/distal (**H**) views; **I, J**, tooth of *Pholidosaurus* sp. (ANG10-369) in labial (**I**) and mesial/distal (**J**) views. Scale bar represents: A-C, 2 mm; D-J, 8 mm.

#### Family BERNISSARTIIDAE Dollo, 1883

*Bernissartiidae* indet.  
(Figs 17E; 19A-C)

##### DESCRIPTION

Several mesiodistally elongate, bulbous and low-crowned isolated teeth have been recovered at Angeac-Charente (Figs 17E; 19A-C) and their morphology is reminiscent of the tribodont condition described for the small neosuchian *Bernissartia* (Buffetaut & Ford 1979; Martin *et al.* 2020). An incomplete left jugal (ANG15R-1205) is inflated on its lateral surface and might also belong to a bernissartiid. A small osteoderm (ANG16-4907) also resemble the dorsal row of osteoderms figured by Buffetaut (1975) in *Bernissartia fagesii*. Here, the specimen is slightly wider than long although it is not as rectangular as in *Bernissartia fagesii*. A double-keel runs on its dorsal surface and an anterolateral process is present. The recently described

bernissartiid *Koumpiodontosuchus aprosdokiti* (Sweetman *et al.* 2015) also shares tribodont teeth with *Bernissartia fagesii* and, for this reason, we cannot yet ascertain a generic or specific attribution for the Angeac-Charente material.

#### PTEROSAURIA Kaup, 1834

##### Superfamily PTERODACTYLOIDEA Plieninger, 1901

*Pterodactyloidea* indet. A  
(Fig. 20A-D)

##### DESCRIPTION

This indeterminate pterodactyloid taxon is represented by small, labiolingually compressed teeth (Fig. 20A-D). The crown is relatively low, triangular and broad-based in labial and lingual views (Fig. 20A-C). The basal part of the labial and lingual faces is devoid of enamel, except along the mesial and distal carinae.



FIG. 20. — Pterosaur teeth from Angeac-Charente: **A**, Pterodactyloidea indet. A (ANG M-24) in labial view; **B**, Pterodactyloidea indet. A (ANG M-10) in lingual view; **C**, **D**, Pterodactyloidea indet. A, (ANG M-42) in lingual (**C**) and mesial (**D**) views; **E**, **F**, Pterodactyloidea indet. B, (ANG M-43) in lingual (**E**) and mesial (**F**) views; **G**, **H**, Pterodactyloidea indet. B, (ANG M-112) in lingual (**G**) and mesial (**H**) views; **I**, Pterodactyloidea indet. B, (ANG M-40) in lingual view; **J**, **K**, Pterosauria indet. (ANG M-41) in labial (**J**) and distal (**K**) views; **L**, **M**, Pterosauria indet. (ANG M-113) in lingual (**L**) and mesial (**M**) views. Scale bar: 500  $\mu$ m.

The crown base is slightly inflated and the recurved apex is more or less slender, so that in labial view the carinae are convex and concave in the basal half and distal half of the crown, respectively. A weak enamel ornamentation consisting of faint vertical folds is present in some teeth. This taxon, characterized by a gradual heterodonty, corresponds to the morphotypes 5-7 reported from the Purbeckian beds of Chassiron (Vullo *et al.* 2014: fig. 17e-g) and to the isolated tooth MPZ2011/46 described from the Valanginian-Hauterivian of Pochancalo 1 in northeastern Spain (Gasca *et al.* 2012: fig. 3k). Since this tooth morphology is present in some archaeoptero-dactyloids (e.g., *Pterodactylus*, *Germanodactylus*) and istiodactyliforms (e.g., *Haupterus*, *Longchengopterus*, *Mimodactylus*) (Lü *et al.* 2008; Wang *et al.* 2008; Kellner *et al.* 2019), we refer this taxon to Pterodactyloidea indet. A.

Pterodactyloidea indet. B  
(Fig. 20E-I)

DESCRIPTION

A second indeterminate pterodactyloid taxon is present at Angeac-Charente (Fig. 20E-I). The teeth mainly differ from those of taxon A by their slenderer crown and narrower base in labial view. In cross section, the lingual face is more convex than the labial face. The enamel distribution is similar to that observed in taxon A. The enamel surface shows some short, irregular vertical folds. This taxon also occurs in the Berriasian of Cherves-de-Cognac (Pouech 2008: fig. 38, pl. 23b).

Pterosauria indet.  
(Fig. 20J-M)

DESCRIPTION

A third morphological group of pterosaurian teeth corresponds to slender, recurved crowns that are characterized by a subcircular cross section and poorly distinct carinae (Fig. 20J-M). The enamel is smooth whereas the basal part of the crown devoid of enamel (i.e., basal portion of labial and lingual faces) shows an irregular rugose texture. Teeth of this morphology can be observed in some non-pterodactyloid taxa (e.g., the Late Jurassic rhamphorhynchid genus *Bellubrunnus*; Hone *et al.* 2012) and archaeoptero-dactyloids (e.g., ctenochasmatids; Perea *et al.* 2018); therefore, this third morphotype cannot be identified beyond Pterosauria indet.

DINOSAURIA Owen, 1842

ORNITHISCHIA Seeley, 1888

DESCRIPTION

With the exception of thyreophorans, the ornithischian dinosaurs of Angeac-Charente are mainly represented by isolated teeth. Most of these teeth show evidence of pre-burial transport and are either broken or eroded. However, the few remaining well-preserved teeth indicate a great diversity of ornithischians, represented by at least five families.

Family HETERODONTOSAURIDAE Kuhn, 1966  
Genus *Echinodon* Owen, 1861

*Echinodon* sp.  
(Fig. 21A-D)

DESCRIPTION

*Premaxillary teeth*

Two well-preserved, isolated heterodontosaurid premaxillary teeth (ANG15-R672 & ANG14-3368) were recovered in Angeac-Charente (Fig. 21A-D). Only the crown, possibly from a shed tooth, is preserved in the first one (Fig. 21A, B), the other also shows a part of the root (Fig. 21C, D). Both crowns are very similar in being swollen and recurved foli-dont (Hendrickx *et al.* 2015a). They are rather short with a mesio-distal basal length of 6 mm and 7.5 mm and a preserved crown height of 8 and 9 mm, respectively. The teeth resemble those of *Echinodon* from the Purbeck Group of England described by Norman & Barrett (2002) and Sereno (2012). The crown is slightly concave lingually and gently convex labially, with an elliptical cross-section at mid-height. The main axis of the crown is recurved distally, so that its apex is slightly distal to the center of the crown base. The apex is blunt and bears a wear facet lingually. In lingual and labial views, the mesial border of the crown is convex with a bulge at its base, whereas the distal border is concave. As in *Echinodon* (Sereno 2012), and in contrast to many ornithischians, the carinae of the premaxillary teeth do not bear denticles (Galton 2009). The marked lingual wear facet, presumably from occlusion with the predeventary bill, is apicobasally oriented (Sereno 2012). The crown enamel ends at the same level on every surface. The enamel has a relatively smooth texture, but exhibits small striations.

At the cervix, a slightly pronounced constriction separates the crown from the base of the root. The latter being incomplete in one specimen and lacking in the other, we cannot assess its length relatively to the length of the crown. The base of the root is large. The root labiolingual width is stable along the preserved section, practically equivalent to the crown mesiodistal basal length, and slightly inferior to the maximum width of the crown. The root is labiolingually narrower than mesiodistally wide. In lingual and labial views, it has subparallel and slightly convex borders. At the fracture point, the root has an oval cross-section with a large pulp cavity.

Family HYPsiLOPHODONTIDAE Dollo, 1882

Hypsilophodontidae indet.  
(Fig. 21E, F)

DESCRIPTION

*Premaxillary tooth*

A well-preserved isolated hypsilophodontid crown (ANG M-119) only lacks its apex (Fig. 21E, F). In general shape, it is very similar to the aforementioned heterodontosaurid premaxillary teeth, but has a less bulbous morphology, bears denticles and lacks a wear facet on the lingual surface of the

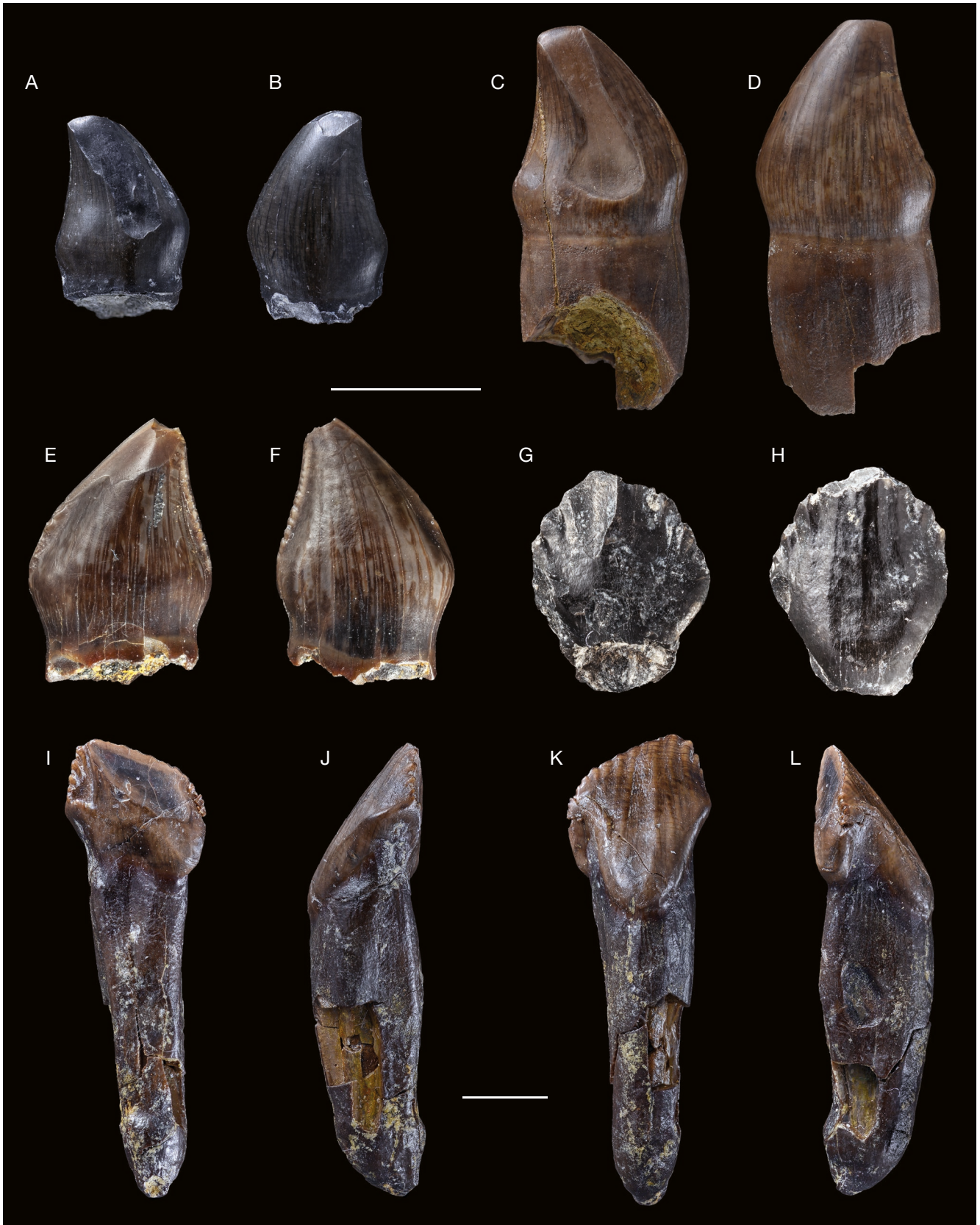


FIG. 21. — Ornithischian teeth from Angeac-Charente: **A, B**, Heterodontosaurid premaxillary tooth of *Echinodon* sp. (ANG15-R671) in lingual (**A**) and labial (**B**) views; **C, D**, Heterodontosaurid premaxillary tooth of *Echinodon* sp. (ANG14-3368) in lingual (**C**) and labial (**D**) views; **E, F**, hypsilophodontid premaxillary tooth (ANG M-119) in lingual (**E**) and labial (**F**) views; **G, H**, hypsilophodontid dentary tooth (ANG15-R927) in labial (**G**) and lingual (**H**) views; **I-L**, hypsilophodontid maxillary tooth (ANG 10-153) in lingual (**I**), distal (**J**), labial (**K**) and mesial (**L**) views. Scale bars: A-D, I-L, 5 mm; E-H, 3 mm.

crown. Based on its shape, it is identified as a premaxillary tooth, the maxillary and dentary teeth being more quadrangular in shape (Norman *et al.* 2004: fig. 18.3). The crown is recurved folioid (Hendrickx *et al.* 2015a) and short, with a mesiodistal basal length of 3 mm and a preserved crown height of 4 mm. It appears quite similar to the premaxillary teeth of *H. foxii* figured by Galton (2009: fig. 2G, L-P). The crown is compressed labiolingually and has a slightly convex surface on both sides. At mid-height, the cross-section is elliptical. The main axis of the crown is recurved, so that in lingual and labial views, the apex appears distal to the midpoint of the base of the crown. Both the mesial and distal margins are mesially and distally expanded respectively at their base. However, the mesial margin is convex, whereas the distal margin is concave for most of its length. The carinae extend from the apex along two-thirds of the crown and bear a series of fine, bulbous denticles. The mesial carina is damaged, but all the denticles are visible on the distal border. The density of the denticles is approximately 6 per mm. The crown surfaces have a relatively smooth texture. The crown enamel does not extend further basally on one particular side as for dentary teeth (see below). There is a visible constriction forming a cervix, at the base of the root.

#### Maxillary tooth

One well-preserved and complete isolated hypsilophodontid maxillary tooth (ANG10-153) (Fig. 21I-L) has been recovered from Angeac-Charente. It is 27 mm long with the root being twice as long as the crown. The crown is sub-quadrangular and short, with a mesiodistal basal length of 6 mm and a crown height of 10 mm. It looks similar to the maxillary crown of *H. foxii* (Galton 1974: fig. 14a, b). The crown is expanded mesiodistally, compressed labiolingually, and has a sub-oval cross section at mid height. The lingual surface is relatively flat, whereas the labial surface bears a longitudinal concavity in the central area of the crown and is convex mesiodistally. In lingual and labial views, the main axis of the crown is straight, but the apex is displaced distally relatively to the midpoint of the crown base. The rounded apex is however not distally bent, but strictly ventrally oriented. The mesial and distal margins are subparallel, even if the mesial margin is slightly convex, whereas the distal one is straight with a small angle at mid-height. The carinae are located on the upper portions of the mesial and distal edges, and on the apical border of the crown. The tooth carinae are covered by small denticles throughout their length, in contrast to the *H. foxii* tooth figured by Galton (1974: fig. 14a, b), in which the apical border is worn and, therefore lacks denticles. The mesial carina is damaged, but probably exhibited denticles. The distal and apical carinae exhibit large and regular denticles, at a frequency of approximately 1 per mm. They are rounded in shape, apicobasally oriented and their size slightly increases towards the apex. The denticles on the apical margin are smoothly worn and, consequently, an extended single and oblique wear facet is visible on the dorsal part of the lingual surface. There is no wear on the labial surface, but small ridges extend ventrally to denticles, towards the crown base.

The longest visible is almost 6 mm long and is directly mesial to the apex. The enamel texture is relatively smooth, except towards the base of the crown where it is more irregular. The crown enamel is clearly more basally extended on the labial side than on the lingual side of the tooth. Consequently, the base of the crown appears swollen on the labial surface and forms an incipient cingulum, as in most basal euornithopods (Norman *et al.* 2004).

At the level of the cervix, there is a constriction in labial and lingual views. It is not particularly pronounced, in which respect it differs from the condition observed in *H. foxii* (Galton 1974: fig. 14a, b). The root is long, tubular and narrower than the crown. Its mesiodistal width decreases towards the apex, whereas its labiolingual thickness is more or less equivalent on most of the root length and only decreases slightly towards the apex.

#### Dentary tooth

An isolated hypsilophodontid dentary crown, only lacking the apex, has also been recovered at Angeac-Charente, (ANG R-927; Fig. 21G-H). The crown is straight folioid (Hendrickx *et al.* 2015a) and short, with a mesiodistal basal length of 4 mm and a preserved crown height of 5 mm. At mid-length, it has a semicircular cross-section. In lingual and labial views it is diamond-shaped, and the proportions and shape are quite similar to the dentary teeth of *H. foxii* (Galton 1974: fig. 15; 2009: fig. 3). The crown is compressed labiolingually, with a convex labial surface and a slightly concave lingual surface. The main axis of the crown is straight, and the apex was most likely directed strictly dorsally. The mesial and distal borders are strongly convex, forming an angle of approximately 100° at mid-height of the crown. The carinae extend from there towards the apex. They bear a series of large denticles. The denticles are regular and semicircular, and have an apicobasal orientation. Ventral to each denticle, a blunt ridge extends towards the crown base on the lingual surface. It seems that the same ridges are also present on the labial surface, but this cannot be assessed with certainty because the tooth is eroded. On the lingual surface, the longest and most pronounced ridge is positioned below the apex. On the labial surface, three subvertical and subparallel ridges are visible on the central area of the crown. The enamel texture is irregular. The crown enamel extends further basally on the labial side than on the lingual side. A marked constriction is visible at the base of the crown, as in the dentary teeth of *H. foxii* (Norman *et al.* 2004: fig. 18.3E).

IGUANODONTIA Dollo, 1888  
Family CAMPTOSAURIDAE Marsh, 1885

Camptosauridae indet.  
(Fig. 22)

#### DESCRIPTION

Several diagnostic features allow the referral of the material described below to Camptosauridae, including: 1) lozenge-



FIG. 22. — Camptosaur remains from Angeac-Charente: **A**, dentary tooth of Camptosauridae indet. (ANG11-1120) in lingual view; **B-E**, left femur of Camptosaurus indet. (ANG14-R563) in anterior (**B**), medial (**C**), posterior (**D**) and lateral (**E**) views. Scale bar: A-D, 5 cm; E, 1 cm.

shaped teeth with prominent vertical keel more strongly developed on maxillary teeth than on dentary teeth, several secondary vertical ridges on sculptured surface of crown with anterior and posterior ridges bordering the non-denticulate half of maxillary tooth crown, posterior ridge on equivalent part of dentary teeth (Galton & Powell 1980); and 2) femur robust, with a dorsally arched shaft, a midshaft positioned and pendant fourth trochanter, and with a dorsally open, trough-like anterior intercondylar groove (Norman & Barrett 2002).

#### Dentary tooth

One extremely well-preserved, isolated camptosaurid tooth (ANG11-1120) exhibits an almost complete crown and a root broken at approximately mid-length (Fig. 22E). The crown is straight folioid (Hendrickx *et al.* 2015a), moderately elongated, and relatively robust. The mesiodistal basal length is 7 mm and the preserved crown height is 17 mm. It appears very similar to dentary teeth from the Kimmeridgian of England described by Galton & Powell (1980) and to the *Owenodon* sp. material figured by Galton (2009). The crown is labiolingually compressed, flat lingually, and strongly convex labially, with a D-shaped cross-section at mid-height. In lingual view, the main axis of the crown is straight, with a crown apex that was most likely pointing strictly dorsally. Both the mesial and the distal margins are symmetrical, with a marked angle at mid-height, conferring to the crown a diamond-shaped aspect in lingual and labial

views. On the distal border, the lower edge of the crown is flexed mesiolingually, forming a pseudo-cingulid, as seen in *Camptosaurus prestwichii* (Norman & Barrett 2002: fig. 5) and *Camptosaurus medius* (Galton 2009: fig. 10D). The carinae extend from the apex to half of the length of the crown, until the mesial and distal angulations. They appear shorter than in some *Camptosaurus* specimens, in which the carinae extend along almost two-thirds of the edges (Norman & Barrett 2002: fig. 5A; Galton 2009: fig. 10D). Both carinae are straight and oblique. Denticles are visible on the entire length of the preserved carinae. The mesial carina is damaged, but it apparently exhibits the same density of denticles as the distal carina with 3 denticles per mm. The denticles are fine, slightly mesially and distally hooked, and apicobasally oriented. They present a marked increase in size, the largest being the most apical. Ventral to the denticles, small ridges extend from their base towards the crown base. Most are approximately 1 mm in length but the longest is almost 5 mm in length and extends from the third well-developed denticle. The longitudinally concave lingual crown surface bears two strongly developed central and apicobasally oriented ridges separated by a flute. In contrast to the condition observed in some dentary teeth of the holotype of *C. prestwichii* (Norman & Barrett 2002: fig. 5A; Galton 2009: fig. 9K) and *C. medius* (Galton 2009: fig. 10D), but as seen in *Owenodon* sp. (Galton 2009: fig. 18J), the ridges are parallel throughout their length. The crown enamel extends more basally in the mesiolingual part



of the crown than in the distolingual part. The enamel has a smooth texture and its surface bears transverse undulations contacting both carinae. They are more marked on the basal half of the crown.

A pronounced constriction occurs at the base of the crown forming a cervix. Breakage of the root renders it impossible to assess whether or not it was longer than the crown. It is, however, clearly narrower. The width of the root is the same throughout the preserved portion, and it is roughly equivalent to the mesiodistal basal length measured at the level of the cervix. The root is labiolingually narrow and exhibits subparallel mesial and distal borders. On its lingual surface, a shallow concavity is visible. At the fracture point, it has a suboval cross section.

#### *Femur*

One subcomplete left femur is part of the material from Angeac-Charente referred to *Camptosauridae*. It is well-preserved, but both ends are crushed and eroded, and a small part of the distal end is missing (Fig. 22B-E). The preserved length of the femur is 265 mm. The diaphysis is relatively stout. In anterior and posterior views, the femur is straight (Fig. 22B, D). In lateral and medial views, the femur is curved with convex anterior and concave posterior margins.

The femoral head is positioned in the same plane relative to the transverse axis of the distal condyles. The femoral head is discrete, unlike that of *C. dispar* (Galton & Powell 1980: fig. 2F) and oval in anterior and posterior views. In those views, it is inclined at approximately 40° with respect to the main axis of the bone. The neck is large and it merges obliquely with the femoral shaft. In some *Camptosaurus* specimens, the neck looks more constricted (Norman & Barrett 2002: fig. 6; Galton 2009: fig. 5T).

The lesser trochanter is located on the anterior surface of the femur, on the proximal extremity. It is eroded, but it still appears as a strong and high protrusion extending proximodistally in the anterolateral angle of the femur. Its proximal extremity is lower than the proximal margin of the femoral head, but it still appears more strongly developed than in most described *Camptosaurus* species (Galton & Powell 1980; Norman & Barrett 2002; Carpenter & Wilson 2008; Galton 2009). There is no deep cleft visible between the lesser trochanter and the greater trochanter, in contrast to the condition observed in *C. aphanoecetes* (Carpenter & Wilson 2008). The greater trochanter is difficult to discern, probably as a result of erosion.

The femur diaphysis has a quadrangular cross section. It is as robust as in other *camptosaurids*. Under the fourth trochanter, the diaphysis is slightly narrower transversely than anteroposteriorly. On the posterior surface of the diaphysis, the pendent fourth trochanter is located on the medial edge of the bone, just above midshaft (Fig. 22C-E). It is strongly developed, as in most species of *Camptosaurus* (Carpenter & Wilson 2008; Galton 2009), and it is blade-shaped in lateral view (Fig. 22E). In posterior view, the base of the trochanter is straight (Fig. 22D). The proximal margin of the trochanter is elongated and gradually rises from the diaphysis, at an

angle of approximately 115° relative to the main axis of the shaft. The distal margin of the fourth trochanter is shorter and steeper.

The distal extremity of the femur is incomplete. A longitudinal bulge is visible above the distal condyles, but the condyles themselves are not preserved. On the anterior surface of the femur, a very shallow intercondylar groove is present. On the posterior surface, the popliteal fossa is visible.

THYREOPHORA Nopcsa, 1915  
ANKYLOSAURIA Osborn, 1923

Ankylosauria indet.  
(Fig. 23A-C)

#### DESCRIPTION

The ankylosaurs are only represented in Angeac-Charente by a single tooth (ANG15-3980) and an osteoderm (ANG18-6585). The tooth (Fig. 23A, B) was collected in 2015 from the unit 3 of the CG3 plot. The osteoderm (Fig. 23C) was found in 2018, in the CG9 plot, at the base of the bonebed (unit 2 of Rozada *et al.* 2021).

ANG15-3980 consists of a nearly complete, but worn tooth crown, with only the basal part of the root attached. The crown height is 9 mm, and the maximum width at the crown base is 8.5 mm. The crown is folioid, labiolingually compressed, and slightly recurved posteriorly. The labial and lingual crown surfaces are smooth and swollen around the base. The base of the crown is raised on the labial side (Fig. 23B), while there is a distinct cingulum at the base of the lingual side (Fig. 23A). A broad primary ridge extends vertically from the swollen base on both sides of the crown to form the apex of the tooth. The mesial and distal carinae bear 6 denticles, but there is no evidence of fluting as in stegosaurs and many Late Cretaceous ankylosaurs. There is a slight constriction of the root just below the crown. ANG15-3980 is nearly identical to NHMUK R2940, which is an isolated tooth from the Purbeck Group of Lulworth Cove, Dorset, referred to an ankylosaur (Galton 1980, 1983). It is also similar to ankylosaur teeth reported from the Valanginian and Barremian of southern England (Blows & Honeysett 2014).

Based on its shape and its size, ANG18-6585 is clearly distinct from other osteoderms found in Angeac-Charente that belong either to turtles, crocodyliformes or scincormorphs (see above). It has a pentagonal shape, with a maximum length of *c.* 10 cm and a thickness of *c.* 15 mm. ANG18-6585 possesses a marked keel on its exterior surface (Fig. 23C), while its base is nearly flat. The exterior surface of the osteoderm is marked with numerous grooves that give it a spongy texture. Such a morphology and structure have been reported in nodosaurid ankylosaurs (Blows 2001), and is very similar to the large ossicles observed on the sacral shield of *Polacanthus* from the Barremian of the Isle of Wight (Hulke 1887; Blows 1987, Pereda-Suberbiola 1994).

Although the material is very limited, the discovery of ankylosaur remains at Angeac-Charente is significant because these animals are very rare in the European fossil record in Purbeckian facies. Except for the Lulworth tooth (Galton 1983) and a cervico-pectoral lateral spine associated with a distal humerus from the Early Valanginian of Gronau in Germany (Sachs & Hornung 2013), there are no other known ankylosaur remains in Europe around the Jurassic/Cretaceous boundary.

STEGOSAURIA Marsh, 1877  
 Family STEGOSAURIDAE Marsh, 1880  
 Subfamily DACENTRURINAE  
 Mateus, Maidment & Christiansen, 2009  
 Genus *Dacentrurus* Lucas, 1902

*Dacentrurus* sp.  
 (Fig. 23D-J)

DESCRIPTION

Stegosaurs are represented at Angeac-Charente by 84 identified skeletal elements, most of which are vertebrae and ribs. Other remains include a few appendicular (phalanges) and skull (squamosal and braincase elements) bones, and one tooth (Fig. 23D-J). Except for the tooth, which was collected following washing and screening, all the other elements are from the same area (Fig. 3[CG4 to CG7 plots]). They very likely belong to the same individual because none of the identified bones represent the same skeletal element. Moreover, the relative proportion of the bones is also consistent with their belonging to a single individual, as suggested by the reconstructed vertebral series (Fig. 23F-J).

The single collected dentary tooth crown (Fig. 23D, E) has the same proportions as the stegosaur tooth from Cherves-de-Cognac described by Billon-Bruyat *et al.* (2010). It has a preserved height of 4.2 mm and a maximum mesiodistal width basally of 4 mm. The root is broken at its base. The presence of a sharp demarcation, either swelling or cingulum, almost at the same level on each crown surface together with the mesiodistal symmetry of the tooth lead us to refer this tooth to a stegosaurian (Billon-Bruyat *et al.* 2010). Nevertheless, the morphology of the crown is quite distinct from that of other known stegosaur teeth. As in *Huayangosaurus*, the base of the crown is sharply differentiated from the root by a prominent swelling, but there is no true ring-shaped cingulum as in other stegosaurs (Serenó & Dong 1992). In labial view, a single rounded median protuberance is present, but there are no well-defined ridges. A broad, 45° angled wear surface is present above the bulbous crown base on the labial side and has truncated a part of the dentary crown, so that the denticles are no longer visible (Fig. 23D). Vertical coarse ridges, semicircular in cross section and divided by narrow grooves are visible in lingual view.

A dozen cervical vertebrae, including the axis as well as four dorsal and two caudal vertebrae have been col-

lected (Fig. 23F-J). The neural arches are often broken, probably due to trampling (Rozada *et al.* 2021), and numerous neural spines or transverse processes are found isolated. The axial skeleton shows some features permitting clarification of the phylogenetic position of the Angeac-Charente stegosaur. The transverse processes of dorsal vertebrae project at a high angle to the horizontal as in all Thyreophoroidea (Fig. 23I), and the prezygapophyses are fused on some dorsal vertebrae as in most Eurypoda. The dorsal centra are wider than long (ANG 15-3937, centrum width 126 mm ; centrum length 95 mm). This is a feature diagnostic of *Dacentrurus* according to Galton (1985) and Maidment *et al.* (2008), and of Dacentrurinae (*Dacentrurus* + *Miragaia*) (Mateus *et al.* 2009; Costa & Mateus 2019). Cervical ribs are fused to para- and diapophyses in at least two cervical vertebrae. This feature is also diagnostic of Dacentrurinae (Mateus *et al.* 2009; Costa & Mateus 2019).

A taxonomic revision of the Late Jurassic to Early Cretaceous European stegosaurs is beyond the scope of this paper. However, if we acknowledge the existence of several species of stegosaurs closely related to *Dacentrurus* (Costa & Mateus 2019), we concur with Cobos *et al.* (2010) that, given the available diagnostic characters, and despite the discovery of a new specimen of *Miragaia* (Costa & Mateus 2019), *Dacentrurus* and *Miragaia* cannot be clearly differentiated at a generic level, at this time. Moreover, we do not understand the taxonomical logic of creating, on the one hand the new European genus, *Miragaia*, and the new sub-family Dacentrurinae, while the original diagnostic characters of *Dacentrurus*, such as dorsal vertebral centra that are wider transversely than they are long anteroposteriorly (see Galton 1985; Maidment *et al.* 2008), largely encompass *Miragaia*, and on the other hand, synonymizing a third American genus *Alcovasaurus* with *Miragaia* (Costa & Mateus 2019). Pending the complete description and revision of the Late Jurassic to Early Cretaceous European stegosaur material and a phylogenetic analysis of the specimens concerned, we still prefer to synonymize *Miragaia* with *Dacentrurus* (Cobos *et al.* 2010), which is not incompatible with the results of phylogenetic analyses (Raven & Maidment 2017). Thus, based on Costa & Mateus (2019), the Angeac-Charente stegosaur may be more closely related to *Dacentrurus longicollum* (comb. nov.), because the cervical transverse processes of a posterior cervical vertebra project ventral to the ventral margin of the prezygapophyses. Nevertheless, it is very difficult to assess the condition of this feature in *D. armatus*, given that only one half of a neural arch is preserved in the type species (Owen 1875; Galton 1985). In any case, the Angeac-Charente taxon is closely related to the English, Spanish and Portuguese stegosaurs, and it is the youngest occurrence of *Dacentrurus*. In addition to bony remains, about 100 stegosaur natural track casts in a range of sizes have been identified and documented on a single bedding plane in the CG3 plot, and assign to the ichnotaxon *Deltapodus* (Rozada 2019; Rozada *et al.* 2021).



FIG. 23. — Thyreophoran remains from Angeac-Charente: **A, B**, ankylosaur maxillary tooth (ANG15-3980) in lingual (**A**) and labial (**B**) views; **C**, ankylosaur osteoderm (ANG18-6585) in dorsal view; **D, E**, dentary tooth of *Dacentrurus* sp. (ANG M-14) in labial (**D**) and lingual (**E**) views; **F**, axis of *Dacentrurus* sp. (ANG18-6203) in ventral view; **G**, anterior cervical vertebra of *Dacentrurus* sp. (ANG12-1878) in ventral view; **H**, reconstructed cervical series of *Dacentrurus* sp. (ANG16-6748, ANG16-4660, ANG12-1749, ANG14-3202, ANG14-2912, ANG14-3094) in ventral view; **I, J**, dorsal vertebra of *Dacentrurus* sp. (ANG18-6548) in anterior (**I**) and right lateral (**J**) views. Scale bars: A, B, 5 mm; C, D, 2.5 mm; E, 2.5 cm; F-J, 5 cm.



FIG. 24. — Sauropod teeth from Angeac-Charente: **A-D**, posterior left maxillary tooth of *Turiasauria* indet. (ANG11-837) in labial (**A**), mesial (**B**), lingual (**C**) and distal (**D**) views; **E-H**, left maxillary tooth of *Turiasauria* indet. (ANG15-R905) in labial (**E**), mesial (**F**), lingual (**G**) and distal (**H**) views; **I-L**, left maxillary tooth of *Turiasauria* indet. (ANG13-2330) in labial (**I**), mesial (**J**), lingual (**K**) and distal (**L**) views; **M-P**, left premaxillary tooth of *Turiasauria* indet. (ANG14-R289) in labial (**M**), mesial (**N**), lingual (**O**) and distal (**P**) views; **Q-T**, dentary tooth of *Turiasauria* indet. (ANG14-3495) in labial (**Q**), mesial (**R**), lingual (**S**) and distal (**T**) views; **U-X**, left dentary tooth of *Turiasauria* indet. (ANG14- R435) in labial (**U**), mesial (**V**), lingual (**W**) and distal (**X**) views; **Y-AA**, maxillary tooth of *Macronaria* indet. (ANG R-1732) in labial (**Y**), distal (**Z**) and lingual (**AA**) views. Scale bar: A-X, 2 cm; Y-AA, 1 cm.



FIG. 25. — Sauropod embryonic or hatchling teeth from Angeac-Charente: **A**, tooth of *Macronaria* indet. (ANGM-18) in lingual view; **B**, **C**, tooth of *Turiasauria* indet. (ANGM-118) in labial (**B**) and lingual (**C**) views. Scale bar: 500  $\mu$ m.

SAURISCHIA Seeley, 1888  
 SAUROPODA Marsh, 1878  
 EUSAUROPODA Upchurch, 1995  
 TURIASAURIA Royo-Torres, Cobos & Alcalá, 2006

*Turiasauria* indet.  
 (Figs 24A-X; 25B, C; 26; 27)

#### DESCRIPTION

Sauropod remains are especially abundant in the Early Cretaceous of Angeac-Charente. The locality has yielded many teeth ( $N = 146$ ), bones ( $N = 784$ ), and track casts of this group of dinosaurs (Néraudeau *et al.* 2012; Rozada *et al.* 2021). All parts of the skeleton are represented including the braincase, some skull bones, teeth, cervical, dorsal and caudal vertebrae, chevrons, pelvic girdle and all the limb bones (Figs 24–27). Based on the number of femurs and their size, as well as the teeth, there are at least seven different individuals preserved in the site. With the exception of two teeth (see below), all this material belongs to a single taxon. All remaining teeth are reminiscent of the *Turiasauria* clade (Allain *et al.* 2013, 2017). We can classify them based on a small number of diagnostic characters. Teeth are heart-shaped in labial and lingual views, with an asymmetric shape induced by a concave distal margin towards the apex (Royo-Torres *et al.* 2006, 2017; Royo-Torres & Upchurch 2012; Mocho *et al.* 2016). This feature has been observed in most of the sauropod teeth that have been collected from Angeac-Charente (Figs 24; 25B, C). A second character permits referral of these teeth to *Turiasauria*. When the root is well preserved, several long longitudinal grooves are visible in *Turiasaurus*, *Losillasaurus* (Royo-Torres *et al.* 2021) and *Moabosaurus* (Britt *et al.* 2017 and RRT personal observation). These grooves are also present in the Angeac-Charente taxon (Fig. 24I–P, U–X) and may be diagnostic for *Turiasauria* (Royo-Torres *et al.* 2021). Moreover, the teeth of Angeac-Charente show a range of crown morphotypes and

this variability of forms has also been described in *turiasaur* teeth from Portugal (Mocho *et al.* 2016) and in *Mierasaurus* (Royo-Torres *et al.* 2017) and *Losillasaurus* (Royo-Torres *et al.* 2021). Teeth, in private collections, identical in every way to those of Angeac-Charente, are also present in the Berriasian of Cherves-de-Cognac (RA, TL pers. obs.).

The caudal vertebrae are also useful in determining the systematic position of the Angeac-Charente sauropod (Fig. 26). The anterior caudal vertebrae are procoelous with a slightly convex posterior articulation (Fig. 26A–I) whereas the middle become amphicoelous or amphiplatyan (Fig. 26J–L). The presence of a convex posterior articulation on sauropod caudal vertebrae was acquired several times during sauropod evolution (Wilson 2002; Upchurch *et al.* 2004; D’Emic 2012; Mannion *et al.* 2017, 2019) and can be seen in diplodocids, titanosaurs and mamenchisaurids. The procoelous condition was also acquired in *Turiasauria*, as described for the Late Jurassic *Turiasaurus* and *Losillasaurus* (Casanovas *et al.* 2001; Royo-Torres *et al.* 2006, 2021). It has also been reported in the posterior series of Early Cretaceous *Mierasaurus* and *Moabosaurus* (Royo-Torres *et al.* 2017; Britt *et al.* 2017). This feature is considered to be synapomorphic for *Turiasauria* in some phylogenetic analyses (Carballido & Sander 2014). The neural arch of anterior caudal vertebrae is restricted to the anterior half of the centrum. This character is shared with *Turiasaurus*, *Losillasaurus*, *Moabosaurus*, *Mierasaurus*, *Cetiosaurus* and the Titanosauriformes (Upchurch *et al.* 2004; D’Emic 2012; Britt *et al.* 2017; Royo-Torres *et al.* 2017). The presence in the Angeac-Charente taxon of caudal vertebrae with short lateral processes (‘caudal ribs’) that do not extend beyond the posterior end of the centrum suggests affinities with Titanosauriformes (Mannion *et al.* 2019; Royo-Torres *et al.* 2021).

Two additional possible synapomorphic characters for *Turiasauria* seen in specimens from Angeac-Charente include slightly opisthocelous posterior dorsal centra, as well as a high neural arch below the postzygapophyses of the posterior dorsal vertebrae (Carballido & Sander 2014).

MACRONARIA Wilson & Sereno, 1998

Macronaria indet.  
(Figs 24Y-AA; 25A)

DESCRIPTION

In addition to the turiasaur, a second sauropod taxon may be present at Angeac-Charente site. It is only represented by a single abraded tooth and a tooth recovered from microremains (Figs 24Y-AA; 25A). They are spatulate and characterized by straight and subparallel distal and mesial edges at the base of the crown, and by the presence of a convex labial and concave lingual surface. Based on these features, these teeth are assigned to a macronarian sauropod probably close to *Camarasaurus* (Wilson 2002; Upchurch *et al.* 2004; Mocho *et al.* 2017).

Sauropod track casts have also been recorded at Angeac-Charente. They are represented by casts of pes and manus footprints (Rozada *et al.* 2021). In 2018, a sauropod footprint cast was observed above and in contact with an *in-situ* broken sauropod radius. It represents a spectacular “instantaneous” preservation of the action of a sauropod pes or manus crushing a sauropod long bone, and inducing bone modifications (breakage, displacement and reorientation) and sediment deformations (Rozada *et al.* 2021). The footprints are identified as Sauropoda indet. because of the general circular morphology of the pes, the characteristic tubular metacarpal arrangement of the manus and also the huge size of the prints (Carrano & Wilson 2001; Wilson 2005).

THEROPODA Marsh, 1881

TETANURAE Gauthier, 1986

Family MEGALOSAURIDAE? Fitzinger, 1843

Megalosauridae? indet.  
(Fig. 28K-N)

DESCRIPTION

All the large (> 3 cm) blade-like theropod teeth found at Angeac-Charente are tentatively referred to a single taxon, although two tooth morphotypes are present. The first morphotype probably corresponds to mesial teeth (Fig. 28K-M), the crown of which are slender and more elongated than in lateral teeth (Fig. 28N). The crown height ratio (Hendrickx *et al.* 2015a) ranges between 1.91 (ANG M-121) for a lateral tooth and 2.43 for a mesial one (ANG 17-5650). Apart from that, the teeth have the same characters. They are strongly compressed labiolingually. The mesial margin is convex and the distal margin is only slightly concave. Both the distal and mesial carinae are denticulate, but the latter only occurs on the apical half to one third of the crown. The carinae are centrally positioned on both the mesial and distal margins of crowns. There are 12 (ANG 17-5650) to 18 (ANG M-121) denticles per 5 mm along the mesial carinae, and 12 to 15 along the distal carinae at two thirds of the crown height. The denticles are longer mesiodistally than they are basoapically high, and they have a horizontal subrectangular outline. Inter-

dental sulci are present. The enamel is transversely wrinkled and both transverse and marginal undulations are present (Hendrickx *et al.* 2015a).

Teeth of large carnivorous dinosaurs, morphologically very close to those of Angeac-Charente, have been reported from the Tithonian of Chassiron and from the Purbeckian of England. The first have been referred with caution to Megalosauridae (Vullo *et al.* 2014), while the latter have been alternately referred to Megalosauridae or Allosauroidea (see Milner 2002). All dental characters described above have been recognized in Megalosauridae (Hendrickx *et al.* 2015b), and we tentatively refer the large dinosaur teeth of Angeac-Charente to this group, but an assignment to another basal tetanuran clade cannot be definitively excluded.

COELUROSAURIA Huene, 1914

ORNITHOMIMOSAURIA Barsbold, 1976

Ornithomimosauria indet.

DESCRIPTION

Ornithomimosauria are by far the most commonly represented vertebrates in Angeac-Charente, with more than 3800 macroremains collected (Figs 29-30), accounting for more than 50% of the identified vertebrate material (Rozada *et al.* 2021). The minimum number of individuals (MNI) is approximately 70 based on the distal end of left tibiae. Ornithomimosaur remains are mainly concentrated in the CG1 and CG3 loci, in which they represent 70 % of all the ornithomimosaur remains identified. Such a concentration and high number of individuals are congruent with a mass mortality event of an ornithomimosaur herd (Allain *et al.* 2011, 2014; Néraudeau *et al.* 2012; Rozada *et al.* 2021). However, no articulated skeletons have been observed due to the intense trampling (dinoturbation) affecting this area (Rozada *et al.* 2021). The only articulated remains of ornithomimosauria found so far come from the northwestern part of the quarry (CG9 plot) and they include the zeugopod and the autopod of the forelimb of a single individual, as well as the the zeugopod and autopod of the hindlimb of another single individual.

Except for the most fragile elements such as the maxillary and palate bones, which have probably suffered from trampling and have not yet been identified, the skeleton of the Angeac-Charente ornithomimosaur is virtually complete (Fig. 31). A complete description of the entire skeleton of this new taxon is beyond the scope of this study. Nevertheless, it seems important to highlight here key anatomical features of the Angeac-Charente ornithomimosaur: first, because this clade was hitherto unknown in Europe at the beginning of the Cretaceous (Allain *et al.* 2014); secondly because it may be the oldest known ornithomimosaur to date (Choiniere *et al.* 2012; Cerroni *et al.* 2019); thirdly, because it shows very close anatomical similarities to *Limusaurus*, which is a Late Jurassic Chinese theropod that is not considered a member of the Ornithomimosauria, but a ceratosaurian (Xu *et al.* 2009). These similarities include a very large external mandibular fenestra and short forelimbs with

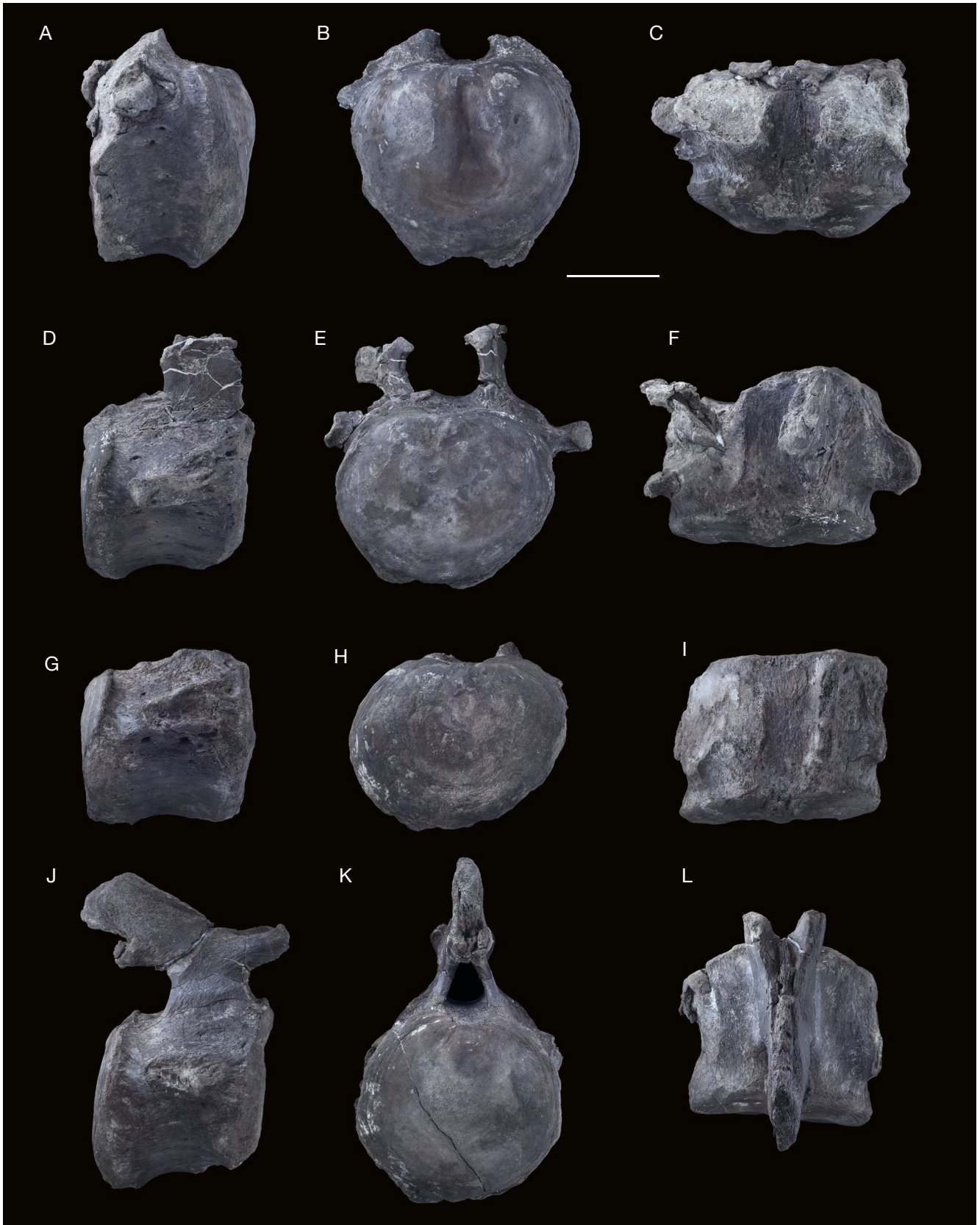


FIG. 26. — Sauropod caudal vertebrae from Angeac-Charente: **A-C**, anterior caudal vertebra of *Turiasauria* indet. (ANG15-R679) in left lateral (**A**), posterior (**B**) and dorsal (**C**) views; **D-F**, anterior caudal vertebra of *Turiasauria* indet. (ANG15-R698) in right lateral (**D**), posterior (**E**) and dorsal (**F**) views; **G-I**, anterior caudal vertebra of *Turiasauria* indet. (ANG15-R921) in right lateral (**G**), posterior (**H**) and dorsal (**I**) views; **J-L**, middle caudal vertebra of *Turiasauria* indet. (ANG15-R652) in right lateral (**J**), posterior (**K**) and dorsal (**L**) views. Scale bar: 10 cm.



FIG. 27. — Femur of *Turiasauria* indet. (ANG19-7000) from the Berriasian of Angeac-Charente discovered during the 2019 campaign. The length of the femur is 2 m. © L. Bocat.



manual digit reduction (RA pers. obs.). Relationships between ceratosaurians and ornithomimosaurians have long been confusing (e.g. Marsh 1895; Janensch 1925; Galton 1982; Holtz 1994; Rauhut 2003). Some taxa, including *Elaphrosaurus*, *Deltadromeus*, *Limusaurus*, *Nqwebasaurus* and probably the Angeac-Charente taxon do not have a clearly established phylogenetic position, and their anatomy may also reflect unexpected and unrecognized relationships between ceratosaurians and ornithomimosaurians. Pending a comparative and detailed phylogenetic study, we provide herein some anatomical features that clearly indicate the ornithomimosaurian affinity of Angeac-Charente material.

Besides the features already mentioned by Allain *et al.* (2014), we mainly used the anatomical characters discussed in the recent reappraisal of the phylogenetic position of *Afromimus* by Cerroni *et al.* (2019). The edentulous and downturned dentary (Fig. 29A) is an ornithomimosaurian synapomorphy convergently acquired by numerous other coelurosaurian groups (Zanno & Makovicky 2010). It is worth noting that outside coelurosaurians only *Limusaurus* displays a toothless skull and mandible in mature individuals (Wang *et al.* 2017). The pedal unguals of the Angeac-Charente theropod have a weak longitudinal curvature and exhibit the reduction of the flexor tubercle to a ventral platform seen in ornithomimosaurians, but also in abelisauroids (Fig. 29B, C; Cerroni *et al.* 2019: fig. 7). Nevertheless, they are more reminiscent of ornithomimosaurians, being slender, and having a triangular cross-section and a single ventral groove (Longrich 2008), whereas pedal unguals of *Afromimus* and *Masiakasaurus* are shorter and possess a dorsal vascular groove.

The centrum of the middle and distal caudal vertebrae is long and low (Fig. 29D-L). The anterior and posterior articular surfaces are slightly wider than tall, with a reniform contour (Fig. 29H, L). A broad and shallow sulcus is present on the ventral surface, and it is laterally delimited by two prominent ridges (Fig. 29E, J). All these features are present in ornithomimosaurians (Osmolska *et al.* 1972; Longrich 2008) but also in *Elaphrosaurus* (Rauhut & Carrano 2016). As in all ornithomimosaurians, the robust and tongue-shaped prezygapophyses of the Angeac-Charente taxon are elongated anteroposteriorly, up to three-quarters the length of the centrum. They are horizontally directed (Fig. 29F, K) and do not diverge laterally from the sagittal plane (Fig. 29D, I). Conversely, the zygapophyses of ceratosaurians are slender, shorter and directed anterodorsally (Carrano *et al.* 2002; O'Connor 2007, Cerroni *et al.* 2019).

The tibia of the Angeac-Charente ornithomimosaur has already been described in detail (Allain *et al.* 2014). Here, we figure new material to highlight the features that best differentiate it from a ceratosaur tibia (Fig. 30A-D). The proximal end of the tibia is markedly different from that of *Ceratosaurus*, *Masiakasaurus*, *Carnotaurus*, *Majungasaurus*, *Afromimus* and *Elaphrosaurus* having a fibular crest clearly separated from the proximal articular surface (Fig. 30A-C), as in tetanuran theropods and thus all the ornithomimosaurians. The elliptical scar present on the posterior surface of the proximal end of the tibia of some ceratosaurians is not visible in the Angeac-Charente taxon (Cerroni *et al.* 2019). As in all ornithomimosaurians, the anterior surface of the distal end of the tibia of the Angeac-Charente taxon bears a tall and transversely expanded flat articular surface for the ascending

process of the astragalus (Fig. 30D). There is no medial buttress to accommodate the ascending process as in many basal tetanurans and ceratosaurians, including *Berberosaurus*, *Masiakasaurus*, *Majungasaurus* and *Ceratosaurus*.

The medial face of the fibula bears a deep and proximodistally elongate elliptical fossa for the insertion of *musculus popliteus*. This fossa opens medially and is anteriorly and posteriorly bounded by sharp rims (Fig. 30E). Such a condition is only known in coelurosaurians and *Elaphrosaurus*, and markedly differs from the condition seen in coelophysoids and ceratosaurians, in which the fossa is covered anterodorsally by the tibial crest and thus opens posteriorly (Rauhut 2003; Allain *et al.* 2007; Rauhut & Carrano 2016; Cerroni *et al.* 2019).

In common with the tibia and fibula, the astragalus has a morphology typical of the coelurosaurians and very different from that of the ceratosaurians (Fig. 30F-H). In contrast to *Ceratosaurus*, *Elaphrosaurus*, *Masiakasaurus*, and abelisauroids, the astragalus is fused neither to the calcaneum nor the tibia or fibula (Fig. 30H). The height of the blade-like ascending process of the astragalus is more than twice the height of astragalar body and the process arises from the complete breadth of the astragalar body (Fig. 30F-G). In contrast, all ceratosaurians exhibit a low and narrow ascending process. In addition, the fibular facet on the astragalus is strongly reduced on the lateral side of the ascending process of the astragalus (Fig. 30H). In contrast, the distal end of the fibula of numerous abelisauroids including *Berberosaurus*, *Masiakasaurus*, *Afromimus* and *Majungasaurus* is transversely expanded and the flared distal end partially overlaps the ascending process of astragalus, the fibular facet of which is large. As previously stated (Néraudeau *et al.* 2012, Allain *et al.* 2013, 2014), all surveyed anatomical features agree with assignment of the Angeac-Charente theropod to Ornithomimosauria.

Cerroni *et al.* (2019) have recently questioned the ornithomimosaurian phylogenetic affinities of the Early Cretaceous African *Nqwebasaurus* (Choiniere *et al.* 2012). If confirmed, it would imply that the Charentais taxon is the oldest known ornithomimosaur, based on the Berriasian age of the Lagerstätte of Angeac-Charente (Benoit *et al.* 2017; Polette *et al.* 2018). Moreover, ornithomimosaurians would then have an exclusively Laurasian distribution. Nevertheless, based on first hand examination of fossil specimens by one of us (R.A.), the phylogenetic affinities of *Limusaurus* and *Deltadromeus* are far from certain. More detailed descriptions regarding their anatomy are required to draw conclusions regarding the origin and evolution of ornithomimosaurians.

## Superfamily TYRANNOSAUROIDEA Osborn, 1905

### Tyrannosauroida indet. (Fig. 28H-J)

#### DESCRIPTION

There are at least eight teeth with a very characteristic morphology. They are D-shaped in cross-section with the mesial carina lingually displaced (Fig. 28H-J). The mesial margin is



Fig. 28. — Theropod teeth from Angeac-Charente: **A-C**, Archaeopterygid tooth (ANG M-09) in lingual (**A**) and labial (**B, C**) views; **D**, Archaeopterygid tooth (ANG M-08) in lingual view; **E, F**, cf. *Nuthetes* sp. (ANG M-45) in lingual (**E**) and distal (**F**) views; **G**, cf. *Nuthetes* sp. (ANG M-61) in lingual view; **H**, tooth of Tyrannosauroida indet. (ANG17-5342) in lingual view; **I, J**, tooth of Tyrannosauroida indet. (ANG M-73) in lingual (**I**) and distal (**J**) views; **K**, Megalosauridae? indet. (ANG17 R-1748) in lingual view (**J**); **L, M**, Megalosauridae? indet. (ANG17-5650) in labial (**L**) and (**M**) lingual views; **N**, Megalosauridae? indet. (ANG M-121) in lingual view. Scale bar: A, B, 1 mm; C-F, 400 µm; G, 5 mm; H-N, 1 cm.

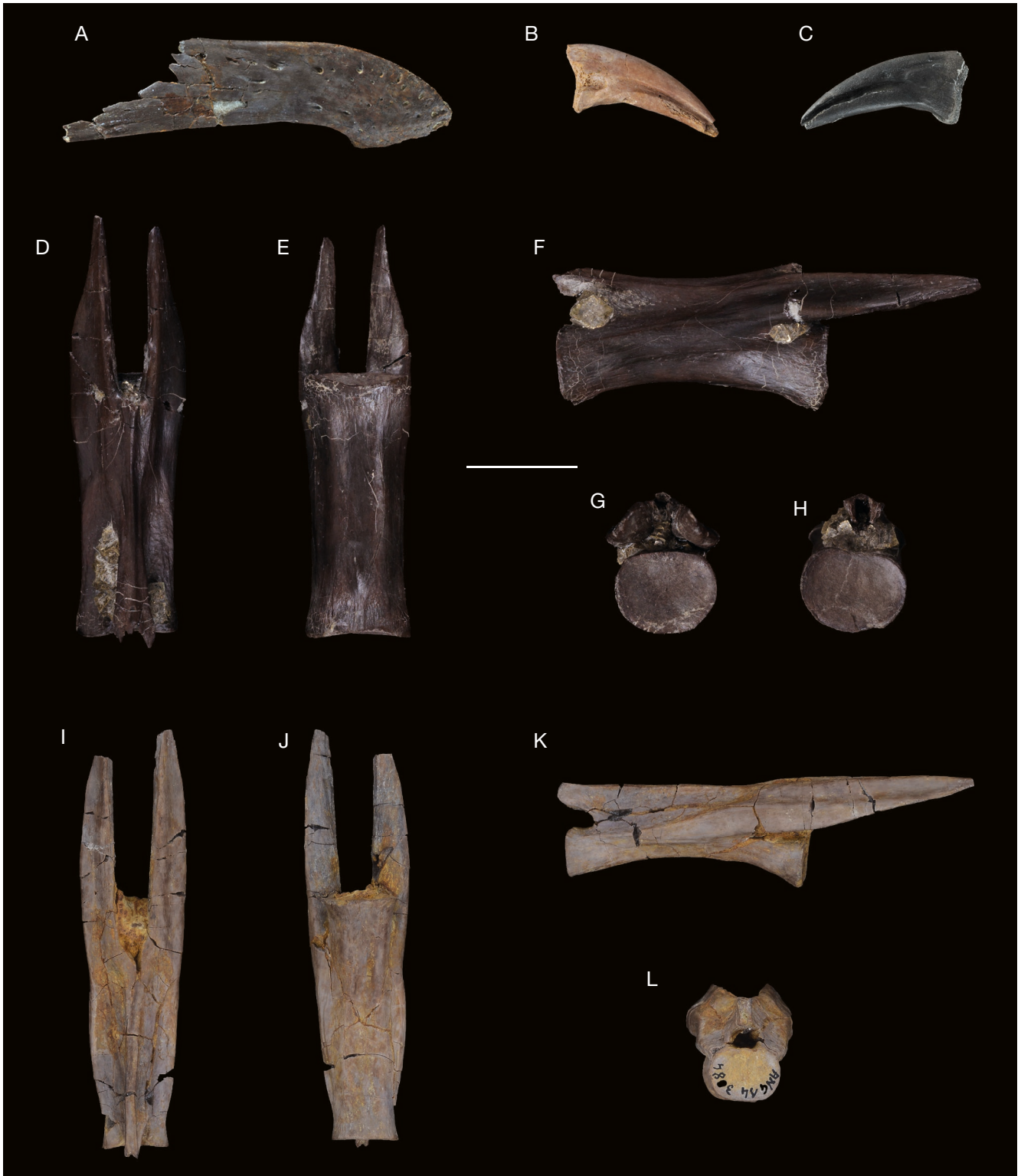


FIG. 29. — Ornithomimosaur remains from Angeac-Charente: **A**, right dentary (ANG11-776) in lateral view; **B**, pedal ungual (ANG11-1335) in lateral view; **C**, pedal ungual (ANG11-898) in lateral view; **D-H**, middle caudal vertebra (ANG12-1622) in dorsal (**D**), ventral (**E**), right lateral (**F**), anterior (**G**) and posterior (**H**) views; **I-L**, distal caudal vertebra (ANG14-3084) in dorsal (**I**), ventral (**J**), right lateral (**K**) and posterior (**L**) views. Scale bar: 2 cm.

only slightly convex. The distal carina is denticulate along its entire length, while the mesial carina is only denticulate on its apical quarter. The denticles extend over the apex. There are 12-13 denticles per 5 mm on mesial and distal carinae.

Two longitudinal grooves are present on the lingual side of ANG M-73, below the denticulate mesial carina (Fig. 28I). When preserved, the enamel texture is irregular (Hendrickx *et al.* 2015a).

The morphology of these teeth and in particular the lingual offset of the mesial carina are typical of tyrannosauroids (Holtz 2004). They are very similar to that described in the Bathonian *Proceratosaurus bradleyi* and the Barremian *Eotyrannus* (Hutt *et al.* 2001; Rauhut *et al.* 2010). This discovery confirms the presence of Tyrannosauroidea in Europe at the beginning of the Early Cretaceous.

Family DROMAEOSAURIDAE Colbert & Russell, 1969  
Genus *Nuthetes* Owen, 1854

cf. *Nuthetes* sp.  
(Fig. 28E-G)

DESCRIPTION

Several isolated dromaeosaurid teeth, including the two reported here (ANG M-61; ANG M-45), were recovered following sampling and screening-washing of a gravel lens, rich in lignite and fossil bone remains (Fig. 28E-G). These teeth lack a serrated mesial carina, as in *Tsaagan mangas* (Norell *et al.* 2006) and some teeth of *Nuthetes destructor* (Milner 2002). ANG M-61 is a complete tooth crown, and is more rounded. It is strongly recurved and its distal carina runs along half the length of the lingual face of the crown (Fig. 28G). There are 32 denticles per 5 mm on distal carina. This tooth is identified as a mesial tooth. ANG M-45 is the apical part of a second tooth (Fig. 28E-F). Its crown is more labiolingually compressed, and this tooth is identified as a lateral tooth. The distal carina bears numerous distinct denticles. In both teeth, the enamel surface is devoid of ornamentation.

Teeth identical in every way to those of Angeac-Charente have also been reported from the Berriasian of Cherves-de-Cognac (Pouech 2008) and from the Tithonian of Chassiron (Vullo *et al.* 2014). All these teeth from Charente are similar to those of the dromaeosaurid *Nuthetes destructor* from the Purbeck Group of southern England (Milner 2002), and are tentatively referred to this genus.

AVES Linnaeus, 1758  
Family ARCHAEOPTERYGIDAE Huxley, 1872

Archaeopterygidae indet.  
(Fig. 28A-D)

DESCRIPTION

Archaeopterygid birds are represented in Angeac-Charente by at least five teeth. One of these teeth is complete (ANG M-09, Fig. 28A-C), whereas the others are broken at the base of the crown (Fig. 28D). The total height of the complete tooth is 3.2 mm. The crown height is only 1.2 mm and its basal length is 0.63 mm. The crown is strongly compressed labiolingually. There are no obvious enamel ornamentation and serrations are totally absent on the slight carinae. The apical quarter of the tooth is strongly distally recurved.

Both the mesial and distal edges of the crown are sigmoid. By comparison with teeth of other theropods, we consider that the most convex side of the tooth corresponds to the labial surface (Fig. 28B-D).

The specimens from Angeac-Charente are nearly identical to the single tooth collected at Cherves-de-Cognac, which in turn was assigned to an indeterminate archaeopterygid, based on the above characteristics (Louchart & Pouech 2017). Angeac-Charente material is the youngest temporal occurrence of this extinct European family of early birds.

SYNAPSIDA Osborn, 1903  
MAMMALIA Linnaeus, 1758

Mammalia indet.  
(Fig. 32C, D)

DESCRIPTION

A tooth from the mammal material of Angeac-Charente, ANG M-34 (Fig. 32C, D), preserves a high, main central cusp, one accessory cusp and one root. Given the strong development of the accessory cusp and the inclination of the main cusp apex, this side of the tooth, and thus the only preserved root, is considered to be distal. The section of the tooth breakage shows that a second, mesial root was present. A symmetrical and similar accessory cusp was maybe present on the mesial side. Such morphology is reminiscent to that of the posterior premolariforms of the Middle Jurassic eutriconodont *Amphilestes* and other “Amphilestidae” (Kielan-Jaworowska *et al.* 2004). However, without the second half of the tooth, it is difficult to reach a conclusion, as it could also correspond to other, more derived mammals. Without any more diagnostic characters, this specimen is thus cautiously identified as Mammalia indet.

Family THEREUODONTIDAE  
Sigogneau-Russell & Ensom, 1998  
Genus *Thereuodon* Sigogneau-Russell, 1989

*Thereuodon* cf. *taraktes*  
(Fig. 32G-I)

DESCRIPTION

An isolated tooth crown (Fig. 32G-I) is assigned to the genus *Thereuodon* of the monogeneric family Thereuodontidae, on the basis of several characters (Sigogneau-Russell 1989; Sigogneau-Russell & Ensom 1998; Kielan-Jaworowska *et al.* 2004): it is labio-lingually narrow, with a great development of the parastylar lobe, forming almost a basin (Fig. 32I); a small vertical concavity can be seen on the anterior face of the paracone; the stylocone is well-developed (Fig. 32G); cusp D occurs just behind the stylocone, although it is heavily abraded on this specimen (Fig. 32G); a vertical ridge, the mediocrista, links the paracone to the cusp D, although it is weakly pronounced (Fig. 32I). Thus, three transversely narrow basins



FIG. 30. — Ornithomimosaur remains from Angeac-Charente: **A-C**, proximal end of right tibia (ANG12-1893) in posterior (**A**), anterior (**B**) and lateral (**C**) views; **D**, distal end of right tibia (ANG10-56) in anterior view; **E**, proximal end of right fibula (ANG11-696) in medial view; **F-H**, Left astragalus and calcaneum (ANG12-1803) in anterior (**F**), posterior (**G**) and dorsal (**H**) views. Scale bar: A-E, 4 cm; F-H, 2 cm.

are present in occlusal view. Moreover, the paracone is high compared to the labial wall and labially but not posteriorly recurved (Fig. 32G, I). This crown is well-preserved, lacking only the metastyle.

Two species are known for the genus *Thereuodon*: the type-species *T. dahmanii* (Sigogneau-Russell 1989) from the Jurassic/Cretaceous transition of the Ksar Metlili Formation, Morocco, and *T. taraktes* (Sigogneau-Russell & Ensom 1998), from the Early Cretaceous (Berriasian) Purbeck Group, England. In the Angeac-Charente specimen,

the great protrusion of the parastylar cusp and the weakly marked mediacrista are reminiscent of *T. taraktes*, but the well-developed metacone is close to what is observed in *T. dahmanii*. The stylocone is closer to cusp D and less sharp than in *T. dahmanii*, but this conformation is similar to that of *T. taraktes*. Finally, as in *T. taraktes* but unlike *T. dahmanii*, there is no cuspule “c”. In conclusion, we tentatively assign this specimen to *Thereuodon* cf. *taraktes*.

Sigogneau-Russell (1989) and Sigogneau-Russell & Ensom (1998) considered the teeth they referred to the

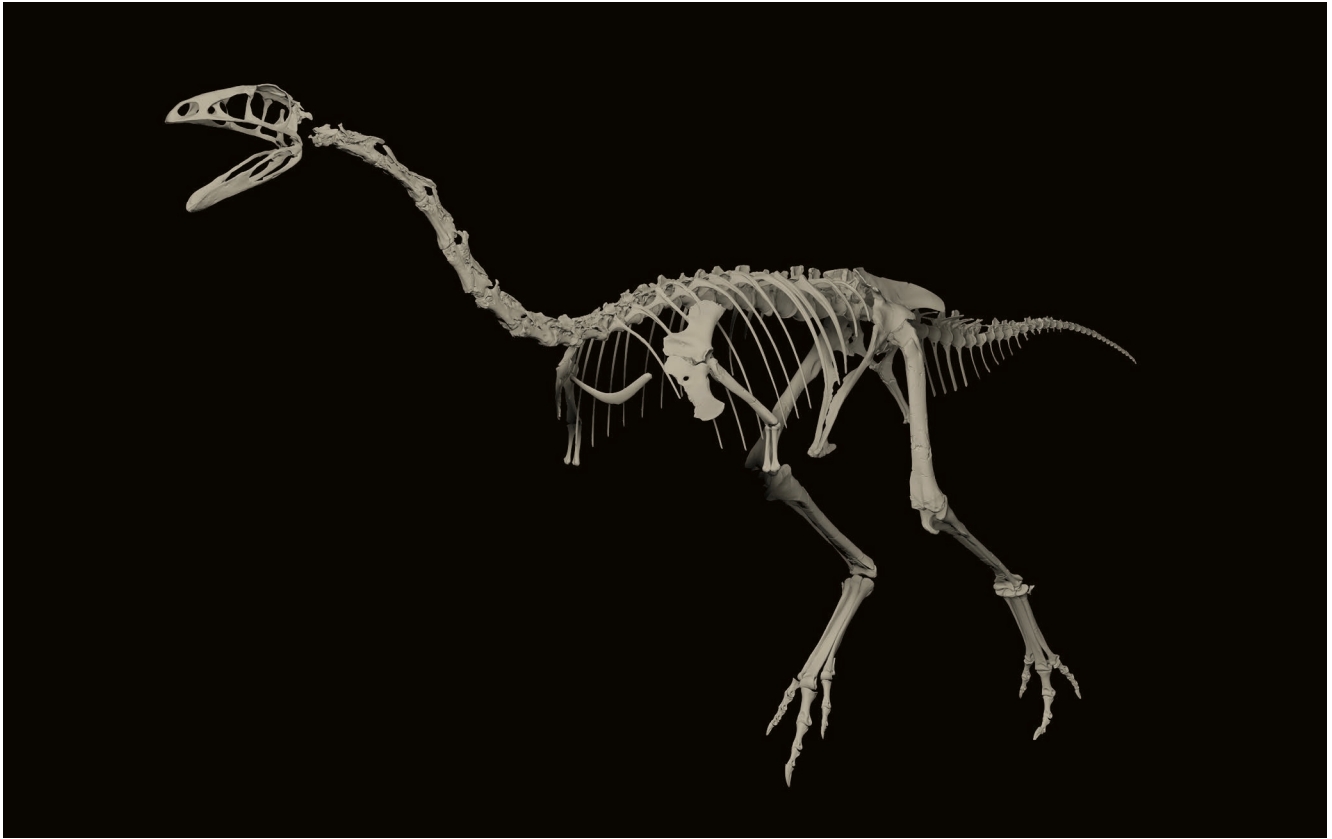


FIG. 31. — Reconstruction of the Angeac Ornithomimosaur, based on 3D surface scans of 232 bones. All the bones of the 3D reconstruction were scaled on the basis of a 40 cm long femur.

two species of *Thereuodon* as “symmetrodontan” permanent molars. However, the upper deciduous premolars of *Nanolestes drescheriae*, a stem-Zatheria from the Late Jurassic of Guimarota, Portugal (Martin 1999, 2002), show some similarities with the teeth of *Thereuodon*. Thus, the DP<sup>23-5</sup> of *N. drescheriae* share with the teeth of *Thereuodon* an obtuse-angled trigone, a low and recurved paracone, and a trigone basin divided by a ridge connecting stylocone and paracone. These characters are diagnostic of Holotheria, a clade that include the last common ancestor to *Kuehneotherium* and Theria, and all of its descendants (Hopson 1994; Wible *et al.* 1995). Martin (2002) thus reinterpreted the teeth of *Thereuodon* as holotherian, probably zatherian upper deciduous premolars. Moreover, Bonaparte (1990) and Sigogneau-Russell & Ensom (1998) observed a gross resemblance between the teeth of *Thereuodon* and the upper cheek teeth of *Barberenia*, from the Late Cretaceous of Argentina. These were subsequently identified by Martin (1999) as upper deciduous premolars, probably belonging to the “dryolestoidan” *Brandonia* from the same formation, an opinion then followed by Bonaparte (2002). Thus, it seems that *Thereuodon* should be considered as a stem-Zatheria (Martin 2002). However, from a nomenclatural point of view, the

fact that *Thereuodon* is known only by milk teeth does not invalidate the genus, which is why we use it here to precise the identification of this specimen.

#### EUTRICONODONTA

Kermack, Mussett & Rigney, 1973  
(Fig. 32A, B, E, F)

#### DESCRIPTION

Some mammalian teeth show a distinctive morphology comprising three main cusps placed serially in anteroposterior alignment on a transversely compressed crown (Fig. 32A, B, E, F). This cusp arrangement and general morphology is typical of eutriconodontans (Kielan-Jaworowska *et al.* 2004).

Orientation of these isolated teeth follows the criteria of Godefroit & Battail (1997). The most convex side of the crown is considered to be the labial face, and the most concave the lingual face. Accessory cusps are usually more numerous or better developed on the distal side, and thus the side bearing the most developed and/or the most differentiated accessory cusps is considered to be distal. The distal inclination of the cusps, when present, also helps to distinguish the mesial and distal faces of the teeth.

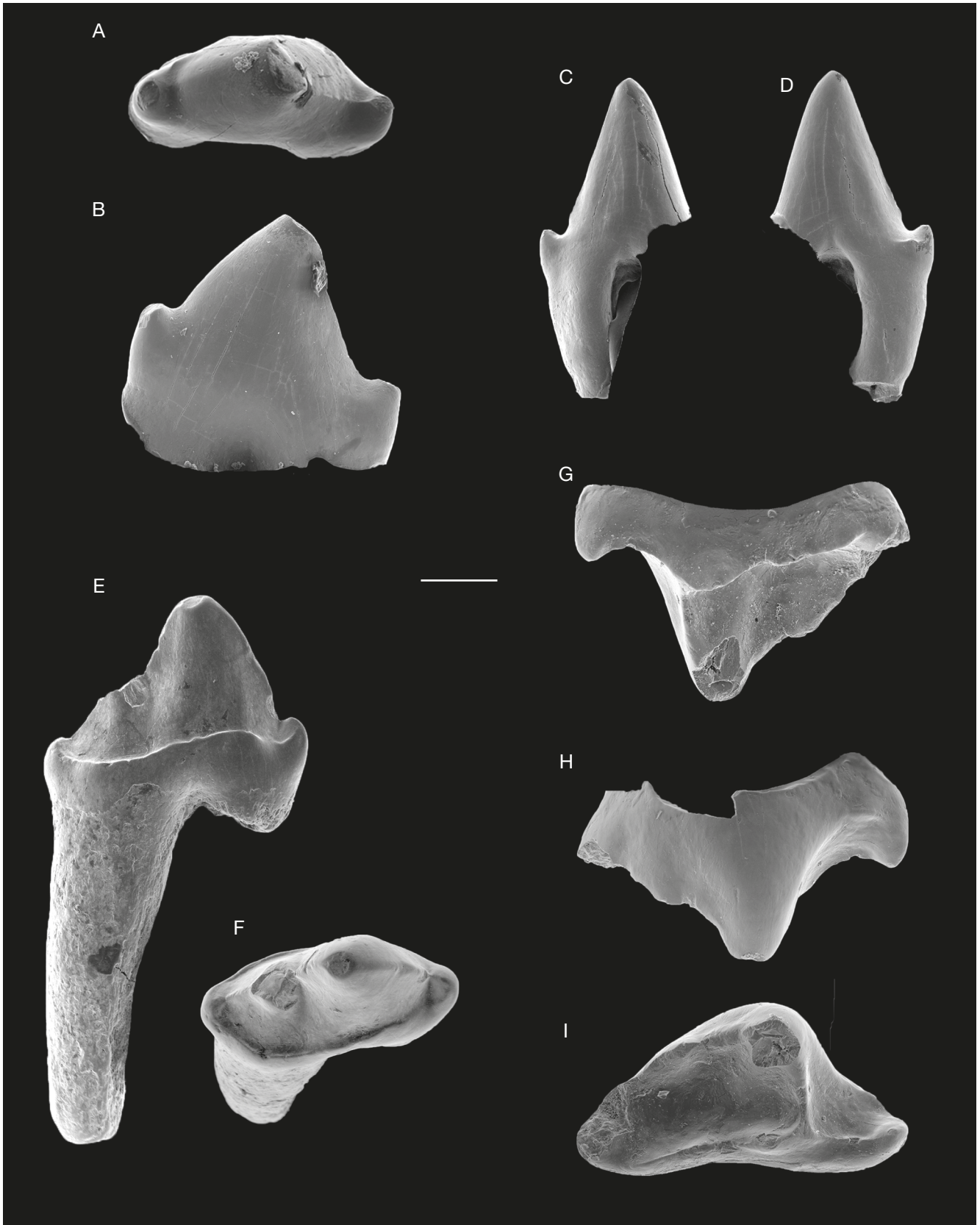


FIG. 32. — Mammal teeth from Angeac-Charente: **A, B**, premolariform or molariform tooth of *Gobiconodon?* sp. (ANG M-21) in occlusal (**A**) and labial (**B**) views; **C, D**, premolariform tooth of *Mammalia* indet. (ANG M-34) in lingual (**C**) and labial (**D**) views; **E, F**, left lower molar of *Triconodon* sp. (ANG M-02) in lingual (**E**) and occlusal (**F**) views; **G-I**, left upper molar of *Thereuodon* cf. *taraktes* (ANG M-23) in labial (**G**), lingual (**H**) and occlusal (**I**) views. Scale bar: 500  $\mu$ m.

Family GOBICONODONTIDAE Chow & Rich, 1984  
Genus *Gobiconodon?* Trofimov, 1978

*Gobiconodon?* sp.  
(Fig. 32A, B)

DESCRIPTION

Within the eutriconodontan material from Angeac-Charente, the specimen ANG M-21 (Fig. 32A, B) consists of an isolated tooth crown, the main central cusp a being surrounded by two unequal cusps b and c (see figures 4.7 and 7.2 by Crompton & Jenkins [1968] and Kielan-Jaworowska *et al.* [2004] respectively for an explanation of the cusp-numbering system). The root is missing but the tooth was probably uniradicate. The crown is labiolingually compressed and the lingual face appears almost planar in occlusal view, while the labial face is convex at its base (Fig. 32A). There is no trace of either a labial or lingual cingulid. Cusp a dominates the crown and is triangular in lateral profile (Fig. 32B). Its mesial surface is rounded, but its distal edge shows a well-defined crest (Fig. 32A). An oval wear facet can be observed on the labiodistal surface of cusp a (Fig. 32A). Cusp b is smaller than cusp c; it is also placed higher relatively to cusp a and less separated from it than cusp c. The apex of cusp c appears to be slightly flexed labially. Both cusps b and c bear small labially oriented wear facets. The presence of a probably single root indicates a tooth from the anterior dentition, but the well-developed accessory cusps show that it is a distal premolar and not a more mesial tooth. Among Laurasian Early Cretaceous mammals, single-rooted distal premolars are only seen within the Gobiconodontidae family (Sweetman 2006). Moreover, the specimen ANG M-21 closely resembles the gobiconodontid distal premolar (possibly right p4) described by Sweetman (2006) in the Early Cretaceous Wessex Formation of the Isle of Wight, southern England, and tentatively referred to *Gobiconodon*. Considering this, and the general morphology of ANG M-21 (tricuspid tooth with mesiodistally aligned cusps; dominant cusp a and small but well-developed accessory cusps; labial inflation of the crown; lack of cingulid), the specimen is identified as a left distal premolar, probably a p3 (as the accessory cusps are less developed than in the possible p4 described by Sweetman [2006]), of a gobiconodontid mammal, and is tentatively referred to *Gobiconodon*.

Family TRICONODONTIDAE Marsh, 1887  
Genus *Triconodon?* Owen, 1859

*Triconodon?* sp.  
(Fig. 32E, F)

DESCRIPTION

The specimen ANG M-02 (Fig. 32E, F) consists of an almost complete tooth, only lacking the mesial root.

The crown is labiolingually compressed and bears three mesiodistally aligned cusps. A main central cusp a is largely dominant. It is triangular in lateral profile and surrounded by two smaller accessory cusps: cusp c (distal) reaches half of the height of cusp a, and cusp b (mesial) is about three times smaller than cusp c. Cusp a is slightly flexed lingually. Cusps a and c bear distolingually oriented wear facets. Both labial and lingual cingulid are present. Thus, considering these characters, ANG M-02 can be identified as an eutriconodontan left lower premolariform. It is somewhat similar to the p3 of *Triconodon* from the Berriasian of Britain (Jäger *et al.* 2021), so the specimen is tentatively referred to this genus.

ALLOTHERIA Mars, 1880

MULTITUBERCULATA Cope, 1884  
(Fig. 33)

PRELIMINARY STATEMENT

Multituberculates are the most commonly represented mammals in Angeac-Charente with nearly fifteen isolated teeth already collected by screening-washing. We follow here the classification of Mesozoic allotherian mammals provided by Kielan-Jaworowska *et al.* (2004). All teeth are provisionally referred to the Pinherodontidae (Hahn & Hahn 1999), except for one P4 (Fig. 33I, J) that is very similar to the holotype of *Sunnyodon notleyi* (Kielan-Jaworowska & Ensom 1992), and one ?P5 that has only two rows of cusps (Fig. 33K-L), whereas there are three in Pinherodontidae (Hahn & Hahn 1999; Kielan-Jaworowska *et al.* 2004) and is thus identified as Multituberculata indet. A systematic revision of European Late Jurassic to Early Cretaceous Multituberculates is beyond the scope of this paper, but it is worthy to note that, for the moment, based only on their morphology, no tooth really suggests the presence of more than two taxa of multituberculates in Angeac-Charente.

Family PINHEIRODONTIDAE Hahn & Hahn, 1999

Pinheirodontidae indet.  
(Fig. 33A-H, M-P)

DESCRIPTION

Most of the multituberculate teeth discovered in Angeac-Charente can be referred to the family Pinheirodontidae, but it has not been possible to refer them to any existing genera. The material figured here includes a left p4 (ANG M-72), a left P1 (ANG M-03), a right P2 (ANG M-06), a left P3 (ANG M-22), a left ?m2 (ANG M-105) and a left M2 (ANG M-32) (Fig. 33A-H, M-P).

The most mesial part of the blade-like p4 (ANG M-72) is missing (Fig. 33A). It possesses at least six serrations, and no basal labial cusp, a diagnostic feature of *Pinheirodon* (Hahn &



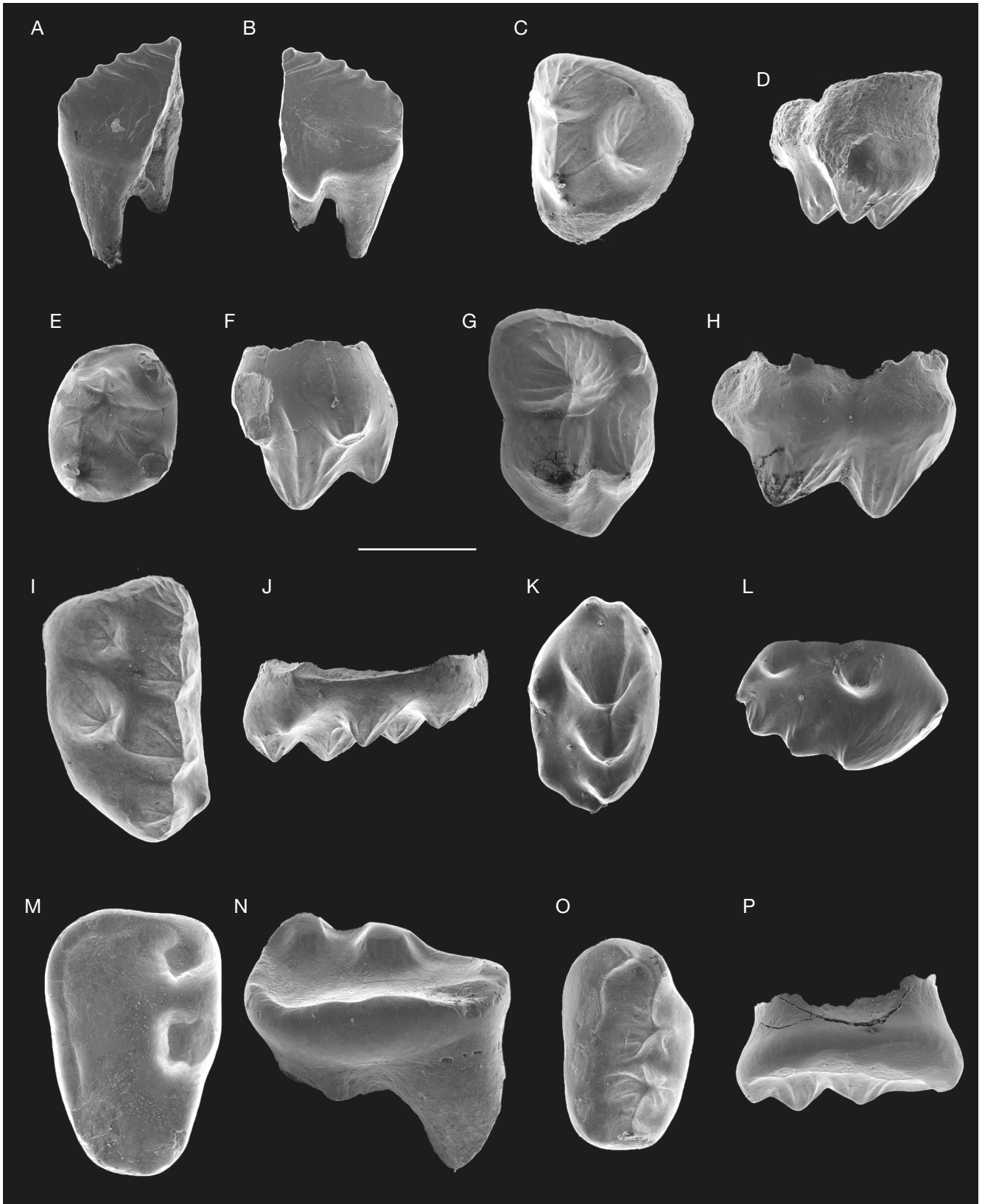


FIG. 33. — Multituberculate mammal teeth from Angeac-Charente: **A, B**, left p4 of Pinheirodontidae indet. (ANG M-72) in lingual (**A**) and labial (**B**) views; **C, D**, left P1 of Pinheirodontidae indet. (ANG M-03) in occlusal (**C**) and distolingual (**D**) views; **E, F**, right P2 of Pinheirodontidae indet. (ANG M-06) in occlusal (**E**) and lingual (**F**) views; **G, H**, left P3 of Pinheirodontidae indet. (ANG M-22) in occlusal (**G**) and lingual (**H**) views; **I, J**, left ?P4 of *Sunnyodon* sp. (ANG M-04) in occlusal (**I**) and labial (**J**) views; **K, L**, left ?P5 of Multituberculata indet. (ANG M-106) in mesio-occlusal (**K**) and occluso-labial (**L**) views; **M, N**, left ?m2 of Pinheirodontidae indet. (ANG M-105) in occlusal (**M**) and labial (**N**) views; **O, P**, right M2 of Pinheirodontidae indet. (ANG M-32) in occlusal (**O**) and lingual (**P**) views. Scale bar: A, B, 1 mm; C, D, 750  $\mu$ m; E-P, 500  $\mu$ m.

Hahn 1999; Kielan-Jaworowska *et al.* 2004). Nevertheless, the Angeac-Charente specimen has a straight, vertical, distal margin (Fig. 33B), while the latter is strongly convex just above the root in *Pinheirodon*.

The ?m2 (ANG M-105) has a well-developed central basin. Labial cusps are missing and there are only two lingual cusps as in *Bernardodon* (Fig. 33N), whereas there are three in *Pinheirodon* (Hahn & Hahn 1999). Nevertheless, the tooth shape is considerably longer than wide, and precludes assigning it to *Bernardodon* (Fig. 33M).

The M2 (ANG M-32) shows a prominent anterolingual shelf (Fig. 33O), like that observed in the molars of *Bernardodon* and *Pinheirodon* (Kielan-Jaworowska *et al.* 2004). As in the latter two genera there are three lingual cusps, but ANG M-32 differs from other pinheirodontids in lacking the labial cusps (Fig. 33P; Hahn & Hahn 1999).

The anterior upper premolars P1 (ANG M-03), P2 (ANG M-06) and P3 (ANG M-22) have 3-4 ribbed cusps arranged in two rows like in other “plagiaulacidans” (Fig. 33C-H; Kielan-Jaworowska *et al.* 2004). They are not very diagnostic and only tentatively assigned here to Pinheirodontidae, based on their similarities with the pinheirodontid teeth described by Hahn & Hahn (1999: fig. 58).

Family ?PAULCHOFFATHIDAE  
Hahn, 1969  
Genus *Sunnyodon*  
Kielan-Jaworowska & Ensom, 1992

*Sunnyodon* sp.  
(Fig. 33I, J)

DESCRIPTION

ANG M-04 is roughly oval in shape and has only two rows of cusps, with four main lingual cusps, and two main labial cusps and one posterior labial cuspule (Fig. 33I, J). It also possesses an incipient distal lingual ridge, with a small cuspule. All these features led us to assign this tooth to the genus *Sunnyodon*, a monospecific genus, *S. notleyi*, based on a single ?P5 from the Berriasian of the Purbeck Group in England (Kielan-Jaworowska & Ensom, 1992). The Angeac-Charente tooth differs from the latter by the labial cusps that are more anteriorly located, whereas they are arranged symmetrically at the middle of the tooth length in *S. notleyi*, and by the absence of the anterior labial cuspule (Fig. 33I). This difference could be explained by the fact that these teeth belong to two different loci and/or two different species. This tooth is considered here to be a ?P4 and it is referred to *Sunnyodon* sp., although the validity of this genus can be debated. An upper posterior premolar of *Sunnyodon* has also been reported from the Berriasian strata of the Rabekke Formation on the island of Bornholm, Denmark (Lindgren *et al.* 2004).

TRECHNOTHERIA  
McKenna, 1975

Family SPALACOTHERIIDAE Marsh, 1887  
Genus *Spalacotherium* Owen, 1854

*Spalacotherium evansae* Ensom & Sigogneau-Russell, 2000  
(Fig. 34A, B)

DESCRIPTION

Three teeth of Spalacotheriidae have been recognized including two molars, which have the characteristic “symmetrodont” pattern with acute angulation of the principal cusps, seen in other spalacotheriids (Fig. 34A; Kielan-Jaworowska *et al.* 2004).

The best preserved of the molars ANG M-26 lacks the posterior root and the hypoconulid (cusp d) (Fig. 34A, B). The protoconid, the metaconid and the paraconid are well-developed. The talonid was probably much reduced. Mesially, a single cusp e is lingually placed on the cingulid (Fig. 34B), and allows the identification of this tooth as a left lower molar. ANG M-26 is very similar, if not identical, to a tooth referred to *Spalacotherium evansae* (DORC GS 360, Ensom & Sigogneau-Russell 2000). Its smaller size compared to that of the molars of other species of *Spalacotherium*, the incompleteness of the labial cingulid associated with the equivalent height of the paraconid and metaconid, are diagnostic features (Ensom & Sigogneau-Russell 2000), that allow us to assign this specimen to *Spalacotherium evansae*. The latter species has been described from various localities of the Purbeck Group, including the Berriasian Lulworth Formation at Sunnydown Farm, U.K.

CLADOTHERIA McKenna, 1975  
Superfamily DRYOLESTOIDEA Butler, 1939  
Family DRYOLESTIDAE Marsh, 1879

Dryolestidae indet. (Fig. 34C-F)

DESCRIPTION

Dryolestidae are represented by only two fragmentary molars lacking the roots and the talonid (Fig. 34C-F). Based on the configuration of the trigonid and the lack of a cuspid in median position on the labial side of the molars, those teeth are considered to be left lower molars (Kielan-Jaworowska *et al.* 2004). Both lower molars are shorter mesiodistally than wide labiolingually, but the most posterior molar (ANG M-01; Fig. 34E-F) is strongly shortened and widened compared to the anterior molar (ANG M-05; Fig. 34C, D). This feature is diagnostic of Dryolestidae (Kielan-Jaworowska *et al.* 2004). The trigonid is well-developed in both lower molars. The paraconid of the posterior molar ANG M-01 is broken at its base, but it is labiolingually more elongated than the metaconid. Both are separated by a narrow incision (Fig. 34E). The metaconid is enlarged and almost as high as the protoconid (Fig. 34F). Based on these features, the dryolestid molars from Angeac-Charente seem more closely related to either *Guimarotodus* from the Kimmeridgian of Guimarota in Portugal (Martin 1999) or *Phascolestes* from the Berriasian of Dorset in England (Owen 1871; Kielan-Jaworowska *et al.* 2004) than any other Dryolestidae. However, additional material is required to allow a more accurate attribution.

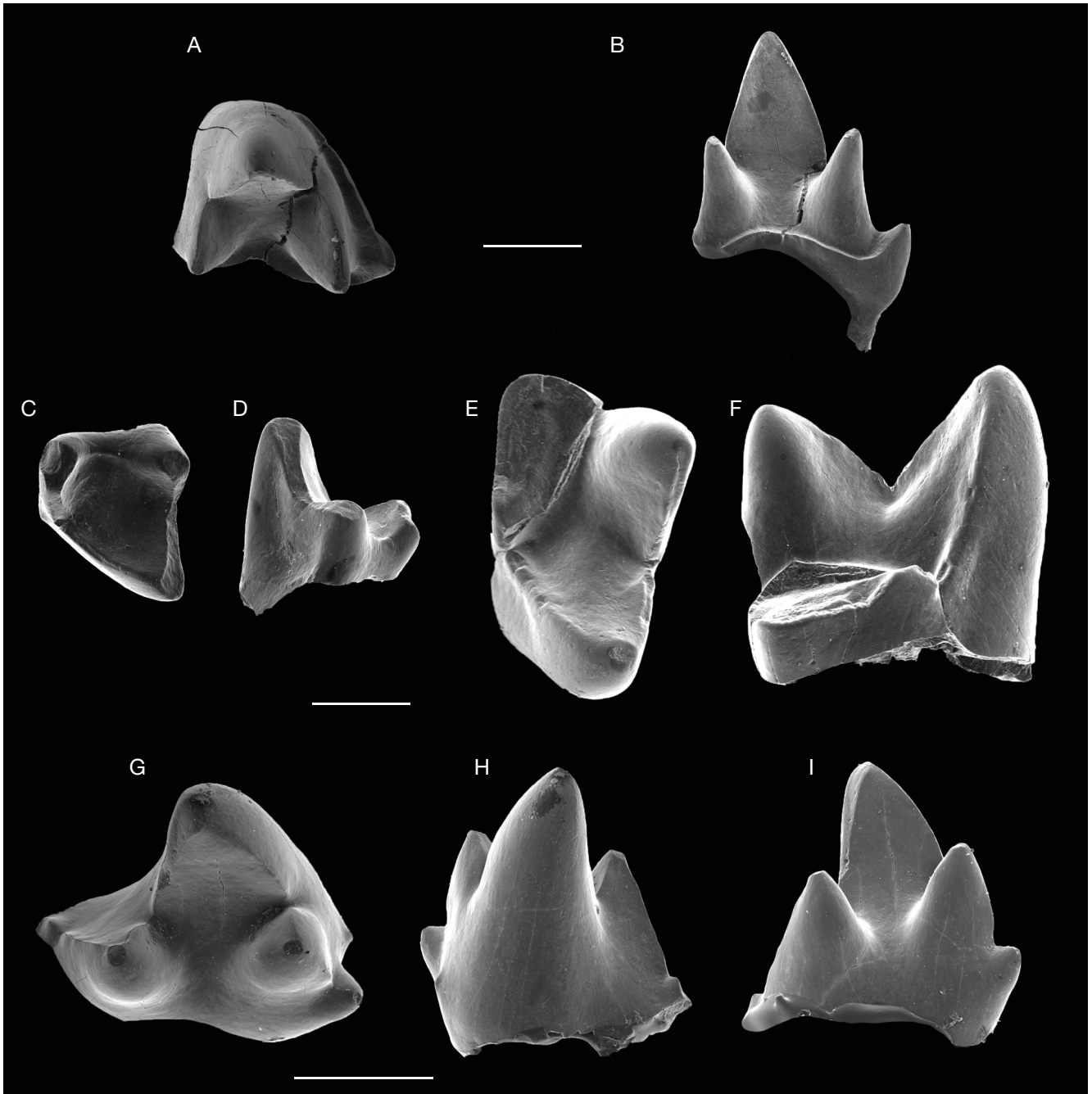


FIG. 34. — Trechnotherian mammal teeth from the Berriasian of Angeac-Charente: **A, B**, left lower molar of *Spalacotherium evansae* Ensom & Sigogneau-Russell, 2000 (ANG M-26) in occlusal (**A**) and lingual (**B**) views; **C, D**, left lower molar (m1 or ?m2) of Dryolestidae indet. (ANG M-05) in occlusal (**C**) and linguodistal (**D**) views; **E, F**, left lower molar (m6 or ?m7) of Dryolestidae indet. (ANG M-01) in occlusal (**E**) and mesial (**F**) views; **G-I**, left lower molar (m3?) of *Peramus* sp. (ANG M-25) in occlusal (**G**) labial (**H**) and lingual (**I**) views. Scale bars: 400 µm.

ZATHERIA McKenna, 1975  
Family PERAMURIDAE Kretzoi, 1946

*Peramus* sp.  
(Fig. 34G-I)

DESCRIPTION

Peramuridae are represented by at least two lower molars. Only

a left lower molar (ANG M-25), the talonid and the roots of which are missing, is figured herein (Fig. 34G-I). The talonid is present on the other molar, and it clearly displays a hypoculid separated from the hypoconid, a diagnostic feature of Peramuridae (Davis 2012). The main cusp of the trigonid, i.e. the protoconid, is slightly inclined posteriorly (Fig. 34H). The paraconid is mesiodistally narrower and apicobasally shorter than the metaconid. It is located higher and in a more labial position.

The metaconid is visible in labial view, whereas it is hidden by the protoconid in the Moroccan genus *Minimus* (Sigogneau-Russell 1999). Both the anterolabial (cusp e) and the anterolateral (cusp f) marginal cuspules are preserved (Fig. 34G). The latter is much more developed than the former. They define a strongly developed hypoconulid embrasure. All these features are more reminiscent of the lower molars (m2 and m3) of *Peramus tenuirostris* and *P. dubius* from the Berriasian of Dorset, England (Clemens & Mills 1971), than to any other peramuran taxon (Sigogneau-Russell 1999). However, the scarcity of material prevents any comparison based on measurements, and does not allow a reliable specific identification (Davis 2012). Thus, we assign this tooth to *Peramus* sp.

## DISCUSSION

### ORIGINALITY OF THE VERTEBRATE FAUNA AND PALEOENVIRONMENTAL IMPLICATIONS *Fossil and taxonomic diversities*

The continental vertebrate fauna from Angeac-Charente is both very diverse and abundant. It includes wide size range of bones and teeth from 0.5 mm to 2.2 m, and includes three types of ichnofossil: coprolites, track casts, and traces on bone surfaces, including trampling and tooth marks (Rozada *et al.* 2021). But above all, what makes this fossil locality so exceptional is the great taxonomic diversity. With at least forty different vertebrate taxa (see the Appendix 1, Systematic paleontology of the complete faunal list and Table 1 below), Angeac-Charente is the most diverse earliest Cretaceous mixed continental bonebed known to date (see Eberth *et al.* 2007). It has been demonstrated that the Angeac-Charente taphocoenosis provides a good picture of the local paleocommunity, because the site represents a ‘snapshot’ of a Lower Cretaceous ecosystem (Rozada *et al.* 2021), but also because both macro- and microremains have been collected (Carrano *et al.* 2016). This paleocommunity also reflects the Purbeckian paleometacomunity as a whole, as all major clades known for the Jurassic/Cretaceous transition in Europe are represented including rare fossils such as birds and mammals (Table 1). Recognizing this diversity was only possible as a result of the time and space scales of fieldwork, the laboratory preparation of all macroremains from one year to the next, and the continuous sorting of microfossils.

### *Abundance*

Besides the diversity, the abundance of fossils is also remarkable. Relative abundances of large vertebrates (*i.e.* macroremains) have been calculated based on the material collected between 2010 and 2017 (Fig. 35A). For microremains, we used the material collected from the gravel lens of the R1 plot (Fig. 3), which was rich in lignite and bones including the complete shell of *Pleurosternon bullockii* (Fig. 13; Gônet *et al.* 2019), and the material collected at the base of the Unit 3, of the R3 plot (Fig. 35B, C). The overall paleoenvironmental interpretation and significance of these relative abundances is presented below in more detail, as well as the paleoecological insights they provide based on their relationships with spatial distribution and taphonomic data.

The ornithomimosaur is the most abundant taxon throughout. However, its spatial distribution over the site is clearly heterogeneous, as 85% of the ornithomimosaur remains are concentrated in the CG1-8 plots (Fig. 3). This high local abundance of exquisitely-preserved bones supports the hypothesis of a mass mortality event of an ornithomimosaur herd (Rozada *et al.* 2021). While their carcasses may have been transported over a short distance after a mass drowning (see Subalusky *et al.* 2017), their complete skeletons were deposited *in situ* before being scattered by trampling (Rozada *et al.* 2021).

Goniopholidid crocodyliforms, pleurosternid turtles and sauropod dinosaurs are both abundant and homogeneously distributed (Fig. 3). It suggests that these taxa were autochthonous, which is supported by the occurrence of 1) plates of *Pleurosternon bullockii* found in close association in R3 and belonging to a nearly complete specimen, 2) a disarticulated *Goniopholis* sp. skeleton found in CG9, and 3) numerous sauropod track casts found at several loci of the site, as well as the hindquarters of a single individual.

Atoposaurid, bernissartiid and pholidosaurid crocodyliforms are mostly represented by teeth. Atoposaurids and bernissartiids mostly occur as microremains, and they are abundant. They are homogeneously distributed, and were likely part of the autochthonous fauna.

Helochelydrid and thalassochelydian turtles and stegosaurs are only known from a small amount of material. Their distribution appears heterogeneous, probably due to their scarcity. Nevertheless, the three taxa are represented by several associated elements belonging to single individuals. Because of the presence of track casts of the *Deltapodus* type, the stegosaur is considered to be an autochthonous taxon, whereas the two turtles may have been parautochthonous.

Isolated megalosaurid teeth are common and have a homogeneous spatial distribution. Most of the teeth are broken at their base (Fig. 28G-N), suggesting that these breakages occurred during feeding in the Angeac-Charente wetland. However, the absence of carnivorous theropod bones in the assemblage indicates that these dinosaurs probably only fed opportunistically and/or seasonally in this area.

Pterosaurs, ankylosaurs, heterodontosaurids, camptosaurids, hysilophodontids, dromaeosaurids, tyrannosauroids, sphenodontians and mammals are only represented by isolated teeth or a single bone (*e.g.* camptosaurid and ankylosaur). They are much rarer, heterogeneously distributed in the field, and often abraded. This suggests short-distance transport and thus parautochthonous origin for these taxa.

As abundant anuran remains are known in some chaotic debris flows (*e.g.*, Plant Debris Beds of the Barremian Wessex Formation, Isle of Wight, southern England; Sweetman & Insole 2010), their low abundance at Angeac-Charente cannot be explained by the fragility of their bones, but rather seems to reflect genuine scarcity. There may have been a more important sorting upstream of the deposit environment, or a local hydrodynamism difference, impacting the conservation of the anuran remains and/or the presence of anurans at the time of deposition.

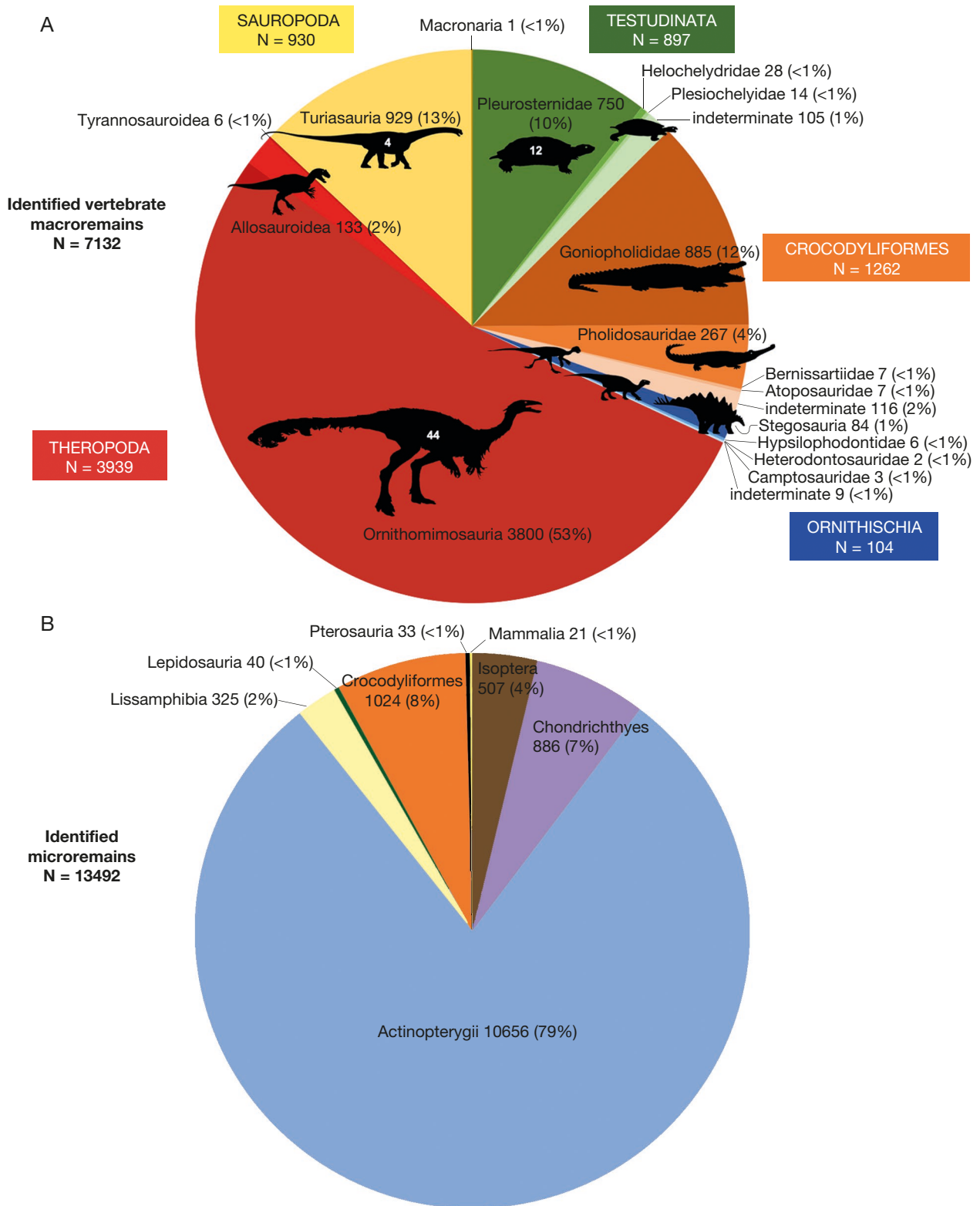


FIG. 35. — **A**, Relative abundance of Angeac-Charente large vertebrate taxa based on identified macroremains collected from 2010 to 2017. White numbers indicate the Minimum Number of Individuals (MNI) (after Rozada *et al.* 2021); **B**, Relative abundance of Angeac-Charente taxa, based on microremains collected in 2017, by water screen-washing (diameter of mesh = 0.8 mm), at the base of the unit 3, of the R3 plot.

*Paleoenvironment*

Sedimentology, mineralogy, and geochemistry as well as non-vertebrate paleontology indicate a continental freshwater

wetland depositional environment for the Angeac-Charente bonebed (Rozada *et al.* 2021). The sedimentological assemblage is dominated by clay in suspension deposited from standing

TABLE 1. — List of vertebrate taxa from the Jurassic–Cretaceous transition of Charente with their relative abundances in each locality, habitat, stratigraphic range and Mesozoic geographical distribution. The black, grey and white squares represent the preferred habitats of each taxon. Abbreviations : **A**, abundant; **C**, common; **CZ**, coastal zone; **FW**, freshwater; **J**, Middle Jurassic; **LC**, Lower Cretaceous; **LJ**, Lower Jurassic; **LP**, Lower Permian; **LT**, littoral; **MT**, Middle Triassic; **NA**, North America; **PR**, paralic; **R**, rare; **SA**, South America; **TR**, terrestrial; **UC**, Upper Cretaceous; **UCa**, Upper Carboniferous; **UJ**, Upper Jurassic; **UP**, Upper Permian; **UT**, Upper Triassic.

Taxa		Locality			Environment					Mesozoic stratigraphic range	Mesozoic geographical distribution	
		Chassiron	Cherves	Angeac	Cont.		Litt.		Mar.			
					TR	FW	PR	LT	CZ			
Chondrichthyes												
Hybodontiformes	<i>Planohyodus</i>	R			x	•	x			Bathonian MJ/Barremian LC	Europe/SA/NA	
	<i>Parvodus celsucuspus</i>	A	A	C	x	•	x			Tithonian UJ/Berriasian LC	Europe	
Rajiformes	<i>Belemnobatis</i>	R					•	x		Bathonian MJ/Aptian LC	Europe	
Osteichthyes Huxley, 1880												
Ginglymodi	indet.	A	A	A	x	•				Kimmeridgian UJ/Aptian LC	Europe/Asia/Africa/NA/SA	
Ionoscopiformes	indet.	C		R	x	•	x			Anisian MT/Cenomanian UC	Europe/Asia/Africa/NA/SA	
Amiiformes	indet.	R	R	C	x	•	x			Ladinian MT/Maastrichtian UC	Europe/Asia/NA/SA	
Mesturidae	<i>Microptycnodon</i>	R		C	x	•	x			Norian UT/Maastrichtian UC	Europe/Asia/Africa/NA/SA	
Pycnodontidae	indet.	R	R	C	x	•	x			Kimmeridgian UJ/Maastrichtian UC	Europe/Asia/Africa/NA/SA	
Aspidorhynchidae	<i>Belonostomus</i>	R					•	x		Tithonian UJ/Maastrichtian UC	Europe/Africa/NA/SA	
Ichthyodectidae	<i>Thrissops</i>	C		R			•	x		Kimmeridgian UJ/Tithonian UJ	Europe	
Lissamphibia Haeckel, 1866												
Allocaudata	Albanerpetontidae	C	R	C	x	•				Bathonian MJ/Maastrichtian UC	Europe/Asia/Africa/NA	
Caudata	indet.	C		R	x	•				Bathonian MJ/Maastrichtian UC	Europe/Asia/Africa/NA	
Anura	indet.	R		R	x	•				Hettangian LJ/Maastrichtian UC	Europe/Asia/Africa/NA/SA	
Reptilia Laurenti, 1768												
Testudinata												
Pleurosternidae	<i>Pleurosternon bullockii</i>	C	C	A	x	•	•	x		Tithonian UJ/Berriasian LC	Europe	
Plesiochelyidae	<i>Jurassichelon</i>	A					x	•	x	Kimmeridgian UJ/Tithonian UJ	Europe	
	<i>Hylaeochelys?</i>	R		R	x	•				Tithonian UJ/Valanginian LC	Europe	
Helochelydridae	indet.	R	R		•	x				Tithonian UJ/Campanian UC	Europe/NA	
Lepidosauria												
Sphenodontia	<i>Opisthias</i>	R				•				Tithonian UJ/Berriasian LC	Europe/NA	
Scincomorpha	<i>Paramacellodus</i>	R				•				Tithonian UJ/Barremian LC	Europe/Africa	
Choristodera	<i>Cteniogenys?</i>	R		R		•				Bathonian MJ/Aptian LC	Europe/Asia/NA	
Crocodylomorpha												
Teleosauridae	<i>Steneosaurus</i>	R					x	•	x	Toarcian LJ/Berriasian LC	Europe/Africa/Asia	
Atoposauridae	<i>Theriosuchus</i>	C	A	C	•					Bathonian MJ/Cenomanian LC	Europe/Asia/Africa	
Bernissartiidae		C	A	C						Berriasian LC/Aptian LC	Europe	
Goniopholididae	<i>Goniopholis</i>	C	C	A			•	x		Kimmeridgian UJ/Berriasian LC	Europe	
Pholidosauridae	<i>Pholidosaurus</i>	C	C	C			•	x		Tithonian UJ/Berriasian LC	Europe	
Dinosauria												
Theropoda	Megalosauridae	R	R	C	•					Bajocian MJ/Berriasian LC	Europe/Asia/Africa/NA/SA	
Dromaeosauridae	<i>Nuthetes</i>	R	R	R	•					Tithonian UJ/Berriasian LC	Europe	
	Ornithomimosauria		A		•					Berriasian LC/Maastrichtian UC	Europe/Asia/NA	
	Tyrannosauroidae		R		•					Bathonian MJ/Maastrichtian UC	Europe/Asia/NA	
	Archaeopterygidae		R		•					Tithonian UJ/Berriasian LC	Europe	
Sauropoda	Turiasauria		C		•					Kimmeridgian UJ/Aptian LC	Europe/Africa/NA	
	Macronaria indet.	R	R	R	•					Bajocian MJ/Maastrichtian UC	Europe/Asia/Africa/NA/SA	
Ornithischia	Camptosauridae	R	R	R	•					Kimmeridgian UJ/Berriasian LC	Europe/NA	
Heterodontosauridae	<i>Echinodon</i>	R			•					Berriasian LC	Europe	
Stegosauria	Hypsilophodontidae		R		•					Bathonian MJ/Maastrichtian UC	Europe/NA	
	<i>Dacentrurus</i>	R	R	R	•					Kimmeridgian UJ/Berriasian LC	Europe	
	Ankylosauria	R			•					Pliensbachian LJ/Maastrichtian UC	Europe/NA/Asia	

TABLE 1. — Continuation.

Taxa	Locality			Environment					Mesozoic stratigraphic range	Mesozoic geographical distribution	
	Chassignon	Cherves	Angeac	Cont.			Litt.				Mar.
				TR	FW	PR	LT	CZ			
Pterosauria											
	Rhamphorhynchidae	R								Hettangian LJ/ Berriasian LC	Europe/Asia/Africa
	Ctenochasmatidae	R								Oxfordian UJ/Aptian LC	Europe/Asia/SA
	Pterodactyloidea A	R	A							Bathonian MJ/Maastrichtian UC	Europe/Asia/Africa/NA/SA
	Pterodactyloidea B	R	C							Bathonian MJ/Maastrichtian UC	Europe/Asia/Africa/NA/SA
Mammalia Linnaeus, 1758											
Thereuodontidae	<i>Thereuodon</i>	R	R							Tithonian UJ/Berriasian LC	Europe/Africa
Eutriconodonta											
Gobiconodontidae	<i>Gobiconodon</i>	R	R							Bathonian MJ/Cenomanian UC	Europe/Asia/Africa/NA
Triconodontidae	<i>Triconodon</i>	R	R							Berriasian LC	Europe
Multituberculata											
	Pinheirodontidae indet.	R	R							Oxfordian UJ/Barremian LC	Europe
	<i>Sunnyodon</i>	R	R							Berriasian LC	Europe
Spalacotheriidae	<i>Spalacotherium evansae</i>	R	R							Berriasian LC	Europe
Cladotheria											
	Dryolestidae indet.	R	R							Bathonian MJ/Campanian UC	Europe/Africa/NA
	<i>Peramus</i>	R	R							Tithonian UJ/Berriasian LC	Europe/Africa

water, locally interrupted by higher energy deposits (Néraudeau *et al.* 2012; Rozada *et al.* 2021). PAAS (Post-Archean Australian Shale)-normalized REY (Rare Earth Element and Yttrium) patterns of sediments and fossil biogenic apatites from the bonebed also indicate that Angeac-Charente sediments and fossils were deposited in a strictly freshwater environment (Rozada *et al.* 2021). Angeac-Charente plant microfossils are dominated by spores of liverworts (marchantiophytes) and lycophytes (lycophytes), with a good diversity of fern spores (monilophytes) and gymnosperm pollen grains (Polette *et al.* 2018). Palynological assemblages are, however, strongly biased by huge differences in the quantity of produced sporomorphs, and there are mostly, if not always, mixocoenoses that include a large regional component. In strong contrast, both plant mesofossils and megafossils show a large dominance of conifers (Néraudeau *et al.* 2012; Daviero-Gomez & Gomez in Allain *et al.* 2017). Mesofossils mostly consist of wood preserved as jet (vitrain) and charcoal (fusain), out of which some belong to the genus *Agathoxylon* Hartig. Apart from wood, there are abundant twigs and isolated leaves of *Brachyphyllum* Brongn., which bear well-preserved cuticles, three-dimensionally preserved cones and seeds, and much rarer fern stipes and frond fragments (Daviero-Gomez & Gomez 2017, unpublished data). Dealing with megafossils, a number of conifer trunks observed in the excavation field remain attached to their rooting systems and branches, and at least one is more than twelve meters in length (Rozada *et al.* 2021: fig. 6B). Overall, the autochthonous and parautochthonous fossil deposit displays a picture of a local plant community dominated by paucispecific, cheirolepidiacean conifer forest.

The fossil algae *Ovoidites parvus* and *Lecaniella* sp. (Néraudeau *et al.* 2012), as well as the large dominance of the fossil charophyte family Clavatoraceae compared to the Porocharaceae (Benoit *et al.* 2017) support a long lasting, fully freshwater, wetland environment. Finally, the abundance of freshwater invertebrates such as viviparid gastropods, and unionoid bivalves preserved in life-position in clay, and ostracods (e.g. *Cypridea* sp.) (Néraudeau *et al.* 2012) are also in agreement with such an environment.

The Angeac-Charente vertebrate fauna is in perfect agreement with and corroborates this sedimentological and paleobotanical-based environmental interpretation (Table 1). Of the about 40 identified vertebrate taxa that compose this fauna, 23 taxa (57.5%) are elsewhere only found in terrestrial environments (helochelydrid turtles, atoposaurid crocodyliforms, dinosaurs, pterosaurs, lepidosaurs and mammals), and 11 (27.5%) in freshwater environments (lissamphibians, pleurosternids, choristoders, bernissartiids, goniopholidids and pholidosaurids). The six remaining taxa (15%) are euryhaline and can live in both freshwater and brackish water. This is the case of the hybodontid shark *Parvodus* as well as all osteichthyan taxa. About 70% of the identified taxa and 98% of the anatomically unidentifiable macroremains collected from Angeac-Charente are derived from terrestrial taxa (Rozada *et al.* 2021). Conversely, microremains are dominated by freshwater taxa (Fig. 35B). Given the overall size of the latter, especially the osteichthyans, this suggests that the water was shallow, which is consistent with the occurrence of dinosaurs tracks and trampling marks, as well as the local record of some mudcracks.

It is worth noting that most of the isolated *Parvodus* teeth found in Angeac-Charente lack a root, which contrasts with what is observed at Cherves-de-Cognac (Rees *et al.* 2013). Taphonomically, this may be explained by the resorption of the root during tooth replacement (Underwood & Cumba 2010). These rootless teeth therefore reflect a loss during the animal's lifetime, in agreement with a wetland connected with a watercourse. It should also be noted that the turtle *Hylaeochelys belli* was recently referred to Thalassochelydia, a group otherwise exclusively composed of coastal marine forms (Anquetin & André 2020). However, this species is always found in sediments of freshwater origin (middle and upper Purbeck and Wealden facies of England) and is apparently the only known freshwater thalassochelydian even if the calcium isotopic composition of its biogenic apatite may indicate this taxon spent time in more saline water and was probably euryhaline.

In summary, the composition of the vertebrate fauna, that comprises a mixture of freshwater and terrestrial taxa, supports the environment of a continental, exclusively freshwater wetland without marine inputs (Fig. 36). Our interpretation is consistent with recent sedimentological, ichnological and geochemical data (Rozada *et al.* 2021), and challenges the previously held assumption of at least occasional, marine water inputs (Néraudeau *et al.* 2012; Benoit *et al.* 2017; Polette *et al.* 2018). The variety of habitats inhabited by the Angeac-Charente vertebrate fauna reflects the complex mosaic of micro-habitats, necessary to sustain a wide range taxa. These include terrestrial, amphibious and aquatic animals in a generally wetland environment. Similar conclusions were drawn concerning the late Barremian freshwater - terrestrial fossil assemblage and environment of Las Hoyas, La Huérguina Formation, Cuenca province, Spain (Buscalioni & Poyato-Ariza 2016).

#### BIOCHRONOLOGICAL IMPLICATIONS

##### *Age of the Angeac-Charente Lagerstätte based on the vertebrate fauna*

Several taxa present in the Angeac-Charente assemblage cannot be identified at low taxonomic levels or are persistent for geologically long periods of time. These taxa do not provide useful information concerning the age of the vertebrate-bearing deposits (e.g. osteichthyans, and pterosaurs). In contrast, many taxa characterized by relatively short stratigraphical ranges can be used as biostratigraphic markers, and we discussed them below.

**Fishes.** Among the ichthyofauna, the hybodont shark *Parvodus celsucuspus* is an endemic species that is so far restricted to the Tithonian-Berriasian of the Charentes region (Rees *et al.* 2013; Vullo *et al.* 2014). Its presence clearly indicates a similar age for the Angeac-Charente assemblage.

**Turtles.** The earliest helochelydrid remains have been reported from the Tithonian of England and France, but they become more common during the Early Cretaceous

(Joyce 2017; Pérez-García *et al.* 2020). The group is only known in Europe and North America and probably went extinct at the end of the Cretaceous (Nopcsa 1928; Laparent de Broin & Murelaga 1996, 1999; Hirayama *et al.* 2000; Joyce *et al.* 2011; Joyce 2017). Earliest Cretaceous, European species are poorly known due to an unsatisfactory fossil record (Joyce 2017; Pérez-García *et al.* 2020). As mentioned above, the shell surface sculpturing observed in the Angeac-Charente helochelydrid material is closer to the ornamentation of '*Helochelydra*' *anglica* from the Berriasian of Dorset and '*Helochelydra*' *bakewelli* from the Valanginian of Sussex, than to that of *Helochelydra nopcsai* from the Barremian of the Isle of Wight in England, and Spain. It also differs to that of *Helochelys danubina* from the Cenomanian of Germany, and from *Plastremys lata* from the Albian-Cenomanian of England. It is therefore consistent with either a Berriasian or Valanginian age for the Angeac-Charente locality.

In Europe, pleurosternids are known by several Kimmeridgian-Albian species (Lydekker 1889; Milner 2004; Pérez-García & Ortega 2011; Pérez-García 2015; Pérez-García *et al.* 2015a; Joyce & Anquetin 2019; Guerrero & Pérez-García 2020). In North America, they are limited to the Late Jurassic (Gaffney 1979; Joyce & Anquetin 2019). The Angeac-Charente pleurosternid material is clearly referable to the species *Pleurosternon bullockii*, which is known from the Tithonian of Boulogne-sur-Mer (France), and from the Tithonian-Berriasian Purbeck Group of Dorset, England (Joyce & Anquetin 2019; Guerrero & Pérez-García 2020).

*Hylaeochelys* is known from the Purbeck (Tithonian-Berriasian) and Wealden (Berriasian-Valanginian) of the UK by the type species *Hylaeochelys belli* (Lydekker 1889; Hirayama *et al.* 2000; Milner 2004; Pérez-García 2012) and in the Tithonian of Portugal by *Hylaeochelys kappa* (Pérez-García & Ortega 2014). The material from Angeac-Charente is more consistent with a tentative referral to *Hylaeochelys belli*, although this awaits confirmation. This suggests that the locality is either Berriasian or Valanginian in age.

In brief, the turtle assemblage from Angeac-Charente is similar to that of the predominantly Berriasian Purbeck Group of England and it supports a Berriasian age for this locality.

**Lepidosaurs.** *Opisthias rarus* is a sphenodontian reptile species from the Late Jurassic Morrison Formation of western North America (Gilmore 1910). An indeterminate species is also known from the latest Tithonian and Berriasian beds of the English Purbeck Group Lulworth Formation (Evans & Fraser 1992; Evans & Searle 2002).

Four species of *Paramacellodus* are known to date, all from Early Cretaceous localities: *P. oweni* and *P. marocensis* from the Berriasian of England and Morocco, respectively, *P. sinuosus* from the Barremian of Spain, and cf. *P. keebleri* from the Aptian-Albian of the United States (Hoffstetter 1967; Richter 1994; Broschinski & Sigogneau-Russell



1996; Evans & Searle 2002; Nydam & Cifelli 2002). In addition, a few indeterminate species tentatively referred to *Paramacellodus* have been reported from various Middle and Upper Jurassic localities (see Evans & Searle 2002). The morphological features of the scarce, fragmentary material from Angeac-Charente suggest that it represents a form close to either *P. oweni* or *P. marocensis*. Although more material is needed to confirm our preliminary identifications, the lepidosaurs from Angeac-Charente tend to indicate a Berriasian age.

**Crocodyliforms.** Atoposaurids are diverse from the Jurassic to the Late Cretaceous in Europe (e.g. Clark 1986; Schwarz & Salisbury 2005; Martin *et al.* 2014a; Tennant & Mannion 2014; Schwarz *et al.* 2017), but also in Asia (Lauprasert *et al.* 2011) and North America (Foster 2018), and they include several genera beyond the genus *Theriosuchus*. Atoposaurids can be preserved as complete skeletons on slabs or, more often, as isolated disarticulated specimens, which makes determination of their taxonomic identity problematic. For this reason, they have a biostratigraphic potential but this has not been defined yet. It is noteworthy that the locality of Cherves-de-Cognac yielded two complete skeletons of *Theriosuchus*, which will be compared in a future work with the relatively complete type material of *Theriosuchus pusillus* from the Purbeck Group of England (Clark 1986).

In Europe, the oldest goniopholidids have been reported from the Late Jurassic. *Goniopholis baryglyphaeus* is from the Kimmeridgian of Guimarota, Portugal (Schwarz 2002) and more fragmentary specimens have been reported from the Late Jurassic near Boulogne-sur-Mer (Buffetaut 1986). The genus *Goniopholis* is a common component of semi-aquatic faunas of the earliest Lower Cretaceous being well-known from the Berriasian Purbeck Group of England (Owen 1879; Salisbury *et al.* 1999; Andrade *et al.* 2011) and from the Obernkirchen Sandstone of Germany (Koken 1887; Salisbury *et al.* 1999). The genus *Nannosuchus* has also been reported from the Purbeck Group (Owen 1879; Salisbury *et al.* 1999; Andrade *et al.* 2011). Other European goniopholidids (*Hulkopholis*, *Anteophthalmosuchus*, *Vectisuchus*) are all younger in age with most of the European record consisting of specimens from the Barremian-Aptian interval (Buffetaut & Hutt 1980; Salisbury & Naish 2011; Martin *et al.* 2016b) or from the Albian (Buscalioni *et al.* 2013; Puértolas-Pascual *et al.* 2015). Although a Late Jurassic age cannot be excluded, the present recognition of *Goniopholis* sp. supports an early Early Cretaceous age for the locality of Angeac-Charente, in agreement with the Berriasian age proposed for the close-by locality of Cherves-de-Cognac (Colin *et al.* 2004).

The genus *Pholidosaurus* is restricted to the latest Jurassic and earliest Cretaceous of Europe, where two species have been named: *P. schauburgensis* von Meyer, 1841 from the Obernkirchen Sandstone of Germany and *P. purbeckensis* (Mansell-Pleydell 1888) from the Purbeck

Group of England (Salisbury *et al.* 1999). The occurrence of *Pholidosaurus* sp. in the Tithonian of Chassiron and of *P. purbeckensis* from the Berriasian nearby locality of Cherves-de-Cognac (Martin *et al.* 2016b) indicates that Angeac-Charente is Tithonian-Berriasian in age.

*Bernissartia fagesii* Dollo, 1883 has been described from the Barremian-Aptian of Belgium. The species was subsequently reported from the Wealden of the Isle of Wight (Buffetaut & Ford 1979), but it has recently been demonstrated that this material pertains to the bernissartiid *Koumpiodontosuchus* (Sweetman *et al.* 2015). *B. fagesii* has also been reported from the Berriasian-Aptian of Galve in Spain (Buscalioni & Sanz 1990). For a review of the distribution of bernissartiids see Martin *et al.* 2020. The Spanish specimen precise age is uncertain but a Berriasian age cannot be discarded. *Bernissartia* cf. *fagesii* has also been reported from the nearby locality of Cherves-de-Cognac (Pouech 2008), which could lend support for a Berriasian age for Angeac-Charente. Nevertheless, given current knowledge concerning bernissartiid stratigraphic distribution, their occurrence in Angeac-Charente can only indicate an Early Cretaceous age without further refinement.

**Dinosaurs.** Among theropods, two taxa (*Nuthetes* and Archaeopterygidae) are exclusively known from the Tithonian-Berriasian of western Europe (Milner 2002; Pouech 2008; Vullo *et al.* 2014; Louchart & Pouech 2017; Rauhut *et al.* 2018). This strongly supports a latest Jurassic-earliest Cretaceous age for the Angeac-Charente assemblage.

The only stratigraphically short-lived ornithischian taxon is the genus *Echinodon*, which is known exclusively from the Berriasian (see Sereno 2012). This corroborates the age provided for the two above-mentioned theropod taxa.

**Mammals.** Isolated mammalian teeth are often highly diagnostic and recognized genera and species are usually stratigraphically short-lived taxa, thus providing useful biostratigraphical information. This is the case for the four taxa *Sunnyodon*, *Thereuodon*, *Spalacotherium evansae* and *Peramus*, which are restricted to the Berriasian stage (Kielan-Jaworowska & Ensom 1992; Sigogneau-Russell & Ensom 1998; Ensom & Sigogneau-Russell 2000; Davis 2012). This is in full accordance with the age deduced from the vertebrate groups discussed above.

**STRATIGRAPHICAL RANGES OF ANGEAC-CHARENTE TAXA**  
The recently proposed earliest Cretaceous (Berriasian) age of the Angeac-Charente locality, based on both charophytes and palynomorphs (Benoit *et al.* 2017; Polette *et al.* 2018), is here confirmed by the vertebrate fauna. Consequently, the stratigraphic range of several taxa is now extended, such as *Parvodius celsucuspus*, Archaeopterygidae, and *Dacentrurus*, the last appearance datum of which is slightly extended since the fauna of Angeac-Charente is slightly younger than that of Cherves-de-Cognac. Conversely, as noted above, the ornithomimosaur from Angeac-Charente may be the oldest representative of its group.

## COMPARISONS WITH OTHER PURBECKIAN LOCALITIES OF SOUTHWESTERN FRANCE

As previously stated, three “Purbeckian” fossil localities have been exploited over the past two decades in southwestern France, namely Chassiron (Vullo *et al.* 2014), Cherves-de-Cognac (Mazin *et al.* 2008) and Angeac-Charente. A comparison between these different Charente Purbeckian localities is all the easier and more relevant, as the same type of fieldwork was carried out at each of the sites, with particular attention paid to both micro and macroremains (Pouech 2008; Vullo *et al.* 2014). The sampling in all three localities was executed in a relatively homogeneous fashion. If there are differences between the fossil record of these three localities, it is therefore related to a biological signal or, to a lesser extent, to the scope of the excavations, but by no means to the excavation techniques used in the field.

The three localities were dated using several independent methods. The Chassiron bonebed was precisely dated to the early Tithonian using brachiopods, dinoflagellate cysts, calcareous nannofossils and magnetostratigraphy (Schnyder *et al.* 2012; Vullo *et al.* 2014). Cherves-de-Cognac is dated to the early-middle Berriasian based on ostracods, charophytes and dinoflagellates (Colin *et al.* 2004; El Albani *et al.* 2004; Benoit *et al.* 2017). Finally, charophytes, palynomorphs and vertebrate fauna suggest a middle to late Berriasian age for the Angeac-Charente bonebed (see above). Thus, the three Charentese localities have all been fairly solidly dated with different markers and these facilitate the establishment of a chronological succession of continental faunas from the end of the Jurassic to the beginning of the Cretaceous.

The depositional environments of Chassiron, Cherves-de-Cognac and Angeac-Charente also show a progressive change in facies, from a paralic coastal environment subject to salinity fluctuations in Chassiron at the end of the Jurassic (Vullo *et al.* 2014), to a hyper-saline lagoonal environment in Cherves-de-Cognac (Buffetaut *et al.* 1989; Colin *et al.* 2004; Mazin *et al.* 2008; Pouech 2008), to a continental wetland environment in Angeac-Charente (Néraudeau *et al.* 2012; Rozada *et al.* 2021). This evolution of the depositional setting is concomitant with the marine regression in Western Europe that characterizes the J/K boundary (Hallam 2001), and is echoed in the paleontological content of each of these localities. The plant assemblages range from small and fragmented, highly transported remains of lycopods (spores), ferns (fronds) and conifers (*Agathoxylon* and *Brachyoxylon* wood, twigs, leaves, cones) and seeds at Chassiron, to rare coniferous remains (*Agathoxylon* wood fragments) at Cherves-de-Cognac, and to abundant native to paranaive well-preserved remains of a very diverse flora at Angeac-Charente (Allain *et al.* 2017). Charophyte assemblages suggest a progressive change from brackish water in Chassiron with abundance of Porocharaceae, to less saline water in Cherves-de-Cognac with the presence of Clavatoraceae, but the dominance of Porocharaceae, and freshwater in Angeac-Charente with the presence of Porocharaceae, but the dominance of Clavatoraceae (Benoit *et al.* 2017).

The vertebrate faunas show the same range. No coastal or marine taxa are present in Angeac-Charente, which contrasts with what is observed in the other two slightly older Charente localities: Cherves-de-Cognac and Chassiron (Table 1). Chassiron includes remains of bony euryhaline fish and taxa from littoral to paralic environments, such as the hybodont shark *Planohybodus*, the thalassochelydian turtle *Jurassichelon* (Pérez-García 2014), and the teleosaurid crocodylomorph *Steneosaurus*. The rich and diverse, terrestrial, and freshwater vertebrate assemblage mainly consists of isolated meso- and microremains (Vullo *et al.* 2014). Cherves-de-Cognac also yields a mixture of coastal and continental organisms with abundant chondrichthyan and osteichthyan remains (Pouech 2008). Macroremains are mostly dominated by crocodylomorphs and, to a lesser extent, turtles. Dinosaurs, pterosaurs, lissamphibians, and mammals are far less abundant, but they comprise a diverse assemblage. They are thought to be allochthonous or parautochthonous to the depositional environment (Pouech *et al.* 2015). This is in stark contrast to the Angeac-Charente ecosystem in which most of the terrestrial taxa, represented by abundant material, have proved to be autochthonous (see above).

Numerous euryhalin, freshwater and/or terrestrial taxa are common to all three localities (Table 1), including Pleurosternidae, *Theriosuchus*, Bernissartiidae, *Goniopholis*, *Pholidosaurus*, Dromaeosauridae, Iguanodontia, Stegosauria, Pinheirodontidae and Cladotheria. This suggests that rather than reflecting faunal turnover between the lower Tithonian and the upper Berriasian, Chassiron, Cherves-de-Cognac and Angeac-Charente vertebrate faunas reflect progressive «terrestrialization» of ecosystems in this area related to the Upper Jurassic regression. Together, they provide a good composite picture of the Purbeckian paleometacommunity of Southwestern France.

## PALEOGEOGRAPHIC INSIGHT

During the Jurassic/Cretaceous transition, the European Archipelago is at the crossroad of Asia, North America and Gondwana (Scotese 2014), and this is reflected in the paleogeographic distribution of the taxa that make up the vertebrate assemblages of Charente (Table 1). Only two taxa of this fauna seem to exhibit a certain endemism: the hybodont shark *Parvodus celsucuspus*, which was only known at its type-locality of Cherves-de-Cognac, but is now reported from Angeac-Charente, and the Angeac-Charente ornithomimosaur. Most of the Charente taxa have a European distribution, and what could be called a Purbeckian signature. They are widespread in western Europe and are represented by abundant specimens, such as *Belemnobatis*, *Thrissops*, *Pleurosternon*, *Jurassichelon*, *Hylaeochelys*, *Goniopholis*, *Pholidosaurus*, Bernissartiidae, *Nuthetes*, Archaeopterygidae, *Echinodon*, *Dacentrurus*, Pinheirodontidae, *Triconodon*, *Sunnyodon* and *Spalacotherium evansae* (Table 1). Nevertheless, at a higher taxonomic rank, most of these taxa have a much more extended distribution,



FIG. 36. — Reconstruction of the Angeac-Charente landscape, 140 Million years ago, © Mazan.

especially in Laurasia, which may suggest a Middle Jurassic Pangaean-inherited distribution, followed by vicariant evolution in western Europe.

The close affinities between the North American (Morrison Formation), European (Iberian Peninsula) and African (Tendaguru) upper Jurassic macrofauna have already been highlighted (Mateus 2006; Mannion *et al.* 2019). For some, they are the result of dinosaur faunal exchanges between North America, Europe and Africa in the Late Jurassic (Mateus 2006), but for others they rather reflect a widespread distribution that occurred as early as the Middle Jurassic (Mannion *et al.* 2019). Faunal interchanges between Europe and North America do not appear to be difficult to envisage during the Jurassic-Cretaceous transition. They are supported by paleogeographic data (Dercourt *et al.* 2000; Scotese 2014) and corroborated by numerous Late Jurassic taxa, including the theropods *Allosaurus*, *Ceratosaurus* and *Torvosaurus* (Mateus 2006), but also by other Early Cretaceous taxa present in Charente, such as *Opisthias*, Pleurosternidae, Helochelydridae, Hypsilophodontidae and Camptosauridae. Faunal exchanges between Europe and Africa, at the end of the Jurassic and at the beginning of the Cretaceous is less consensual, as there has been no clearly established land connection between the two continents (Mannion *et al.* 2019). Such a connection

between Laurasia and Gondwana cannot be ruled out, however, and seems to have been possible via the Mediterranean Tethyan Sill during low eustatic levels (Vrielynck *et al.* 1995; Dercourt *et al.* 2000; Gheerbrant & Rage 2006). In fact, Lasseron *et al.* (2020) proposed the existence of a terrestrial route across the Tethys, based on several taxa, most of which have been found in Charente.

This is the case for the squamate *Paramacellodus*, which is known from the Kimmeridgian of United States, and the Tithonian-Berriasian of England, France and Morocco (Hoffstetter 1967; Richter 1994; Broschinski & Sigogneau-Russell 1996; Evans & Chure 1998). It is also worth noting that a paramacellodid dentary from the Late Jurassic of Tanzania has been referred to *Becklesius*, a second genus otherwise known from the Kimmeridgian-Barremian of Europe (Broschinski 1999). Two mammalian genera, *Thereuodon* and *Peramus*, show the same paleogeographic distribution pattern as paramacellodids. The presence of *Thereuodon* and *Peramus* at Angeac-Charente first underlines the affinities of this site with those from the Purbeck Group, since the Charente species seem more closely related to English taxa than to any other taxon (see above), but both genera are also present at Anoual, Morocco, on the southern edge of Tethys (Lasseron *et al.* 2020). It is very likely that

the distribution of these taxa, in both Europe and Africa, results from dispersal events from Laurasia to Gondwana via ephemeral land connections during the Late Jurassic and/or the beginning of the Early Cretaceous. Indeed, a sampling bias can hardly be invoked to explain the absence of these taxa in Africa during the Middle Jurassic since the recently discovered Guelb el Ahmar fossiliferous sites in the Bathonian Anoual Formation of Morocco have been intensively sampled and have yielded a riche vertebrate fossil assemblage, including mammals (Haddoumi *et al.* 2016; Lasseron *et al.* 2020). Neither has any of these three taxa been recovered from the Middle Jurassic of Madagascar (Flynn *et al.* 2006).

The Gobiconodontidae from Angeac-Charente represent the first occurrence of this group in France, and only the fourth occurrence in Europe, with a specimen from the Bathonian of Britain (Butler & Sigogneau-Russell 2016) and two others from the Barremian of Britain (Sweetman 2006) and Spain (Cuenca-Bescós & Canudo 2003; Martin *et al.* 2015). Outside of Europe, Gobiconodontidae are known from Asia, North Africa and North America (Kielan-Jaworowska *et al.* 2004; Sweetman 2006; Butler & Sigogneau-Russell 2016), in a stratigraphic range comprised between the Lower Jurassic and the Lower Cretaceous (Butler & Sigogneau-Russell 2016). It has been widely accepted that the gobiconodontids originated and diverged in central and eastern Asia (Chow & Rich 1984; Cuenca-Bescós & Canudo 2003). Cuenca-Bescós & Canudo (2003) also concluded that the currently known distribution of this family was the result of at least two dispersal events, both of which originated in central Asia, a first one towards Europe during the Barremian and a second one, later, towards North America. Thus, the gobiconodontids would be the only taxon from the Angeac-Charente fauna to have affinities with Asian taxa. However, the discovery of gobiconodontids in the Upper Jurassic-Lower Cretaceous of Morocco (Sigogneau-Russell 2003) and in the Middle Jurassic and the Lower Cretaceous of Britain (Sweetman 2006; Butler & Sigogneau-Russell 2016) questioned the scenario of their dispersal, and maybe their area of origin. Their presence in the Berriasian of Angeac-Charente confirms that faunal interchanges between Asia and Europe did occur well before the Barremian and suggests that the Gobiconodontidae distribution was at least Laurasian at the beginning of the Cretaceous and maybe since the Middle Jurassic. This is further supported by the presence of the genus *Huastecodon* in the Lower Jurassic of Mexico (Montellano *et al.* 2008), which has been tentatively referred to the Gobiconodontidae.

In summary, the vertebrate fauna from Angeac-Charente has above all a Purberckian character. Many exclusively European genera and species belong to families with an essentially laurasian paleogeographic distribution. Some taxa nevertheless suggest dispersal events between Africa and Europe at the Jurassic/Cretaceous transition. In contrast, none of the fossil taxa in Charente have close affinities with Asian taxa.

## IS THERE A TURNOVER OF THE CONTINENTAL FAUNA AT THE J/K BOUNDARY?

The definition of the Jurassic/Cretaceous boundary has been a pervasive problem for many decades and still awaits a widely accepted outcome (Remane 1991; Enay 2020). The main debate focuses on whether the Berriasian represents the upper stage of the Jurassic or the lower stage of the Cretaceous. It has been shown that the J/K boundary does not correspond to any significant faunal change in the marine environment at a small scale, making it difficult to set a clear boundary, unlike the Triassic/Jurassic and Cretaceous/Paleogene boundaries (Remane 1991; Enay 2020). No fewer than eleven possible biological markers for the J/K boundary have thus been proposed (Wimbledon *et al.* 2011), and with the exception of the disappearance of three species of the calpionellid *Crassicolaria*, there does not seem to be any real turnover among marine microfossils (Granier 2019a, b). Moreover, the marine fauna shows significant provincialism induced by the Purbeckian regression and a long-range correlation is difficult between the Austral, Tethyan, and Boreal domains (Enay 2020).

The age of the J/K boundary is all the more important since this boundary has long been considered a possible mass-extinction event with a 20% level of extinction (Raup & Sepkoski 1982; 1984). Subsequently, the lack of conclusive evidences of a drastic biotic change and/or a remarkable catastrophic event at the J/K boundary led some authors to downplay the importance of the extinction episode at that time (Hallam 1986; Hallam & Wignall 1997; Bambach *et al.* 2004). Recently, based on a large data set, the hypothesis of an important faunal turnover at the J/K boundary has been resurrected (Tennant *et al.* 2017).

In this context, the Angeac fauna does not in any way allow us to definitively settle the debate on the definition of the Jurassic/Cretaceous boundary, but it does bring, to the continental scale, elements that could be taken into consideration. It also undermines the hypothesis of significant changes in the continental fauna at the J/K boundary as currently defined, (the Tithonian/Berriasian boundary). At the current time, Angeac-Charente is the only known Lagerstätte from the Berriasian and is thus of great importance in the study of extinction/faunal turnover during the J/K transition. The main interest of the Chassiron, Cherves-de-Cognac and Angeac-Charente localities is that they follow one another chronologically from the Lower Tithonian to the Berriasian-Valanginian. Thus, they record continental faunal changes on either side of the J/K boundary in a relatively fine way, especially since the assemblages also include microvertebrates. Most of the taxa recored in Angeac-Charente are known before the Jurassic-Cretaceous boundary. Of the 38 Charente vertebrate taxa that were identified to family or genus rank, none became extinct at the Tithonian/Berriasian boundary, except ramphorhynchid pterosaurs (Table 1). Three taxa at a generic level seem to originate during the Berriasian: the heterodontosaurid dinosaur *Echinodon*, the multituberculate *Sunnyodon* and the spalacotheriid *Spalacotherium*. The Spalacotheriidae is unknown before the Berriasian whereas

the Heterodontosauridae and the Paulchoffatiidae are known respectively from the Early and Late Jurassic. As shown above, rather than reflecting an important faunal turnover between the Tithonian and the Berriasian, the three Charente localities appear to record faunal changes related to local environmental changes resulting from the marine regression that characterized the Jurassic/Cretaceous transition.

The same pattern and close affinities with Middle to Late Jurassic faunas have also been suggested for other less diverse earliest Cretaceous continental faunas around the world, including those from the Berriasian-Hauterivian Kirkwood Formation of South Africa (Rich *et al.* 1983; McPhee *et al.* 2016), the Tithonian-Berriasian Ksar Metlili Formation of Morocco (Haddoumi *et al.* 2016; Lasseron *et al.* 2020), and the ?Berriasian-Barremian Teete vertebrate locality in Western Yakutia, in Russia (Averianov *et al.* 2018; Skutschas *et al.* 2018). Conversely, many groups of large vertebrates are recorded neither in the fauna of the late Jurassic nor in that of Angeac-Charente, although, after the Berriasian, they are known in numerous European localities such as the Wessex Formation in England (Batten 2011) and the Late Barremian Lagerstätte at Las Hoyas in Spain (Poyato-Ariza & Buscalioni 2016). Among these groups are ornithocheirid, tapejarid and istiodactylid pterosaurs; spinosaurid, neovenatorid, and carcharodontosaurid theropods; rebbachisaurid sauropods; and birds.

Paleontological data from Charente thus do not support the hypothesis of a biological turnover at the Tithonian/Berriasian boundary, at least in Europe. This appears to have taken place between the end of the Berriasian and the Barremian, although the fossil record from this interval is very poorly known (Benson *et al.* 2013). Data on the latest Jurassic and earliest Cretaceous continental faunas suggest a reversion of the system boundary to Orbigny's (1841) and Opper's (1865) historical position who defined the J/K boundary as Berriasian-Valanginian based on faunal turnover at that time (Granier 2019b; Enay 2020).

## CONCLUSIONS

Angeac-Charente is an exceptional locality in many ways. In view of the extent and intensity of the fieldwork undertaken there and the number of fossils that have been recovered, it comprises one of the largest and most productive earliest Cretaceous localities in the world. Excavation areas will be further extended over the next decade, since 5000 m<sup>2</sup> of land has been made available by the Audoin et Fils company.

The vertebrate assemblage of Angeac-Charente consists of at least 40 vertebrate taxa, of which about 15 are represented by microvertebrate remains. The taxa that make up this very diverse fauna are synchronous, and autochthonous or parautochthonous. They comprise freshwater or terrestrial vertebrates that are clearly indicative of a continental wetland ecosystem, with no direct connection to the sea. The functioning and trophic dynamics of this ecosystem, and the associated paleoclimate, are being studied through multi-isotopic geochemical analyses. The taphocoenosis is

dominated by an ornithomimosaur herd of at least 70 individuals, but turiasaur sauropods, pleurosternid turtles and goniopholidid crocodyliforms are also abundant. Detailed anatomical and taxonomic descriptions of this material are in preparation, and will be published according to the discoveries in the field, and the degree of completeness of the skeletons of the taxa concerned.

To date Angeac-Charente is the only known Lagerstätte from the Berriasian. It thus fills a gap in the fossil record, providing abundant and varied data on a continental wetland ecosystem at the beginning of the Cretaceous. Combined with data from the Charentese Chassiron and Cherves-de-Cognac localities, these data make it possible to follow the evolution of biodiversity, on a regional scale, at the Jurassic-Cretaceous boundary. The taxonomic composition of the Angeac-Charente locality shows strong similarities to Late Jurassic assemblages. It raises important questions regarding terrestrial faunal turnover across the Jurassic/Cretaceous boundary and the possible redefinition of the Jurassic/Cretaceous boundary placing it at the base of the Valanginian stage.

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## APPENDIX

APPENDIX 1. — Systematic paleontology of the complete faunal list of the Angeac-Charente locality.

- Arthropoda von Siebold, 1848  
 Crustacea Brünerich, 1772  
 Ostracoda Latreille, 1802  
*Cypridea* gr. *tuberculata* Sowerby, 1836  
*Cypridea laevigata* Dunker, 1846  
*Damonella pygmaea* Anderson, 1941  
*Damonella ellipsoidea* Wolburg, 1962  
*Darwinula oblonga* Roemer, 1839  
*Alicenula leguminella* Forbes, 1855  
*Fabanella boloniensis* Jones, 1885  
*Mantelliana* sp. Anderson, 1966
- Isoptera Brullé, 1832  
 Family indet.  
*Microcarpolithes hexagonalis* Vangerow, 1954  
 (termite coprolithes)
- Mollusca Linnaeus, 1758  
 Gastropoda Cuvier, 1795  
 Viviparidae Gray, 1847  
 Viviparidae indet.  
 Bivalvia Linnaeus, 1758  
 Unionoidea Stoliczka, 1871  
 cf. *Margaritifera* sp.
- Vertebrata Lamarck, 1801  
 Chondrichthyes Huxley, 1880  
 Hybodontiformes Owen, 1846  
 Lonchidiidae Herman, 1977  
*Parvodus celsucuspus* Rees, Cuny, Pouech & Mazin, 2013
- Osteichthyes Huxley, 1880  
 Actinopterygii Klein, 1885  
 Ginglymodi Cope, 1872  
 Ginglymodi indet.  
 Ionoscopiformes Grande & Bemis, 1998  
 Ionoscopiformes indet.  
 Amiiiformes Huxley, 1861  
 Amiiiformes indet.  
 Pycnodontiformes Berg, 1937  
 cf. *Micropycnodon* sp.  
 Pycnodontidae indet.
- Amphibia Linnaeus, 1758  
 Lissamphibia Haeckel, 1866  
 Lissamphibia indet.  
 Albanerpetontidae Fox and Naylor, 1982  
 Albanerpetontidae indet.  
 Anura Fischer von Waldheim, 1813  
 Anura indet.  
 Caudata Scopli, 1777  
 Caudata indet.
- Reptilia Laurenti, 1768  
 Testudinata Klein, 1760  
 Perichelydia Joyce, 2017  
 Helochelydridae Nopsca, 1928  
 (*sensu* Joyce *et al.* 2016)  
 Helochelydridae indet.  
 Paracryptodira Gaffney, 1975  
 Pleurosternidae Cope, 1868  
*Pleurosternon bullockii* (Owen, 1842)  
 Thalassochelydia Anquetin *et al.*, 2017  
*Hylaeochelys belli?* (Mantell, 1844).
- Lepidosauria Haeckel, 1866  
 Squamata Opper, 1811  
 Scincomorpha Camp, 1923  
 cf. *Paramacellodus* sp.  
 Rhynchocephalia Günther, 1867  
 Sphenodontia Williston, 1925  
 cf. *Opisthias* sp.
- Archosauromorpha von Huene, 1946  
 Choristodera Cope, 1876  
 cf. *Cteniogenys* sp.
- Archosauria Cope, 1870  
 Crocodyliformes Hay, 1930  
 Atoposauridae Gervais, 1871  
*Theriosuchus* sp.  
 Atoposauridae indet.  
 Bernissartiidae Dollo, 1883  
 Bernissartiidae indet.  
 Goniopholididae Cope, 1875  
*Goniopholis* sp.  
 Pholidosauridae Eastman, 1902  
*Pholidosaurus* sp.
- Dinosauria Owen, 1842  
 Theropoda Marsh, 1881  
 Megalosauridae Fitzinger, 1843  
 Megalosauridae indet.  
 Ornithomimosauria Barsbold, 1976  
 New taxon  
 Tyrannosauroida Osborn, 1905  
 Tyrannosauroida indet.  
 Dromaeosauridae Matthew and Brown, 1922  
 cf. *Nuthetes* sp. Owen, 1854  
 Archaeopterygidae Huxley, 1872  
 Archaeopterygidae indet.
- Sauropoda Marsh, 1878  
 Macronaria indet.  
 Turiasauria Royo-Torres, Cobos & Alcalá, 2006  
 New taxon
- Thyreophora Nopsca, 1915  
 Stegosauria Marsh, 1877  
*Dacentrurus* sp.  
 Ankylosauria Osborn, 1923  
 Ankylosauria indet.

APPENDIX 1. — Continuation.

- Heterodontosauridae Kuhn, 1966  
*Echinodon* sp.
- Ornithopoda Marsh, 1881  
Hypsilophodontidae  
Hypsilophodontidae indet.
- Camptosauridae  
Camptosauridae indet.
- Pterosauria Kaup, 1834  
Pterosauria indet.
- Pterodactyloidea Plieninger, 1901  
Pterodactyloidea indet. A  
Pterodactyloidea indet. B
- Synapsida Osborn, 1903  
Mammalia Linnaeus, 1758  
Mammalia indet.
- Thereuodontidae Sigogneau-Russell & Ensom, 1998  
*Thereuodon* cf. *taraktes*
- Eutriconodonta Kermarck, Mussett & Rigney, 1973  
Gobiconodontidae Chow & Rich, 1984  
*Gobiconodon* sp.
- Triconodontidae Marsh, 1887  
*Triconodon* sp.
- Allotheria Mars, 1880  
Multituberculata Cope, 1884  
Paulchoffatiidae Hahn, 1969  
*Sunnyodon* sp.
- Pinheirodontidae Hahn et Hahn, 1999  
Pinheirodontidae indet.
- Trechnotheria McKenna, 1975  
Spalacotheriidae Marsh, 1887  
*Spalacotherium* sp.
- Cladotheria McKenna, 1975  
Dryolestoidea Butler, 1939  
Dryolestidae Marsh, 1879  
Dryolestidae indet.
- Zatheria McKenna, 1975  
Peramuridae Kretzoi, 1946  
*Peramus* sp.