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Palaeontology of the Purbeck-type (Tithonian, Late Jurassic) bonebeds of Chassiron (Oléron Island, western France)

*Paléontologie des bonebeds de type purbeckien (Tithonien, Jurassique supérieur) de Chassiron (île d'Oléron, Ouest de la France)*

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ABSTRACT

The paralic flora and fauna from the Late Jurassic of Chassiron (Oléron Island, western France) are described. The Tithonian-aged bonebeds of Purbeck facies of this locality have yielded a rich and diverse vertebrate assemblage including fishes, amphibians, reptiles and mammals, alongside numerous plant and invertebrate remains. The Chassiron locality thus appears as a peculiar Konzentrat-Lagerstätte in which most of the palaeoecosystem's biological components (both aquatic and terrestrial) have been preserved. The depositional environment was probably subject to salinity fluctuations, as indicated by the co-occurrence of freshwater and euryhaline organisms. This is one of the richest localities and the first mammal-bearing site known from the Jurassic of France.

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R É S U M É

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La flore et la faune paraliques du Jurassique supérieur de Chassiron (île d'Oléron, Ouest de la France) sont décrites. Dans cette localité, les *bonebeds* d'âge Tithonien et de faciès purbeckien ont livré, aux côtés de nombreux restes de plantes et d'invertébrés, un assemblage de vertébrés riche et diversifié, incluant poissons, amphibiens, reptiles et mammifères. La localité de Chassiron apparaît comme un Konzentrat-Lagerstätte remarquable, dans lequel la plupart des composants biologiques du paléocécosystème ont été préservés, aussi bien aquatiques que terrestres. Le milieu de dépôt était probablement soumis à des fluctuations de salinité, comme l'indique la présence simultanée d'organismes dulçaquicoles et euryhalins. Il s'agit, pour l'ensemble du Jurassique français, d'une des localités les plus riches et du premier site à mammifères.

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1. Introduction

Bonebeds are relatively uncommon in the Late Jurassic of France, where most vertebrate fossils are only isolated remains. With the exceptions of the famous Konservat-Lagerstätten of Cerin and Canjuers, the best-known vertebrate assemblages have been found in the Oxfordian of Lisieux (Buffetaut et al., 1985), the Kimmeridgian of Fumel (Sauvage, 1902) and the Tithonian of Boulogne-sur-Mer (Cuny et al., 1991; Sauvage, 1880). In the late nineties, the discovery by one of us (DA) of an accumulation of vertebrate remains in the Purbeck beds (Early Tithonian in age) of the “Phare de Chassiron” section (Oléron Island, western France) has led to the collection of a large number of specimens (Billon-Bruyat et al., 2001). This material (including both macroremains and microremains) consists of numerous bones and teeth belonging to sharks, bony fishes, amphibians, turtles, crocodylians, dinosaurs, pterosaurs, lizards, choristoderes, and mammals. Such a concentration of vertebrate remains in a few beds of the series, found in association with abundant plant and invertebrate fossils briefly described here, allows the Chassiron locality to be recognized as a Konzentrat-Lagerstätte. The fossil assemblage of the Chassiron bonebeds can be compared with that from the nearby, slightly younger (Berriasian) locality of Cherves-de-Cognac (Buffetaut et al., 1989; Colin et al., 2004; Mazin et al., 2006, 2008).

2. Geological setting

The “Pointe de Chassiron” corresponds to the extreme northern point of the Oléron Island, off the Atlantic coast of France (Fig. 1). The 80-m-thick “Phare de Chassiron” section displays a mixed siliciclastic and carbonate sedimentary succession of Late Kimmeridgian to Late Tithonian–Earliest Cretaceous age. The section is composed of four alternatively carbonate-dominated and clay-dominated informal members (Fig. 2). Carbonate-dominated intervals represent open-marine platform environments, whereas clay-dominated intervals represent more proximal, shallow-water to emergent facies (Colombié et al., 2012; Schnyder et al., 2012). The sedimentary succession reflects a long-term, regressive (progradational) sedimentary sequence of Late

Kimmeridgian to Early Tithonian age, followed by a transgressive (retrogradational)–regressive (progradational) sedimentary cycle of Early Tithonian to Late Tithonian–Earliest Cretaceous age (Colombié et al., 2012; Schnyder et al., 2012) (Fig. 3).

The section begins with beige to grey nodular, irregular limestones beds with thin marly intervals representing an open-marine platform subjected to storms (Member 1, 0 to 24.2 m) (Colombié et al., 2012; Schnyder et al., 2012). This interval is precisely dated by ammonite biostratigraphy of the Late Kimmeridgian Autissiodorensis Zone and the Early Tithonian Gigas Zone (Bousquet, 1967; Hantzpergue, 1989; Hantzpergue et al., 2004) (Fig. 2). Marine influences are progressively less from base to top of Member 1, as testified by evidence of episodic emergence above 18 m (dinosaurian footprints, mud-cracks and fenestrae) and occurrences of charophytes between 20 m and 24.2 m. This sedimentary sequence is terminated by a 0.4 m thick conglomerate with a clayey matrix and limestone clasts, covered in turn by an accumulation of conifer wood fragments. It separates the open-marine deposits below (Member 1) from the shallower, occasionally emergent facies, of the Purbeck beds above (Member 2 to 4, Fig. 2). Purbeck beds lack of ammonites, and their age assignment is based on ostracods (Donze, 1960; Hantzpergue et al., 2004), brachiopods (Hantzpergue et al., 2004), foraminifera (Bousquet, 1967), dinoflagellate cysts, calcareous nannofossils and magnetostratigraphy (Schnyder et al., 2012). Most Purbeck beds appear to be of Early Tithonian age (Fig. 2, Schnyder et al., 2012).

Several layers yielding rich vertebrate fauna concentrations, which are the topic of this paper, occur within black to blue clays and marls deposited at the base of the Purbeck beds between 24 and 33 m, above the conglomeratic layer (Base of Member 2, Figs. 2 and 3). The richest vertebrate assemblages come from beds 1000 and 1005 (Fig. 3). Accompanied by occurrences of charophyte gyrogonites (Martín-Closas et al., 2008), and local wood fragment accumulations, those deposits are related to shallow-water embayment and tidal facies with frequent freshwater discharges from the continent (Schnyder et al., 2012). These clay and marl packages with vertebrate concentrations were deposited at low sea-level during an early phase of a long transgression (Fig. 2).

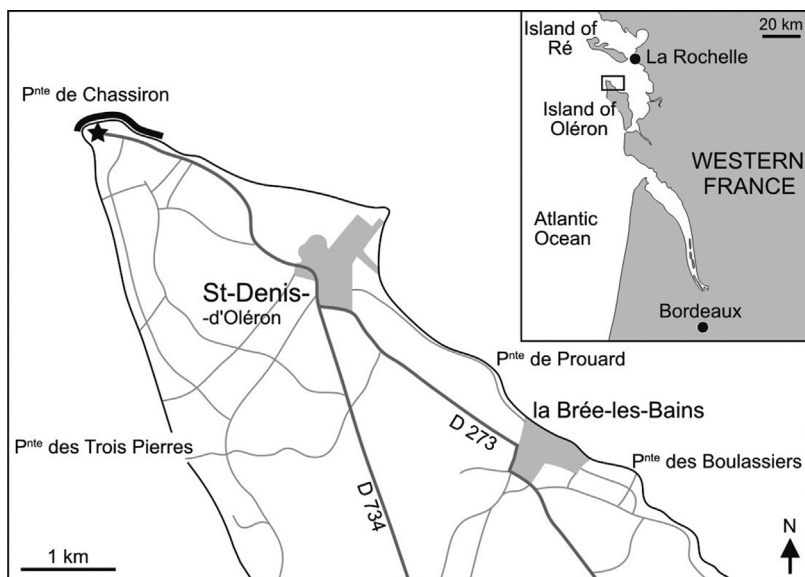


Fig. 1. Location of the “Phare de Chassiron” section.

Fig. 1. Localisation de la coupe du phare de Chassiron. Modifié d’après Schnyder et al. (2012).
Modified after Schnyder et al. (2012).

3. Palaeontology

Specimen repository: all the material studied is deposited in the collections of the “Musée de l’île d’Oléron” (MO), Saint-Pierre-d’Oléron, France (see Table 1 for catalogue numbers of figured vertebrate specimens; plant, invertebrate and eggshell specimens are still unnumbered).

3.1. Palaeobotany

3.1.1. Charophyte algae

The charophyte assemblage of the Chassiron bonebeds has been recently described and discussed in detail (Martín-Closas et al., 2008). It consists of abundant gyrogonites of *Latochara latitruncata* (Nitellaceae), as well as less common gyrogonites of *Mesochara gr. voluta* (Characeae).

3.1.2. Cuticles and mesofossil remains

The plant assemblage mostly consists of rich and abundant mesofossil remains. They are preserved as compressions, either charcoals or cuticles, and many have close-to-original three-dimensional shape. The most common remains are vegetative fragments of conifers. They represent isolated leaves and leafy stems with spirally-arranged scale-like leaves (Fig. 4F). They belong to at least two taxa based on the examination of cuticles under the light and scanning electron microscopes, particularly the stomatal distribution and the wall shape of the ordinary epidermal cells. Several types of cones are also recognized based on the number of scales, and the shape and size of cones and scales (Fig. 4G–I). Seeds are abundant and diverse, and show hilum and micropyle (Fig. 4J–N). Ferns represent a minor component showing fragments of rachis bearing pinnules and distal circinate fronds, and pinnules

bearing sori (Fig. 4A–E). Also, the occurrence of three types of lycopsid megaspores is noteworthy (Fig. 5).

3.1.3. Wood

Wood fragments are also abundant, and two morpho-genera can be recognized. The first wood shows a radial pitting generally biseriata and araucarioid cross-fields with numerous contiguous oculipores (Fig. 6). It is referred to *Agathoxylon* sp., a common and widespread morphogenus of conifer wood (Philippe and Bamford, 2008). The second wood seems to display a mixed type (both araucarian and abietinean) of radial pitting. It is therefore tentatively assigned to *Brachyoxylon* sp., another morphogenus of conifer wood (Philippe and Bamford, 2008).

3.2. Invertebrates

3.2.1. Molluscs

Molluscs are very abundant in the Chassiron bonebeds. They are represented by two or three bivalve species and four or five gastropod taxa. One or two rounded species of the brackish genus *Neomiodon* (close to *N. fasciatus* and *N. angulatus*) (Fig. 7A) constitute the main part of the bivalve assemblage, in association with some more elongated and angular shells assignable to “*Psammobia*” *tellinoides* (Fitton, 1836; Mörter, 1984).

Most of gastropod specimens are planorbids. They include an indeterminate calcitised and smooth species, as well as a pyritised, carinate and finely costulate form assigned to *Gyraulus* (= *Planorbis*) cf. *loryi*. The gastropod assemblage also includes a few specimens of *Provalvata* cf. *sabaudiensis*, *Viviparus* cf. *inflatus*, and probably an indeterminate viviparid (Arkell, 1941) (Fig. 7B).

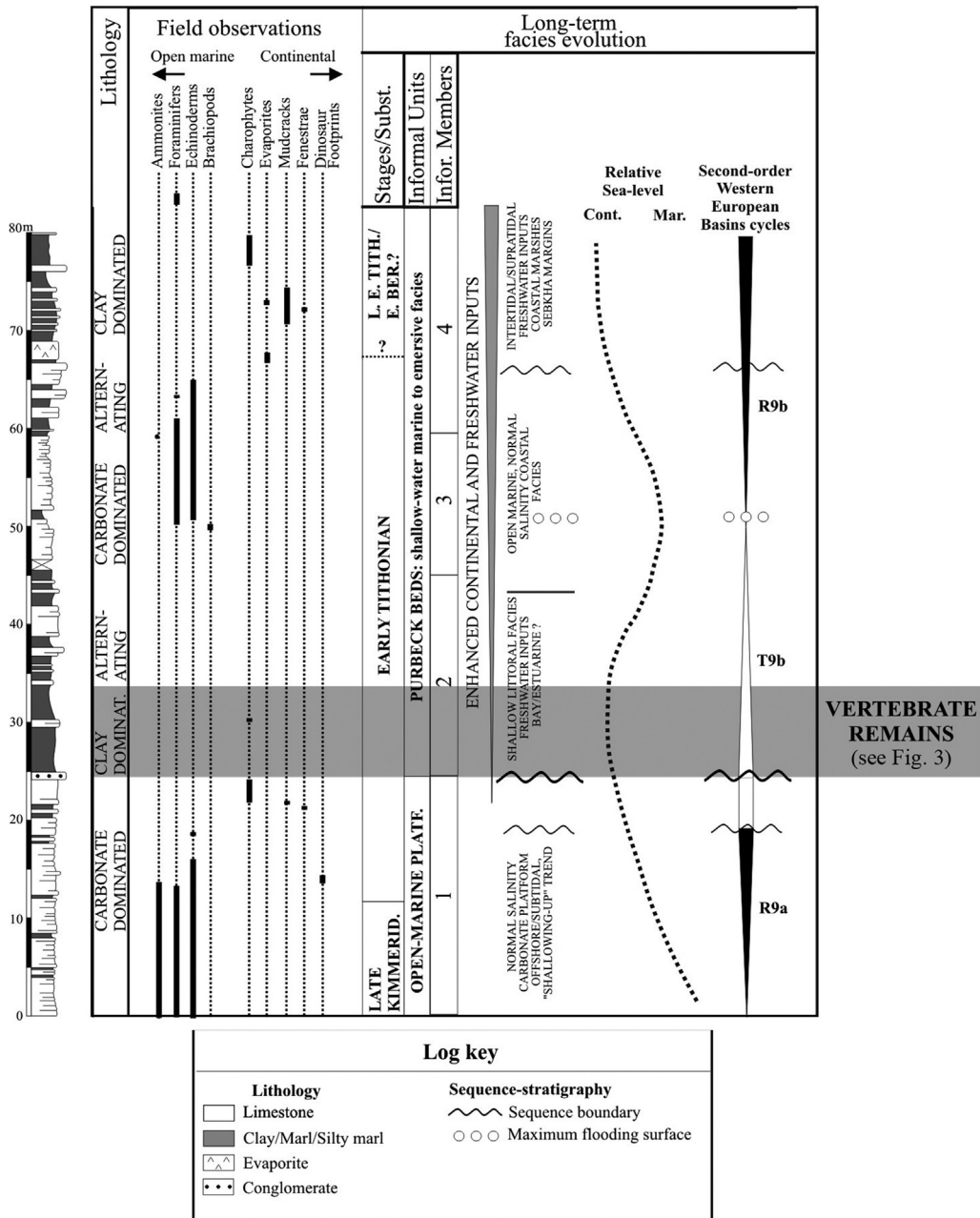


Fig. 2. Age-assignment, long-term facies evolution and sequence-stratigraphy interpretations of the “Phare de Chassiron” section, modified after Schnyder et al. (2012). The grey shaded area denotes the stratigraphic interval including vertebrate remain concentrations and detailed in Fig. 3.

Fig. 2. Coupe du phare de Chassiron : âges, évolution de faciès et stratigraphie séquentielle, modifié d’après Schnyder et al. (2012). La partie grisée indique l’intervalle stratigraphique contenant les concentrations de restes de vertébrés et détaillé sur la Fig. 3.

Similar freshwater to oligohaline molluscan associations are common in the Purbeck Group of southern England (Arkell, 1941; Morter, 1984) and equivalent beds in northwestern Germany (Huckriede, 1967). Interestingly, the molluscan assemblage of the Chassiron bonebeds markedly differs from the one found at Cherves-de-Cognac. In the latter, unionoid mussels and hydrobiid snails are present whereas neomidontids, provalvatids

and planorbids seem to be absent (El Albani et al., 2004).

3.2.2. Ostracods

Ostracod crustaceans are common and diverse (about 20 species) in the studied bonebeds. However, the ostracod fauna is dominated by the following taxa: the euryhaline

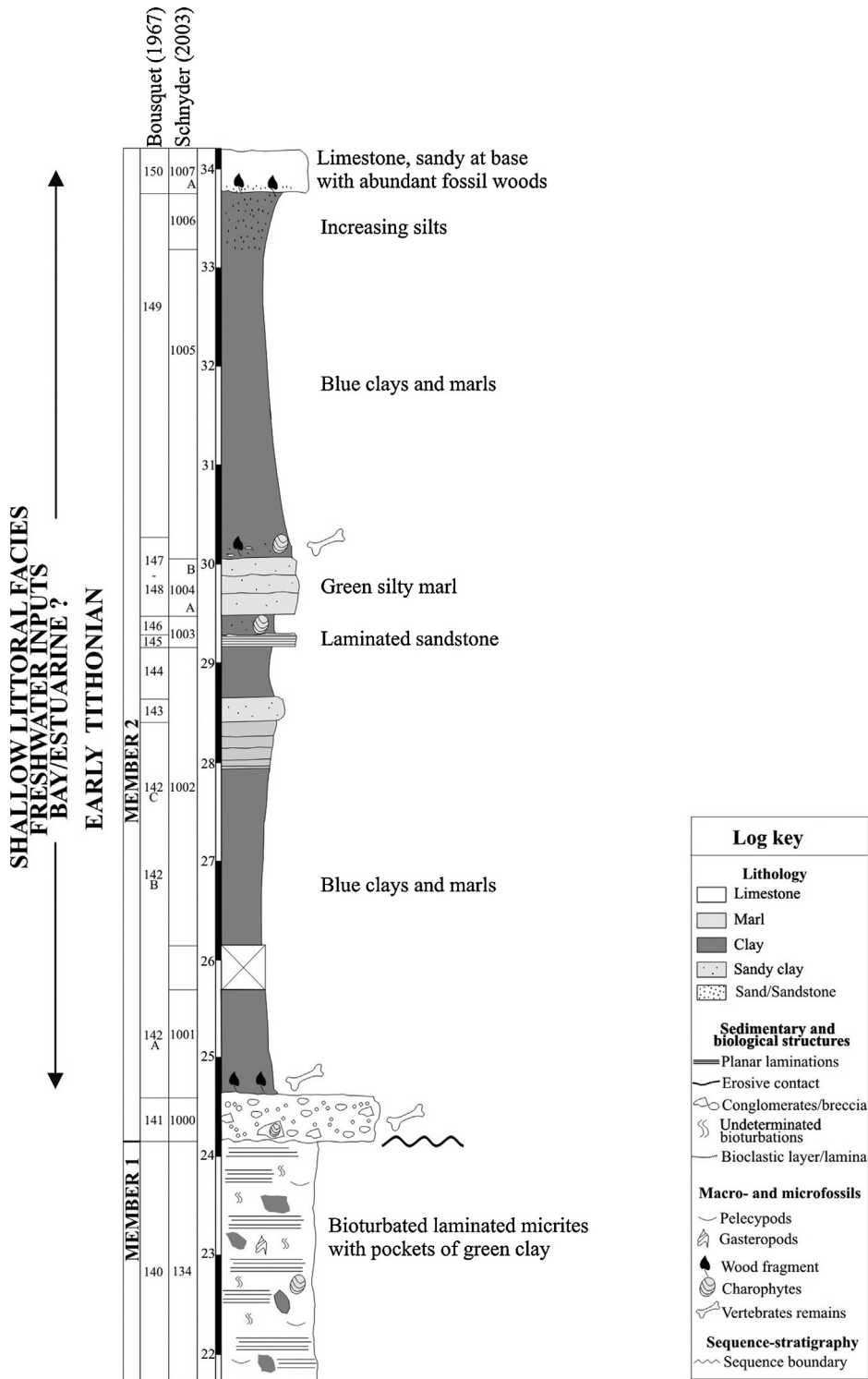


Fig. 3. Detailed sedimentary log of the stratigraphic interval with vertebrate remains concentrations. Log after Schnyder et al. (2012). Bed numbering of Bousquet (1967) and Schnyder (2003) are figured. Bed numbering of Schnyder (2003) is used in this paper.

Fig. 3. Coupe stratigraphique détaillée de l'intervalle contenant les concentrations de restes de vertébrés. Coupe d'après Schnyder et al. (2012). Les numérotations des bancs de Bousquet (1967) et Schnyder (2003) sont indiquées, la seconde étant employée dans la présente étude.

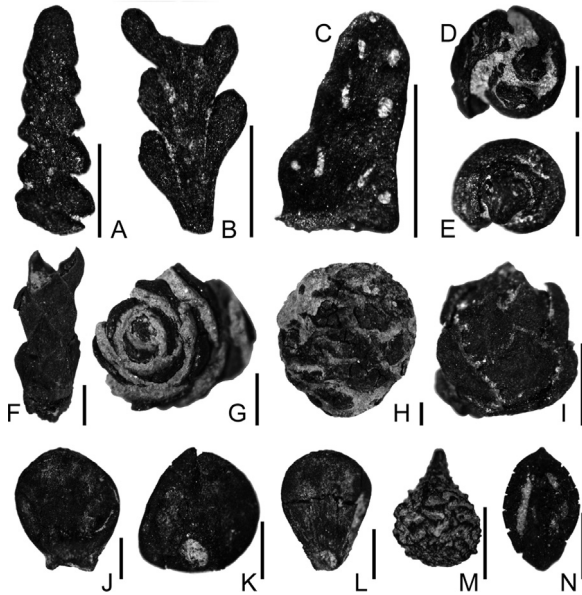


Fig. 4. Plant cuticles and mesoremain. A–E, tiny fragments of ferns: rachis bearing pinnules (A, B), pinnule lower side showing six sori (C), circinate distal part of fronds (D, E). F–I, conifers: leafy stem bearing spirally-arranged scale-like leaves (F), cones (G–I). J–N, seeds showing hilum and micropyle. Scale bars: 1 mm.

Fig. 4. Cuticules et mésorestes divers de plantes. A–E, petits fragments de fougères : rachis portant des pinnules (A, B), face inférieure d'une pinnule montrant six sores (C), partie distale circinée de frondes (D, E). F–I, conifères : tige feuillue portant des écailles disposées en spirale (F), cônes (G–I). J–N, graines montrant le hile et le micropyle. Barres d'échelle : 1 mm.

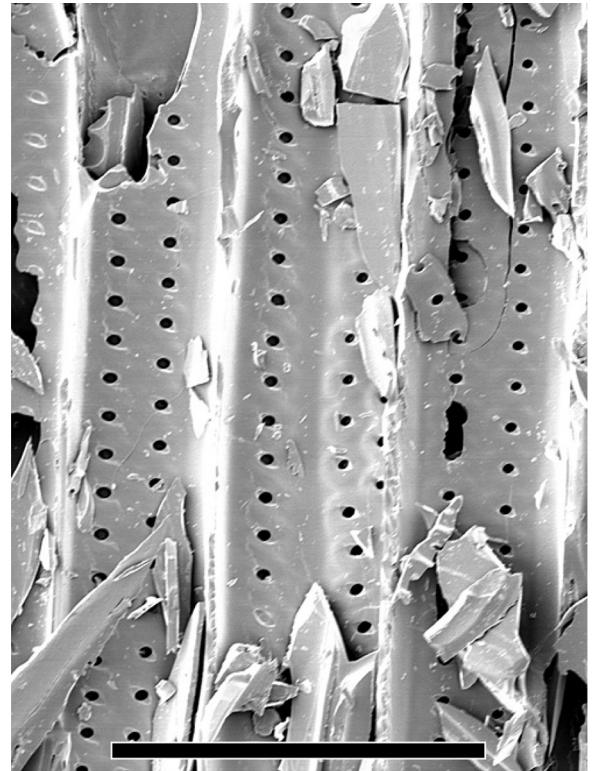


Fig. 6. Conifer wood fragment: *Agathoxylon* sp. Scale bar: 100 μm .

Fig. 6. Fragment de bois de conifère : *Agathoxylon* sp. Barre d'échelle : 100 μm .

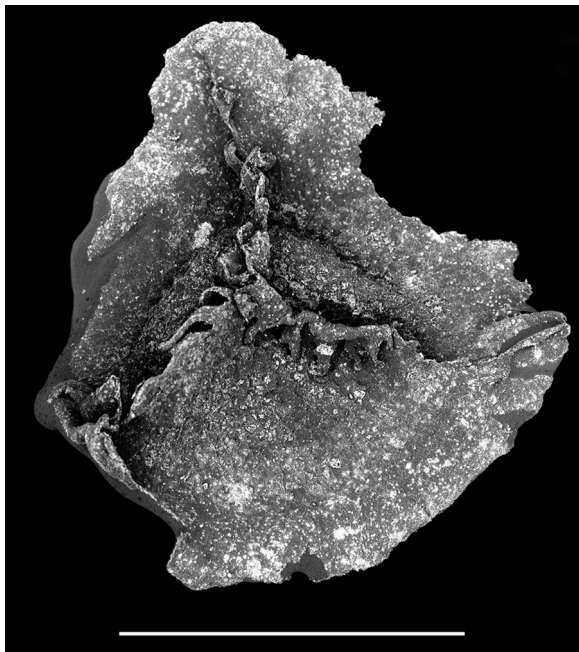


Fig. 5. Lycopsid megaspore. Scale bar: 500 μm .

Fig. 5. Mégaspore de lycopside. Barre d'échelle : 500 μm .

form *Fabanella boloniensis ornata* and the limnic form *Mantelliana* cf. *perlata* (Martín-Closas et al., 2008).

3.3. Vertebrates

3.3.1. Chondrichthyans

Elasmobranch remains are abundant in the Chassiron bonebeds and consist of oral teeth, dermal denticles, and cephalic and dorsal fin spines (Fig. 8). However, all these remains can be assigned to only two taxa of the order Hybodontiformes. The most common taxon by far is the lonchidiid *Parvodus* (Fig. 8A, B), here represented by a species close to *Parvodus celsucuspis* from the nearby Berriasian locality of Cherves-de-Cognac (Rees et al., 2013). It is also very similar to “*Hybodus*” *parvidens*, a widespread species of uncertain generic affinity that may belong to the genus *Parvodus* (Rees et al., 2013; Woodward, 1916). Teeth are small (generally not more than 5 mm in mesiodistal width) and the crown is ornamented by a few vertical folds and bears up to three pairs of lateral cusplets. The main cusp of the anterior teeth is high and slender (Fig. 8A), whereas lateral teeth are smaller and have a lower, more robust cusp and cusplets (Fig. 8B). This indicates that this species of *Parvodus* is characterized by a strong monognathic heterodonty, like *P. celsucuspis* (Rees et al., 2013).

The occurrence of a second taxon, the hybodontid *Planohybodus* (Fig. 8C), is established by the discovery of a few teeth characterized by their larger size, their

Table 1

List of vertebrate taxa from the Tithonian bonebeds of Chassiron, relative abundances (A: abundant; C: common; R: uncommon to rare), and catalogue numbers of figured specimens.

Tableau 1

Liste des taxons de vertébrés des *bonebeds* tithoniens de Chassiron, abondances relatives (A : abondant ; C : commun ; R : peu commun à rare) et numéros d'inventaire des spécimens figurés.

Taxa	Relative abundances	Catalogue numbers of figured specimens
Chondrichthyes		
<i>Parvodus</i> sp.	A	MO-CHA-1 (Fig. 8A) MO-CHA-2 (Fig. 8B) MO-CHA-3 (Fig. 8D) MO-CHA-4 (Fig. 8C)
<i>Planohybodus</i> sp.	R	
Osteichthyes		
<i>Scheenstia mantelli</i>	A	MO-CHA-5 (Fig. 9A) MO-CHA-6 (Fig. 9B) MO-CHA-7 (Fig. 9C) MO-CHA-8 (Fig. 9E) MO-CHA-9 (Fig. 9F)
Ionoscopiformes indet.	C	
Caturidae indet.	R	
Amiidae? indet.	R	MO-CHA-10 (Fig. 9D)
Ichthyodectidae indet.	C	MO-CHA-11 (Fig. 9G)
Pycnodontidae indet.	R	
Lissamphibia		
Albanerpetontidae indet.	C	MO-CHA-12 (Fig. 10A) MO-CHA-13 (Fig. 10B)
Caudata indet. (morph 1)	C	MO-CHA-14 (Fig. 11A) MO-CHA-15 (Fig. 11B)
Caudata indet. (morph 2)	C	MO-CHA-16 (Fig. 11C) MO-CHA-17 (Fig. 11D)
Anura	R	MO-CHA-18 (Fig. 10C) MO-CHA-19 (Fig. 10D)
Chelonii		
<i>Pleurosternon</i> sp.	C	MO-CHA-20 (Fig. 12B)
Pleurosternidae indet.	R	MO-CHA-21 (Fig. 12A)
Plesiochelyidae indet.	A	MO-CHA-22 (Fig. 12C) MO-CHA-23 (Fig. 12D)
cf. <i>Eurysternum</i> sp.	R	MO-CHA-24 (Fig. 12E)
Crocodyliformes		
<i>Steneosaurus</i> sp.	R	
<i>Goniopholis</i> sp.	C	MO-CHA-25 (Fig. 13A) MO-CHA-26 (Fig. 13B) MO-CHA-27 (Fig. 13C) MO-CHA-28 (Fig. 13D) MO-CHA-29 (Fig. 13E)
<i>Theriosuchus</i> cf. <i>pusillus</i>	C	MO-CHA-30 (Fig. 14A) MO-CHA-31 (Fig. 14B) MO-CHA-32 (Fig. 14C)
<i>Pholidosaurus</i> sp.	C	MO-CHA-33 (Fig. 14D)
<i>Bernissartia</i> sp.	C	MO-CHA-34 (Fig. 14E) MO-CHA-35 (Fig. 14F) MO-CHA-36 (Fig. 14G) MO-CHA-37 (Fig. 14H) MO-CHA-38 (Fig. 13F)
	Additional indeterminate crocodylian specimen:	
Dinosauria		
Stegosauridae indet.	R	MO-CHA-39 (Fig. 15A)
Iguanodontia indet.	R	MO-CHA-40 (Fig. 15B)
Spinosauridae indet.	R	MO-CHA-41 (Fig. 16A)
Megalosauridae? indet.	R	MO-CHA-42 (Fig. 16B)
Allosauroidae? indet.	R	
Dromaeosauridae indet.	R	MO-CHA-43 (Fig. 16C)
Troodontidae? indet.	R	MO-CHA-44 (Fig. 16D)
Sauropoda? indet.	R	
Pterosauria		
Rhamphorhynchidae indet. (morph 1)	R	MO-CHA-45 (Fig. 17A)
Rhamphorhynchidae? indet. (morph 2)	R	MO-CHA-46 (Fig. 17B)

Table 1 (Continued)

Taxa	Relative abundances	Catalogue numbers of figured specimens
Ctenochasmatidae (or Boreopteridae?) indet. (morph 3)	R	MO-CHA-47 (Fig. 17C)
Ctenochasmatidae (or Boreopteridae?) indet. (morph 4)	R	MO-CHA-48 (Fig. 17D)
Pterodactyloidea indet. (morph 5)	R	MO-CHA-49 (Fig. 17E)
Pterodactyloidea indet. (morph 6)	R	MO-CHA-50 (Fig. 17F)
Pterodactyloidea indet. (morph 7)	R	MO-CHA-51 (Fig. 17G)
	Additional indeterminate pterodactyloid specimen:	MO-CHA-52 (Fig. 17H)
Lepidosauria		
Squamata indet.	R	
Choristodera?		
<i>Cteniogenys?</i> sp.	R	MO-CHA-53 (Fig. 18)
Mammalia		
Multituberculata indet.	R	MO-CHA-54 (Fig. 19A)
Stem Cladotheria indet.	R	MO-CHA-55 (Fig. 19B)
Incertae sedis		
Vertebrata indet.	R	MO-CHA-56 (Fig. 20)

more densely folded crown, and at least one pair of well-developed lateral cusplets (a second, smaller pair can be present). *Planohybodus* teeth from Chassiron differ from those of the Purbeck–Wealden species *P. ensis* by its more developed labial ornamentation (i.e., vertical folds reaching up to half the height of the main cusp) (Bermúdez-Rochas, 2009).

Only one type of dorsal fin spines occurs at Chassiron. These spines (Fig. 8D) display an ornamentation consisting of a few well-marked longitudinal ridges, as observed in several Late Jurassic–Early Cretaceous hybodont taxa (Bermúdez-Rochas, 2009; Patterson, 1966; Rees et al., 2013; Woodward, 1916). The cephalic spines are also represented by a single morphotype at Chassiron. The basal plate shows three rounded lobes and a recurved crown displaying an apical barb and some strong, anastomosed basal folds. These cephalic and dorsal fin spines are especially

similar to those of *Parvodus celsucuspus* (Rees et al., 2013) and are therefore tentatively referred to *Parvodus* sp. Several morphotypes of dermal denticles (or placoid scales) are present. These denticles are ornamented and more or less compressed laterally; they represent the different morphotypes described by Rees (2002).

Parvodus and *Planohybodus* are both usual components of the elasmobranch faunas of the Purbeck–Wealden facies of western Europe (Ansoerge, 1990; Bermúdez-Rochas, 2009; Patterson, 1966; Underwood and Rees, 2002; Woodward, 1916).

3.3.2. Osteichthyans

Bony fishes are mostly represented by abundant teeth and ganoid scales of the ginglymodian *Scheenstia mantelli* (Fig. 9A–C), a lepisosteiform species previously referred to the “wastebasket” genus *Lepidotes* (López-Arbarello, 2012).

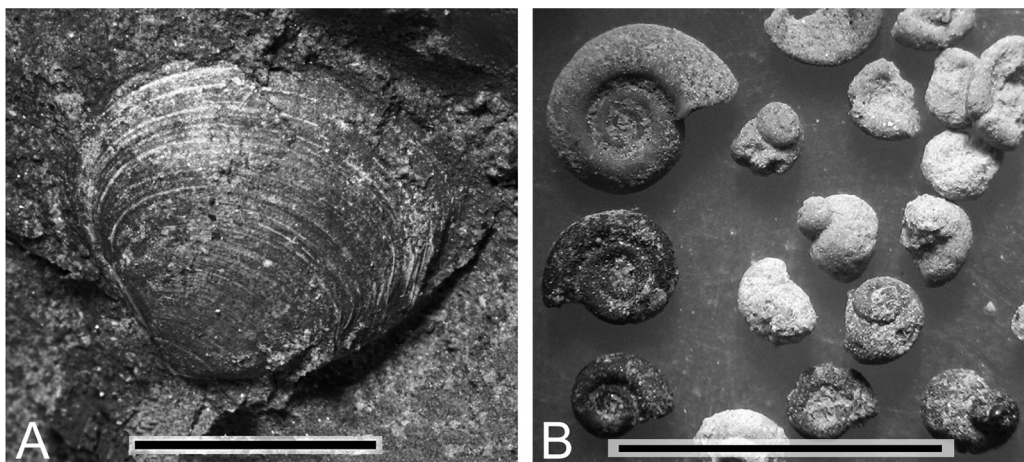


Fig. 7. Molluscs. A, Shell of the neomiodontid *Neomiodon*. B, Gastropod specimens including the planorbid *Gyraulys* (left) and the provalvatid *Provalvata* (right). Scale bars: 5 mm.

Fig. 7. Mollusques. A, Coquille du néomiodontidé *Neomiodon*. B, Spécimens de gastéropodes incluant le planorbidé *Gyraulys* (à gauche) et le provalvatidé *Provalvata* (à droite). Barre d'échelle : 5 mm.

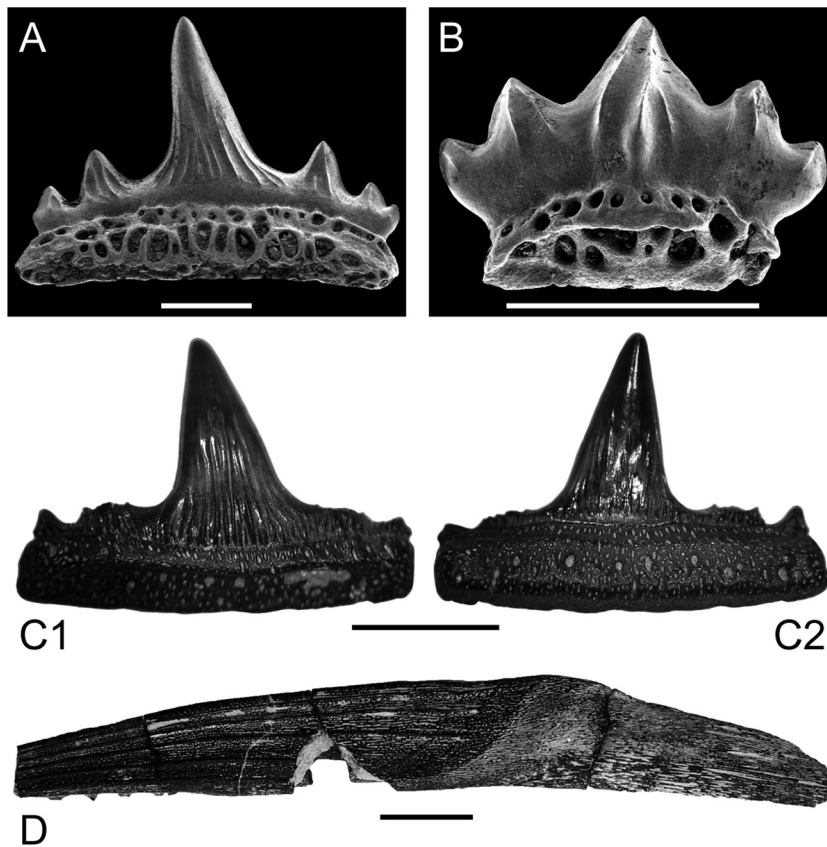


Fig. 8. Hybodont sharks. A, B, *Parvodus* sp.: anterior (A) and lateral (B) teeth in lingual and labial views, respectively. C, *Planohybodus* sp.: tooth in labial (C1) and lingual (C2) views. D, dorsal fin spine of hybodont shark (*Parvodus?* sp.) in lateral view. Scale bars: 1 mm (A, B), 5 mm (C) and 10 mm (D).

Fig. 8. Requins hybodontes. A, B, *Parvodus* sp.: dents antérieure (A) et latérale (B) en vues linguale et labiale, respectivement. C, *Planohybodus* sp.: dent en vues labiale (C1) et linguale (C2). D, épine de nageoire dorsale de requin hybodont (*Parvodus?* sp.) en vue latérale. Barres d'échelle : 1 mm (A, B), 5 mm (C) et 10 mm (D).

Teeth are typically hemispherical to conical and can reach up to 10 mm in diameter. Scales are rhomboid and the enamelled outer surface is smooth or ornamented with small tubercles.

A small edentulous jaw fragment is tentatively referred to an indeterminate amiid on the basis of the shape of the alveoli (oval to subrectangular) (Fig. 9D).

Tiny isolated teeth (Fig. 9F), as well as some minute toothed jaw fragments and small, thin, rhomboid ganoid scales (with sometimes a denticulate posterior margin; Fig. 9E) can be assigned to ionoscopiforms, including ionoscopids (*Ionoscopus*) and possible ophiopsids (*Ophiopsis*) (Woodward, 1918). Other microteeth indicate the presence of caturids (*Caturus*) and ichthyodectids (*Thrissops*) (Fig. 9G). In addition, some rare molariform, oval-shaped teeth indicate the presence of an indeterminate small pycnodontid. Most of these fish taxa are euryhaline forms, commonly found in the coastal marine to brackish environments of the Late Jurassic–Earliest Cretaceous (Rees, 2002; Thies and Mudroch, 1996).

3.3.3. Lissamphibians

3.3.3.1. *Allocaudatans*. Albanerpetontids are represented by fragments of maxillae and dentaries (Fig. 10A), one

incomplete humerus (Fig. 10B), and perhaps a fragment of frontal. On the dentaries, the opening for the Meckelian canal is restricted to the posterior portion of the bone. The surface that supports the tooth bases progressively rises posteriorly; as a result, posterior teeth are less tall than more anterior ones. Teeth are pleurodont, cylindrical, straight, non-pedicellate and closely spaced. On the posterior teeth, the preserved apices are conical, without any trace of accessory cusps (assuming they are not abraded). On more anterior fragments of dentaries, teeth are weakly tricuspid. The distal half of a humerus has a slender and straight diaphysis. The humeral condyle is well ossified and spherical. It is flanked by a large medial epicondyle and a smaller lateral one. The epicondyles do not reach the level of the distal limit of the humeral condyle. A triangular, elongate and well-defined cubital fossa extends on the diaphysis; a foramen opens at its proximal extremity.

The above described characters of the dentaries and humerus clearly support assignment to the Albanerpetontidae (e.g., Gardner et al., 2003). Only the morphology of the apices of the posterior teeth appears to be peculiar in lacking any distinct cuspid; if this does not result from abrasion, this character is certainly significant within the family.

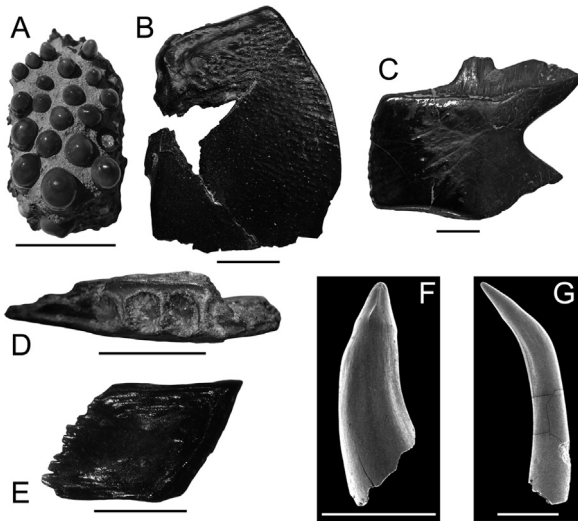


Fig. 9. Bony fishes. A–C, *Scheenstia mantelli*: jaw (A), opercular (B), scale (C). D, amiid?: jaw fragment. E–F, ionoscopiform: scale (E), tooth (F). G, *Thriassops* sp.: tooth. Scale bars: 1 mm (E–G), 5 mm (C, D) and 10 mm (A, B).
Fig. 9. Poissons osseux. A–C, *Scheenstia mantelli*: mâchoire (A), operculaire (B), écaille (C). D, amiid?: fragment de mâchoire. E–F, ionoscopiforme: écaille (E), dent (F). G, *Thriassops* sp.: dent. Barres d'échelle: 1 mm (E–G), 5 mm (C, D) et 10 mm (A, B).

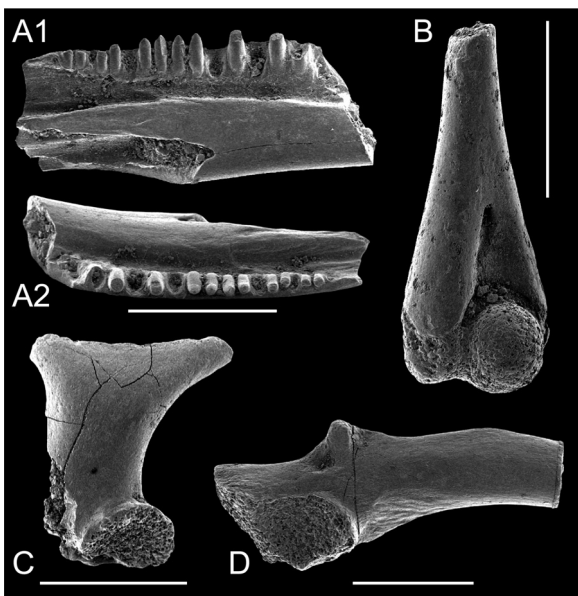


Fig. 10. Allocaudatan and anuran lissamphibians. A, B, Albanerpetontid: posterior part of dentary in lingual (A1) and occlusal (A2) views, distal part of humerus (B). C, D, anuran: scapula (C), ilium (D). Scale bars: 1 mm.
Fig. 10. Lissamphibiens Allocaudata et anoures. A, B, albanerpetontidé: partie postérieure de dentaire en vues linguale (A1) et occlusale (A2), partie distale d'humérus (B). C, D, anoure: scapula (C), ilion (D). Barre d'échelle: 1 mm.

Unfortunately, elements significant for identification at the genus level (premaxillae, frontals) are lacking.

Albanerpetontidae are primarily Laurasian amphibians that range from the Middle Jurassic (Bathonian) to the Early Pliocene. They lived in various environments, but they were

dependent on the presence of freshwater or at least moisture (Gardner and Böhme, 2008).

3.3.3.2. Caudatans. Numerous small atlantal vertebrae with posteriorly concave centra, amphicoelous vertebrae (Fig. 11) and perhaps some fragments of dentaries belong to salamanders. As mainly suggested by atlantal vertebrae, at least two morphs can be distinguished; they represent at least two taxa. In morphotype 1, the atlas is elongate and narrow, and dorsal vertebrae are lightly built and elongate (Fig. 11A, B). In morphotype 2, the atlas is shorter and wider, and dorsal vertebrae are more heavily built and relatively shorter (Fig. 11C, D). In both morphs, the ventral and dorsal rib-bearers are clearly separated from each other. In morphotype 1, the dorsal rib-bearer is clearly shifted posteriorly with regard to morphotype 2; this difference appears to be beyond intracolumnar variation. It is not possible to state securely whether spinal foramina are present. It should be noted that, in the atlas of the two morphs, the odontoid process is formed by the merging of the two anterior cotyles. A marked sagittal groove remains between the two parts. It runs on the dorsal, anterior and dorsal faces of the process; anteriorly, the groove is deep and the two halves of the process are markedly separated. The ventral face of the odontoid process of the salamandroid *Valdotriton* from the Early Cretaceous of Spain (Evans and Milner,

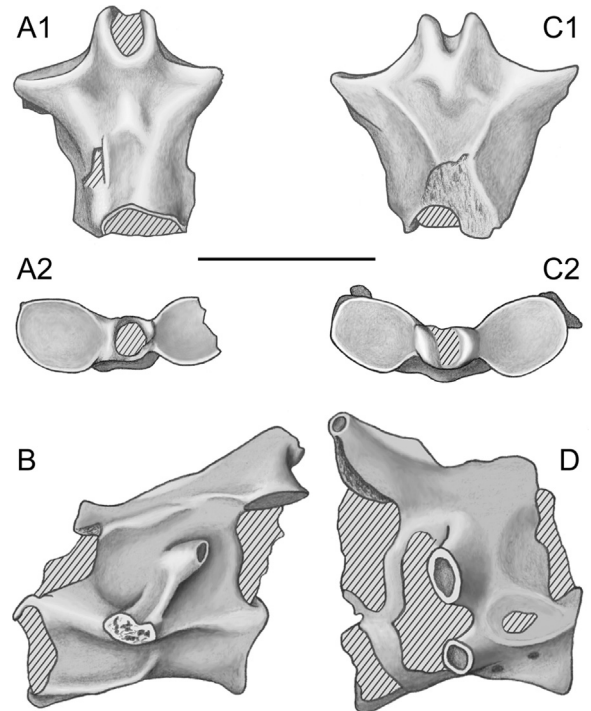


Fig. 11. Caudatan lissamphibians. A, B, Morphotype 1: atlas in ventral (A1) and anterior (A2) views, B, dorsal vertebra in left lateral view. C, D, morphotype 2: atlas in ventral (C1) and anterior (C2) views, D, dorsal vertebra in right lateral view. Scale bar: 1 mm.

Fig. 11. Lissamphibiens urodèles. A, Morphotype 1: atlas en vues ventrale (A1) et antérieure (A2). B, vertèbre dorsale en vue latérale gauche. C, D, morphotype 2: atlas en vues ventrale (C1) et antérieure (C2), D, vertèbre dorsale en vue latérale droite. Barre d'échelle: 1 mm.

1996) displays a similar morphology and *Kiyatriton* from the Early Cretaceous of Russia is more or less reminiscent of this condition (Averianov and Voronkevich, 2002). The odontoid process lacks articular facets of its own in both morphs. The ventral face of the atlas of the shorter morph is clearly limited laterally, which is somewhat reminiscent of the midventral ridge reported in *Apricosiren* from the Earliest Cretaceous of England (Evans and McGowan, 2002).

The two forms from Chassiron differ from *Kiyatriton*. However, the only difference between *Valdotriton* and the elongate form from Chassiron is the presence of spinal foramina in a part of the caudal region in the Spanish taxon. Because vertebrae from Chassiron are isolated, this character cannot be confidently checked. The two morphs from Chassiron are easily distinguished from *Apricosiren*: in the latter, the atlantal odontoid process is markedly depressed and it lacks a sagittal groove. Where comparisons are possible, the two fossils from Chassiron differ from other Jurassic salamanders. More specifically, they differ from *Marmor-erpeton* (Bathonian; Evans et al., 1988), the only named Jurassic salamander from Europe, the odontoid process of which has no sagittal groove and whose dorsal vertebrae are more massive. These salamanders required at least moisture, or more likely freshwater.

3.3.3.3. *Anurans*. Two humeri suggest that two distinct anurans may be present. In one form, the humeral condyle is in line with the diaphysis and the medial epicondyle extends almost to the distal border of the condyle. In the other form, the condyle is slightly shifted laterally and the medial epicondyle does not approach the distal part of the condyle. One scapula (Fig. 10C) preserves a tall *pars suprascapularis*, which is surprising in this early frog because in basal anurans this part of the scapula is generally short or sometimes mid-sized. A single available ilium (Fig. 10D) lacks a dorsal crest but bears a well-developed, triangular *tuber superius*; the morphology of this ilium appears to be peculiar. Several incomplete maxillae are also assigned to anurans.

If two forms are present, the proper association of bones cannot be determined. The environmental requirements were likely similar to those of the above reported salamanders.

3.3.4. Turtles

Turtle remains are abundant in the Early Tithonian deposits of Chassiron, represented mainly by isolated shell plates; some limb and girdle bones and vertebrae are also present. They belong to the paracryptodiran Pleurosternidae and eucryptodiran Plesiochelyidae (*s.l.*).

3.3.4.1. *Pleurosternids*. A dozen more or less complete isolated shell plates, including one neural 8, one suprapygal 2 (Fig. 12B), several peripherals and costals have their outer surface covered with small, clearly defined and relatively regular cupules. Clear striations perpendicular to the margins are visible close to the border of the plate; they are characteristic of Pleurosternidae. The ornamentation of regular cupules is similar to that of the pleurosternids *Pleurosternon bullockii* from the Purbeck Limestone Group of Dorset, England (Lydekker and Boulenger, 1887; Milner,

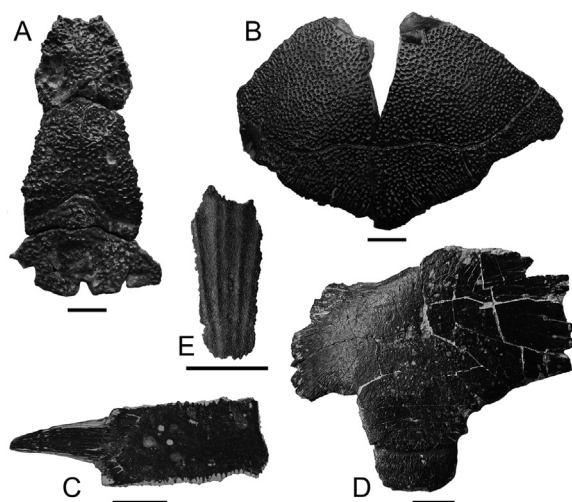


Fig. 12. Turtles. A, Pleurosternid: neural 8 and suprapygals 1–2. B, *Pleurosternon* sp.: suprapygal 2. C, D, plesiochelyid: costal (C), right hyoplastron (D). E, plesiochelyid cf. *Eurysternum*: neural. Scale bars: 10 mm.

Fig. 12. Tortues. A, Pleurosternid: neurale 8 et suprapygales 1–2. B, *Pleurosternon* sp.: suprapygale 2. C, D, plésiochélyidé: costale (C), hyoplastron droit (D). E, plésiochélyidé cf. *Eurysternum*: neurale. Barres d'échelle: 10 mm.

2004; Owen, 1853) and *Selenemys lusitanica* from the Late Kimmeridgian of the Lusitanian Basin, Portugal (Pérez-García and Ortega, 2011). As in *P. bullockii* and *S. lusitanica*, the vertebral scutes are wide, the lateral marginal scutes extend onto the costal plates and the marginal scutes 11 and 12 cover the posterior part of the suprapygal 2. The intervertebral sulcus between the vertebrae 4 and 5 is located on neural 8 as in *P. bullockii*, unlike *S. lusitanica* in which this sulcus is situated on suprapygal 1 (Pérez-García and Ortega, 2011). These turtle remains seem to be more similar to *P. bullockii* than to *S. lusitanica*, they are tentatively assigned to *Pleurosternon* sp.

A partial skeleton includes a neural 8, a suprapygal 1, an incomplete suprapygal 2 (Fig. 12A), several peripherals and costals, a partial left hyoplastron and mesoplastron, girdle and limb bones and caudal vertebrae. The pelvic girdle is of cryptodire type and unattached to the shell. The outer surface of the shell is covered with a strong ornamentation. Parallel striations perpendicular to the margins are visible on the border area of the hyoplastron and mesoplastron. The well-defined cupules are coarser and more irregular than those of *P. bullockii*, *S. lusitanica* and *Pleurosternon* sp. from the same locality mentioned above. They also differ from the ornamentation composed of vermiculated ridges seen in pleurosternids *Glyptops plicatulus*, *Compsemys victa* and *Berruchelus russelli* and from the radiating plications in *Desmemys bertelsmanni*. In Solemydidae, the shell surface is covered either with vermiculated crests or isolated pustules (Gaffney, 1979; Joyce et al., 2011; Milner, 2004; Pérez-García, 2012; Pérez-García and Ortega, 2011; Wegner, 1911). The mesoplastron is a large plate, though damaged on both medial and lateral ends; when complete, it would meet its counterpart at the midline. The morphology of this plate is reminiscent of some primitive turtles

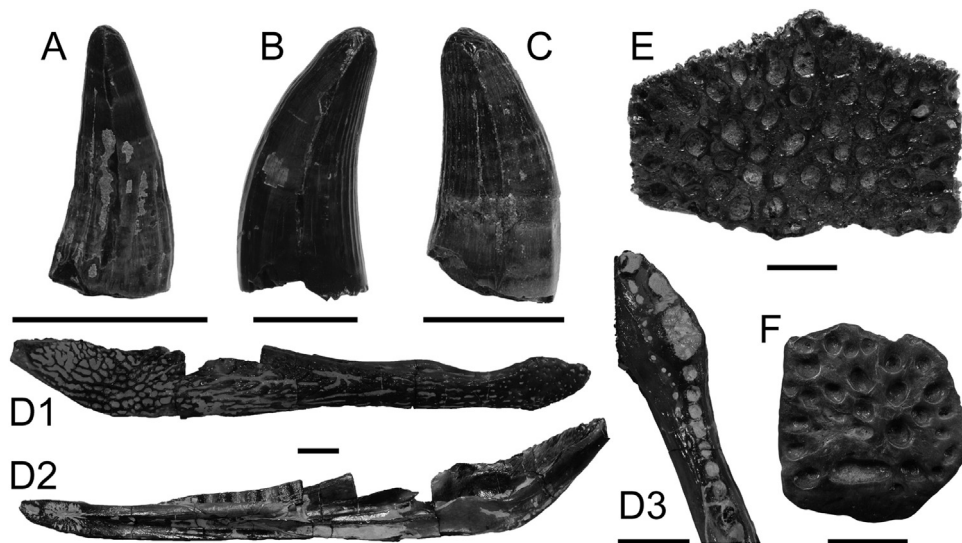


Fig. 13. Crocodylians. A–E, *Goniopholis* sp.: teeth (A–C) in mesiodistal view, mandible (D) in lateral (D1) and medial (D2) views (D3: anterior part in dorsal view), osteoderm (E). F, indeterminate crocodylian osteoderm. Scale bars: 10 mm.

Fig. 13. Crocodyliens. A–E, *Goniopholis* sp. : dents (A–C) en vue mésiodistale, mandibule (D) en vues latérale (D1) et médiale (D2) (D3 : partie antérieure en vue dorsale), ostéoderme (E). F, ostéoderme de crocodylien indéterminé. Barres d'échelle : 10 mm.

known in the Jurassic and Cretaceous of Europe, such as Pleurosternidae and Solemydidae. This is a moderate sized turtle, with a carapace length estimated at about 30 cm. The specimen is a juvenile or neotenic individual, with lateral fontanelles present on both the carapace and plastron, as indicated by the free medial margin of the dorsal and ventral sheets of bridge peripherals. It is referable as to Pleurosternidae and probably represents a new taxon.

3.3.4.2. Plesiochelyid (*s.l.*). Isolated shell plates of Plesiochelyidae (*s.l.*) with a smooth surface are by far the most abundant elements in the Chassiron locality. Isolated neurals, costals, peripherals as well as plastral elements are preserved. The neurals are elongate and narrow with a flat outer surface. The costal plates, even when of relatively large size, have a free lateral border and a free distal rib end (Fig. 12C). The lateral peripherals are slender with a free medial margin. The morphology of the costal and peripheral plates indicates that lateral carapacial fontanelles remained in individuals of relatively large size. Some features such as the short and broad peripheral 1, the relatively wide vertebral scutes and the vertebral 1 which is clearly narrower than other vertebrals closely resemble *Thalassemys* *moseri* known from the Tithonian of Oléron Island and from the Late Kimmeridgian of Solothurn, Switzerland (Bräm, 1965; Rieppel, 1980). The plastral elements (one hyoplastron, three hypoplasra and one xiphiplastron), of several individuals of small size, all belong to juveniles (Fig. 12D). Large midline and lateral fontanelles are present on the plastron, and reminiscent of Eurysternidae, such as *Eurysternum*, *Idiochelys*, *Solnhofia* (Joyce, 2000); however, this may represent a juvenile feature in *T.* *moseri*. The systematic position of this taxon is uncertain (Lapparent de Broin et al., 1996), and the whole group of Plesiochelyidae (*s.l.*) needs a thorough revision.

Some elements, recently discovered, attest to the presence of a second taxon of Plesiochelyidae (*s.l.*), distinct from *Thalassemys* *moseri*. They mostly consist of isolated neural and costal plates that indicate the presence of lateral carapacial fontanelles. Unlike *Thalassemys*, the vertebral scutes are wide and display a peculiar radiating pattern, visible on neural plates (Fig. 12E) and proximal part of costal plates. These features can be found in *Eurysternum*, known from the Late Jurassic of Germany and France (Broin, 1994; Joyce, 2003; Meyer, 1839). The second plesiochelyid (*s.l.*) taxon of Chassiron is probably close to this genus.

The turtle fauna from Chassiron includes freshwater turtles (Pleurosternidae) and shallow marine turtles (Plesiochelyidae *s.l.* and Eurysternidae). This assemblage presents close affinities with the turtle faunas from the Late Jurassic–Early Cretaceous of the western margin of Europe, in particular that of the Purbeck Limestone Group of England. The good preservation of the isolated shell plates and partial skeleton of pleurosternids indicate a short transport of these elements, thus suggesting that the Chassiron locality was located close to the land.

3.3.5. Crocodylians

3.3.5.1. Teleosaurids. A few teeth (crown height ranging from 8 to 18 mm) of the thalattosuchian genus *Steinosaurus* have been collected. They have a slender, slightly sigmoid crown ornamented with numerous, fine longitudinal ridges. Carinae are very weak or absent. Such teeth (morphotype A3 *sensu* Vignaud, 1997) correspond to a longirostrine species. For instance, this dental morphotype is found in *S. priscus* from the Tithonian of western Europe (Vignaud, 1997). The smallest teeth (less than 10 mm) present in the Chassiron material would indicate the presence of juvenile individuals.

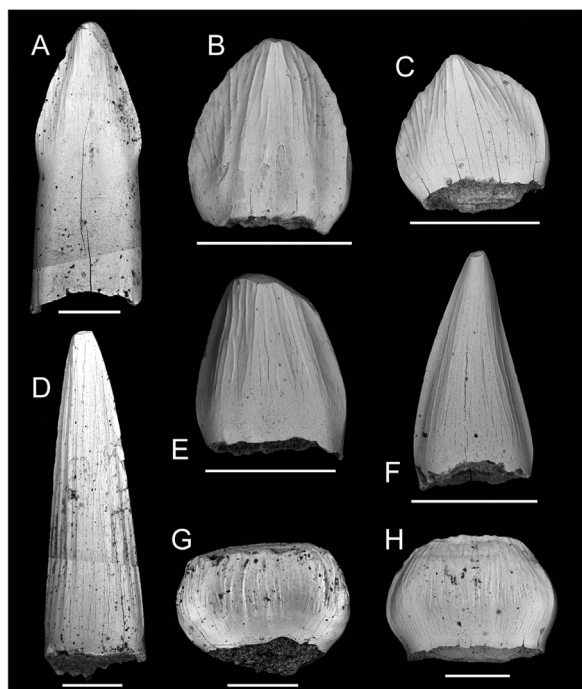


Fig. 14. Crocodylians. A–C, *Theriosuchus* cf. *pusillus*: teeth. D, *Pholidosaurus* sp.: tooth. E–H, *Bernissartia* sp.: teeth. All specimens in lingual view. Scale bars: 1 mm.

Fig. 14. Crocodyliens. A–C, *Theriosuchus* cf. *pusillus*: dents. D, *Pholidosaurus* sp.: dent. E–H, *Bernissartia* sp.: dents. Tous les spécimens en vue linguale. Barres d'échelle: 1 mm.

3.3.5.2. Goniopholidids. The Chassiron bonebeds have yielded numerous teeth of the goniopholidid *Goniopholis*. Their robust, conical crown is ornamented with regular vertical wrinkles (Fig. 13A–C). In addition, an edentulous lower jaw (Fig. 13D), vertebral centra and rather large osteoderms (Fig. 13E) can be assigned to this genus (Owen, 1878, 1879; Salisbury, 2002). Smaller, thinner osteoderms (Fig. 13F) might belong to goniopholidids, but could also be assigned to the other neosuchian taxa described below.

3.3.5.3. Atoposaurids. The family Atoposauridae (Fig. 14A–C) is characterized by lanceolate to leaf-shaped crowns, labiolingually compressed and mesiodistally stretched, with two mesial and distal sharp carinae. Enamel ornamentation, more pronounced on the lingual face, is made of vertical wrinkles diverging toward the carinae, giving these carinae a more or less festooned edge. These teeth can be referred to the genus *Theriosuchus*. Three *Theriosuchus* species are known in the European Late Jurassic and Early Cretaceous: *T. pusillus*, *T. ibericus*, and *T. guimarotae* (Brinkmann, 1992; Owen, 1879; Schwarz and Salisbury, 2005). According to the pronounced heterodonty and the carinae moderately festooned, the specimens from Chassiron can be referred to *Theriosuchus* cf. *pusillus* (Owen, 1879; Salisbury, 2002; Schwarz and Salisbury, 2005). *Theriosuchus* seems to have been common in western Europe during the Late Jurassic and Early Cretaceous (see Schwarz-Wings et al., 2009).

3.3.5.4. Pholidosaurids. The family Pholidosauridae (Fig. 14D) is represented by several teeth showing a more slender conical crown that is lingually curved. The enamel is ornamented with regular vertical wrinkles running from the base to the apex of the crown, as the two weak carinae. These teeth can be referred to the genus *Pholidosaurus*, which is known from the Purbeck and Wealden facies of southern England (Salisbury, 2002), southwestern France (Mazin and Pouech, 2008), Germany, and Denmark (Bonde, 2004).

3.3.5.5. Bernissartiids. The family Bernissartiidae (Fig. 14E–H) is represented by numerous tribodont teeth classically referred to Bernissartiidae indet. or *Bernissartia* sp. (Brinkmann, 1992; Buffetaut and Ford, 1979; Cuny et al., 1991). The crown is low, rounded, labiolingually compressed, and elliptic to kidney-shaped in apical view, with a constriction at the root–crown contact. The enamel ornamentation is made of strong parallel vertical wrinkles. These bulbous isolated crowns correspond to the posterior teeth of bernissartiids (Fig. 14G–H). Teeth showing the same ornamentation and two mesial and distal well-marked carinae, but with higher or conical crown, are also found as microremains (Fig. 14E–F). They should correspond to more anterior teeth of the typical heterodont dentition of the bernissartiids. Bernissartiid macroremains are not common since only three specimens have been described from the Early Cretaceous of Europe (Buffetaut, 1975; Buscalioni and Sanz, 1990; Buscalioni et al., 1984; Dollo, 1883). However, isolated teeth referred to this family show a higher stratigraphical extension and geographical range since they are described from the Kimmeridgian to the Barremian, and from Portugal, Spain, France, Belgium, England, Denmark (see Schwarz-Wings et al., 2009). In northern Africa, a possible bernissartiid tooth have been reported from the Albian of Tunisia (Cuny et al., 2010).

3.3.6. Dinosaurs

Dinosaurs are represented at Chassiron by a few skeletal remains and abundant teeth.

Skeletal remains include a fragment of a large bone indicating an animal of large size. The only observable character is a fairly marked compression, which suggests that it may be a fragment of a rib or a neural spine. This specimen is referred to Dinosauria because of its size, but its state of preservation does not allow a more accurate identification. Several vertebrae are present in the collection, some referable to ornithopods, others to theropods (see below). The most abundant dinosaur remains at Chassiron are isolated teeth, showing various types of preservation, from more or less worn fragments to complete specimens. Three groups have been identified on the basis of unambiguous specimens: Stegosauria, Ornithopoda and Theropoda. In addition, a tooth fragment can be tentatively referred to Sauropoda indet.

3.3.6.1. Stegosauria. Stegosaurids are represented by a single tooth (Fig. 15A). The crown is separated from the root by a well-marked constriction. A strong cingulum is present at the base of the crown on both the labial and the lingual

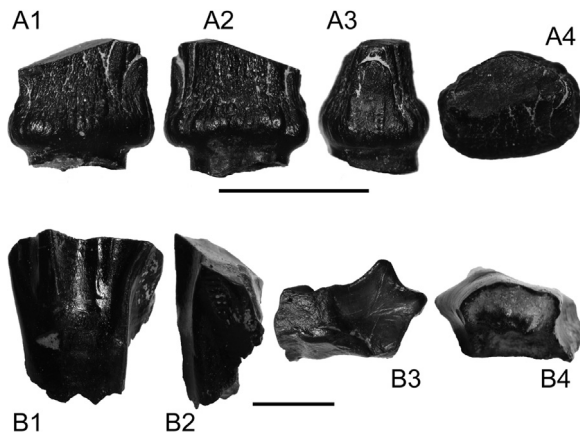


Fig. 15. Ornithischian dinosaurs. A, Stegosaurid: tooth in labial (A1), lingual (A2), mesiodistal (A3) and apical (A4) views. B, Iguanodont: dentary tooth in labial (B1), mesiodistal (B2), apical (B3) and basal (B4) views. Scale bars: 5 mm.

Fig. 15. Dinosaures ornithischiens. A, Stégosauridé : dent en vues labiale (A1), linguale (A2), mésiodistale (A3) et apicale (A4). B, Iguanodonte : dent inférieure en vues labiale (B1), mésiodistale (B2), apicale (B3) et basale (B4). Barres d'échelle : 5 mm.

faces. Above, the crown shows a strong fluting, with broad ridges which are especially distinct and divergent at the mesial and distal ends of the tooth. They end in strong denticles, which however are no longer visible along most of the apical part of the tooth because of strong wear resulting in an oblique facet. This tooth shows all the distinctive characters of stegosaurid teeth, and seems especially reminiscent of *Stegosaurus* from the Late Jurassic of North America (Galton and Upchurch, 2004). It is also similar to the single tooth recently described from the Berriasian of Cherves-de-Cognac (Billon-Bruyat et al., 2010), but the latter has a more pronounced cingulum.

3.3.6.2. Ornithopoda. This group is represented by a few, very worn dental remains, obviously shed in the course of tooth replacement (Fig. 15B). These specimens show both an extremely advanced resorption of the root and a very broad apical wear facet, so that both the apical area and the basal region are markedly concave. On some slightly less worn specimens, one of the faces shows ridges which slightly diverge toward the apex; two of them, in respectively mesial and distal positions, are more strongly marked and bracket other, weaker, ridges. Similar specimens were described as early as 1825 by Mantell from the Wealden of England and identified as worn *Iguanodon* teeth. However, it should be noted that worn teeth of *Camptosaurus*, from the Late Jurassic of the United States (Gilmore, 1909), are also morphologically very close to the specimens from Chassiron. The characters of the ornithopod teeth from Chassiron therefore lead to identify them as Iguanodontia indet.

A few isolated vertebral centra, lacking the neural arch, are platycoelous, with a more or less marked constriction of the centrum, subrectangular articular faces and small facets for the chevron bones. They may belong to small ornithopods.

3.3.6.3. Theropoda. This group of dinosaurs is by far the most abundantly represented at Chassiron, by numerous teeth which can be divided into several morphotypes, possibly corresponding to four families:

Spinosauridae (Fig. 16A): this family is represented by a tooth crown which is weakly compressed mediolaterally and shows well-marked ridges on the lingual face, whereas the labial face is much less ornamented. The carinae bear fairly large denticles (3 denticles per mm) and the enamel is finely wrinkled. This tooth closely resembles some specimens from Tendaguru (Latest Jurassic of Tanzania) considered by Buffetaut (2008) as belonging to basal spinosaurids, and redescribed as *Ostafrikasaurus crassiserratus* (Buffetaut, 2013). It is therefore referred to this family.

Megalosauridae? (Fig. 16B): several relatively large teeth (crown height reaching several centimetres) are strongly compressed labiolingually and show distinctly denticulated mesial and distal carinae (2 to 3 denticles per mm). Interdental sulci are present. The mesial carina extends over only part of the height of the crown (1/3 to 1/2 depending on the specimens). The mesial margin is convex, the distal margin is slightly concave. The enamel is very finely shagreened and some specimens show transversal wrinkles, concave toward the apex, on the faces of the crown. The morphology of these teeth is strongly reminiscent of that of *Megalosaurus* teeth, and they are tentatively referred to the family Megalosauridae. A few fragments indicating significantly larger teeth show generally similar features. As more complete specimens, which might exhibit significant differences, are not available, these fragments are also referred with caution to the Megalosauridae. It must be noted that some of these large teeth might also belong to another basal tetanuran clade, such as the Allosauroidea.

Dromaeosauridae (Fig. 16C): several small teeth (crown height usually not exceeding 10 mm) have a crown that is strongly compressed labiolingually and recurved, with a very convex mesial margin and a markedly concave distal margin. The distal carina bears distinct denticles (about 4 per mm), whereas the mesial carina either is devoid of denticles or bears very small ones. These teeth show the morphological characters of Dromaeosauridae. A few small teeth from Chassiron have a D-shaped cross-section and may be from the premaxillae of Dromaeosauridae.

Troodontidae? (Fig. 16D): some small teeth from Chassiron have an approximately straight, rather than concave, distal margin, bearing fairly large denticles, whereas the mesial margin is rounded, not forming a carina. These specimens may belong to the Troodontidae (cf. Rauhut, 2000).

A few small posterior caudal vertebrae, with an elongate and laterally compressed centrum, may belong to indeterminate theropods.

3.3.6.4. Sauropoda?. A small tooth fragment, 5.5 mm long, shows a slight curvature and a thick enamel layer (~0.5 mm). The enamel surface is irregular and displays some small, shallow pits. These features suggest that this specimen can be referred to an indeterminate sauropod.

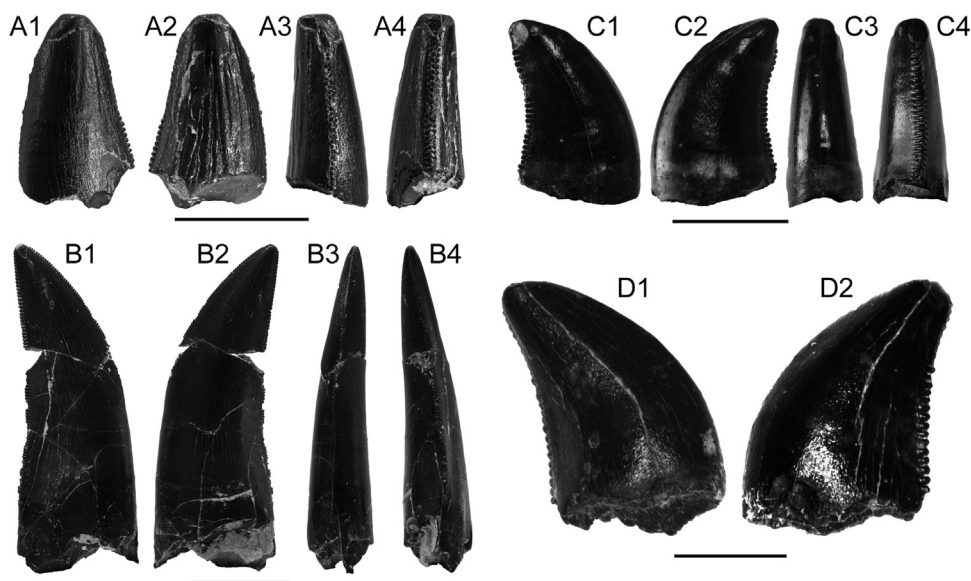


Fig. 16. Saurischian dinosaurs. A, Spinosaurid: tooth in labial (A1), lingual (A2), mesial (A3) and distal (A4). B, Megalosaurid?: tooth in labiolingual (B1, B2), mesial (B3) and distal (B4) views. C, Dromaeosaurid: tooth in labiolingual (C1, C2), mesial (C3) and distal (C4) views. D, Troodontid?: tooth in labiolingual (D1, D2) views. Scale bars: 1 mm (D), 5 mm (C) and 10 mm (A, B).

Fig. 16. Dinosaures saurischiens. A, Spinosauridé : dent en vues labiales (A1), linguales (A2), mésiales (A3) et distales (A4). B, Mégalosauridé ? : dent en vues labiolinguales (B1, B2), mésiales (B3) et distales (B4). C, Dromaeosauridé : dent en vues labiolinguales (C1, C2), mésiales (C3) et distales (C4). D, Troodontidé ? : dent en vues labiolinguales (D1, D2). Barres d'échelle : 1 mm (D), 5 mm (C) et 10 mm (A, B).

The dinosaur assemblage from Chassiron, which mainly consists of isolated teeth, probably does not provide a complete image of the Late Jurassic dinosaurian fauna in the region in question, because some important groups could not be identified (e.g., Ankylosauria) or definitely recognized (e.g., Sauropoda). The available specimens nevertheless reflect some diversity, especially among the theropods (note that the present study is only preliminary; to obtain more accurate identifications, it will be necessary to use various morphological and morphometric methods, such as those used by Cillari, 2010). The theropod assemblage shows similarities with Late Jurassic faunas, especially that from the Kimmeridgian of Guimarota, in Portugal (Rauhut, 2000). It is also similar to the Tithonian–Berriasian assemblage from Riodeva, in Spain (Gascó et al., 2012). The basal spinosaurid is an especially interesting find, suggesting similarities with the more or less coeval fauna from Tendaguru. The occurrence of an iguanodont is also notable, even though its exact systematic position remains uncertain and it is not possible to decide whether it is more closely related to Late Jurassic or to Early Cretaceous forms, because of the advanced wear of the available teeth. The discovery of a stegosaur tooth at Chassiron is also worth noting because this group is poorly represented in the French dinosaur record. On the whole, the dinosaur assemblage from Chassiron is in good agreement with the Late Jurassic age of the locality. However, it is worth noting that a similar dinosaur assemblage has been recovered from the Earliest Cretaceous (Berriasian) deposits of the Cherves-de-Cognac locality (Mazin et al., 2006, 2008), indicating that no major faunal changes occurred among dinosaurs during the Jurassic–Cretaceous transition.

3.3.7. Pterosaurs

Pterosaurs are represented at Chassiron by numerous teeth and a few bone fragments. The discovery of seven dental morphotypes indicates the presence of at least four groups.

Rhamphorhynchidae are represented by a few slender, labiolingually compressed, slightly curved teeth (morphotype 1: Fig. 17A) that do not exceed 10 mm in height. Mesial and distal carinae are present. Larger teeth (up to 20 mm high) of similar morphology (morphotype 2: Fig. 17B) may also belong to this family, but are also reminiscent of those of pterodactyloids such as ornithocheirids (*s.l.*) (Vullo, 2001; Vullo et al., 2009). Because similar teeth are present in some large rhamphorhynchid taxa (Andres et al., 2010; Averianov et al., 2005), the occurrence of ornithocheirids (*s.l.*) at Chassiron cannot be confirmed without more diagnostic material. Therefore, the dental morphotype 2 is tentatively referred to Rhamphorhynchidae indet.

The largest teeth found at Chassiron are broken apically and may have originally reached up to 30 mm in height (morphotype 3: Fig. 17C). They are slightly curved, oval to circular in cross-section, and devoid of carinae. Such teeth are present in ctenochasmatids (Martill et al., 2011; Sweetman and Martill, 2010) and boreopterids (Lü, 2010: pl. 1b). Ctenochasmatid pterosaurs are known in the Purbeck Group of southern England with the genus *Plataleorhynchus*, the teeth of which are unfortunately not preserved on the single specimen known to date (Howse and Milner, 1995). Another type of slender teeth (morphotype 4: Fig. 17D), much smaller (less than 5 mm high), is common at Chassiron. Like teeth of the morphotype 3, they display a lingually curved crown and a circular cross-section, but mesial and distal carinae are present here. The

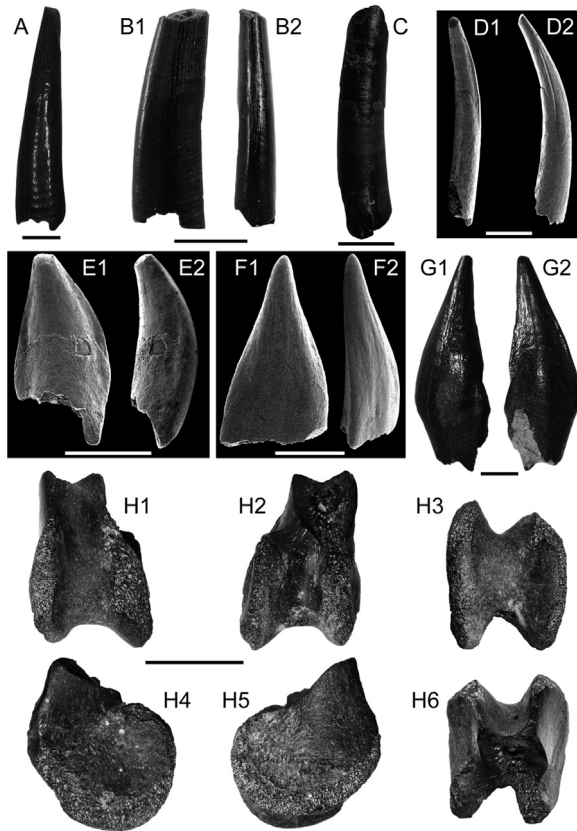


Fig. 17. Pterosaurs. A, Rhamphorhynchid: tooth morphotype 1 in labial view. B, Rhamphorhynchid?: tooth morphotype 2 in labial (B1) and mesial (B2) views. C, Ctenochasmatid (or boreopterid): tooth morphotype 3 in lingual view. D, Ctenochasmatid (or boreopterid): tooth morphotype 4 in lingual (D1) and mesiodistal (D2) views. E, Pterodactyloid: tooth morphotype 5 in lingual (E1) and mesial (E2) views. F, Pterodactyloid: tooth morphotype 6 in labial (F1) and distal? (F2) views. G, Pterodactyloid: tooth morphotype 7 in labial (G1) and lingual (G2) views. H, Pterodactyloid?: distal extremity of left metacarpal IV in anterior (H1), posterior (H2), distal (H3), dorsal (H4), ventral (H5) and proximal (H6) views. Scale bars: 1 mm (A, D–G), 5 mm (B, C) and 10 mm (H).

Fig. 17. Ptérosaures. A, Rhamphorhynchidé: morphotype dentaire 1 en vue labiale. B, Rhamphorhynchidé?: morphotype dentaire 2 en vues labiale (B1) et mésiale (B2). C, Cténochasmatidé (ou boréoptéridé?): morphotype dentaire 3 en vue linguale. D, Cténochasmatidé (ou boréoptéridé?): morphotype dentaire 4 en vues linguale (D1) et mésiodistale (D2). E, Ptérodactyloïde: morphotype dentaire 5 en vues linguale (E1) et mésiale (E2). F, Ptérodactyloïde: morphotype dentaire 6 en vues labiale (F1) et distale? (F2). G, Ptérodactyloïde: morphotype dentaire 7 en vues labiale (G1) et linguale (G2). H, Ptérodactyloïde?: extrémité distale de métacarpien IV gauche en vues antérieure (H1), postérieure (H2), distale (H3), dorsale (H4), ventrale (H5) et proximale (H6). Barres d'échelle: 1 mm (A, D–G), 5 mm (B, C) et 10 mm (H).

enamelled part of the tooth shows a few slight longitudinal folds. This morphotype occurs in the Middle Jurassic (Bathonian) of England and was assigned to an indeterminate “rhamphorhynchoid” (Metcalf et al., 1992: fig. 10i). Like the previous morphotype, the morphotype 4 could also represent ctenochasmatids or boreopterids.

Lastly, the morphotypes 5 to 7 (Fig. 17E–G) include small, short, labiolingually compressed teeth. The crown is triangular in lateral view and displays an apex that is more or less slender and sigmoidal. Distal and mesial carinae are

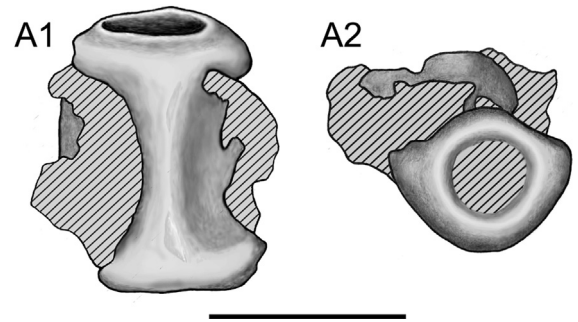


Fig. 18. Choristoderes?. *Cteniogenys?* sp.: dorsal vertebra in ventral (A1) and posterior? (A2) views. Scale bar: 1 mm.

Fig. 18. Choristodères?. *Cteniogenys?* sp.: vertèbre dorsale en vues ventrale (A1) et postérieure? (A2). Barre d'échelle: 1 mm.

present. Similar teeth have been described in Late Jurassic and Early Cretaceous pterodactyloids known by complete skeletons, such as *Pterodactylus*, *Germanodactylus*, *Hapterus* and various istiodactylids (Lü et al., 2008; Wang et al., 2008). Interestingly, an isolated tooth identical to the dental morphotype 6 has been recently described from the Valanginian–Hauterivian of northeastern Spain (Gasca et al., 2012: fig. 3k). Similarly, Bakker (1998) described from the Tithonian of Wyoming a pterosaur jaw fragment bearing teeth reminiscent of the dental morphotype 7.

An extremely well-preserved distal extremity of a left wing metacarpal (metacarpal IV) has been found (Fig. 17H). It corresponds to a rather large pterosaur (wingspan ~2.5–3 m). It is similar in size and shape to the wing metacarpal described by Martill et al. (2013) from the Purbeck Group of southern England and regarded as a possible azhdarchid.

In addition, a few centimetric mid-shaft portions of long bones have been collected. They are almost straight, oval in cross-section, thin-walled, and display no internal trabecular structures. These non-diagnostic shaft fragments are similar to the specimen originally described as *Ornithocheirus nobilis* (*nomen dubium*) (Sweetman and Martill, 2010: fig. 4).

3.3.8. Squamates

A procoelous trunk vertebra and fragments of bones bearing teeth belong to indeterminate pleurodont lizards.

3.3.9. Choristoderes?

An amphicoelous vertebral centrum is tentatively assigned to a choristodere, as suggested by the thick rims of the two cotyles (Fig. 18). It resembles those of *Cteniogenys* from the Middle Jurassic of Britain (Evans, 1991). Small jaw fragments bearing thecodont teeth might also belong to this taxon. The genus ranges from the Bathonian to the Kimmeridgian–Tithonian on the European–North American block. However, it was also reported, with caution, from the Late Cretaceous (Campanian) of North America (Gao and Brinkman, 2005). *Cteniogenys* lived in shallow fresh-water environments.

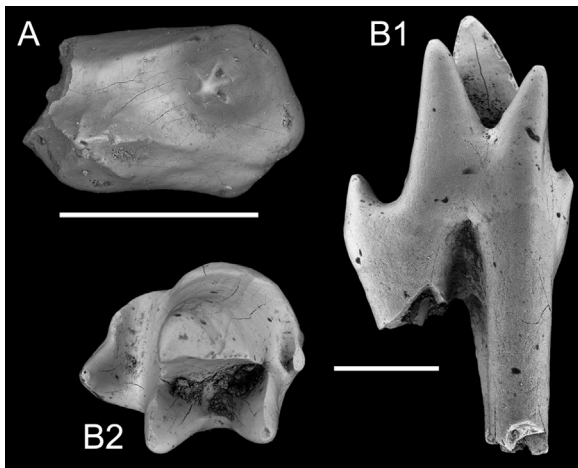


Fig. 19. Mammals. A, multituberculata: anterior upper tooth in occlusal view. B, stem cladotherian: left lower molar in lingual (B1) and occlusal (B2) views. Scale bars: 500 μ m.

Fig. 19. Mammifères. A, Multituberculé : dent supérieure antérieure en vue occlusale. B, Cladotherien basal : molaire inférieure gauche en vues linguale (B1) et occlusale (B2). Barres d'échelle : 500 μ m.

3.3.10. Mammals

Among all the vertebrate microremains collected at Chassiron, seven specimens can be attributed to mammals, which is the first report in the Jurassic of France. At least two groups can be identified, each being represented by two or three complete or fragmentary teeth.

Allotherian mammals are represented by two teeth. Both specimens display clear enamel ornamentation, made of ridges radiating from the apex of the well-individualized cusps. The first tooth (Fig. 19A) is an almost complete small crown, subrectangular in occlusal view, without root. The presence of only two subequal, well-differentiated and ornamented cusps suggests an upper anterior tooth (first premolars) of an indeterminate multituberculata. The second specimen is a single little cusp on a root fragment, and could be part of a multituberculata incisor.

Stem cladotherian mammals (former “eupantotherians”) are represented by three teeth. The best-preserved specimen, a left lower molar (Fig. 19B), shows an excellent state of preservation. The trigonid, composed of three well-developed, thin and acute cusps, as well as the talonid, well-differentiated but single-cusped and basin-less, suggest it belongs either to dryolestoids or to stem zatherians (Kielan-Jaworowska et al., 2004; Sigogneau-Russell, 1999). Two other teeth, less well-preserved or fragmentary, might be premolars of the same taxon.

In addition, two incomplete teeth with the main cusp broken are for the moment referred to Mammalia indet. It is worth noting that multituberculatas and dryolestid mammals are also present in the slightly younger beds of the Cherves-de-Cognac locality (Pouech, 2008; Pouech et al., 2006). These taxa are well represented in the mammalian assemblage of the Purbeck Group in southern England (Sigogneau-Russell and Kielan-Jaworowska, 2002).

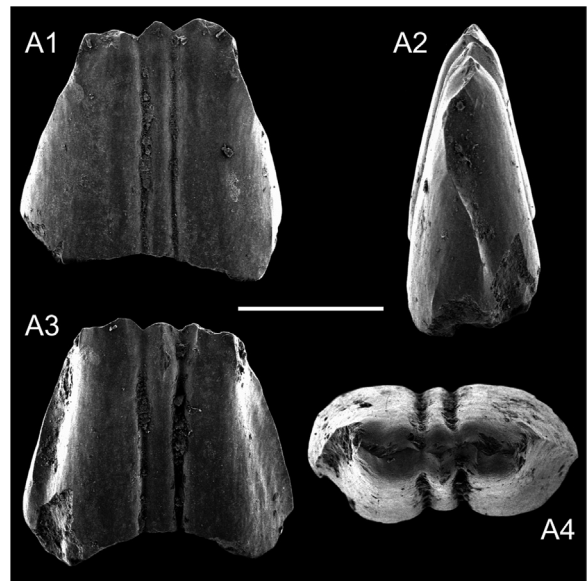


Fig. 20. Vertebrate incertae sedis: tooth in labiolingual (A1, A3), mesiodistal (A2) and apical (A4) views. Scale bar: 500 μ m.

Fig. 20. Vertébré incertae sedis : dent en vues labiolinguales (A1, A3), mésiodistale (A2) et apicale (A4). Barre d'échelle : 500 μ m.

3.3.11. *Vertebrata incertae sedis*

A small, enigmatic tooth has been recovered (Fig. 20). Its crown is labiolingually compressed and has a tri-cusped apex. These cusps are aligned mesiodistally. The central cusp is slightly less developed than the mesial and distal ones. On both labial and lingual faces, a parallel vertical groove is present from the central cusp to the base of the crown. Two carinae are present mesiodistally: one is sigmoid, whereas the other is straight. In apical view, the crown shows a slight medial constriction, and worn apices let appear a relatively thick enamel layer.

3.3.12. Eggshells

Despite their small size, several distinct types of reptile eggshells have been recognized. The first type comprises thick fragments (around 1 mm) with compactituberculata ornamentation (closely spaced nodes: Fig. 21A2) and composed of distinct fan-shaped crystalline units (Fig. 21A1–A4), a typical organisation of dinosaur megaloolithid eggshells (Garcia et al., 2006). The second type, which is the most common, belongs to the Testudoolithidae, an egg family corresponding to chelonians (Hirsch, 1996). The shell structure consists of a single layer (between 0.45 and 0.6 mm) with aragonitic crystallines originating from a central core (Fig. 21B1) and structured in clearly distinct spherulitic units (Fig. 21B2). Furthermore, two other types have been identified: scarce smooth prismatic fragments with three structural arrangements of calcite crystals (Fig. 21C) and thin eggshells (less of 0.3 mm) with crocodiloid microstructure features (Mikhailov, 1997), i.e. discrete and poorly interlocked units with irregular inverted triangular crystalline wedges (Fig. 21D1) and a horizontal layering of tabular crystallines (Fig. 21D2).

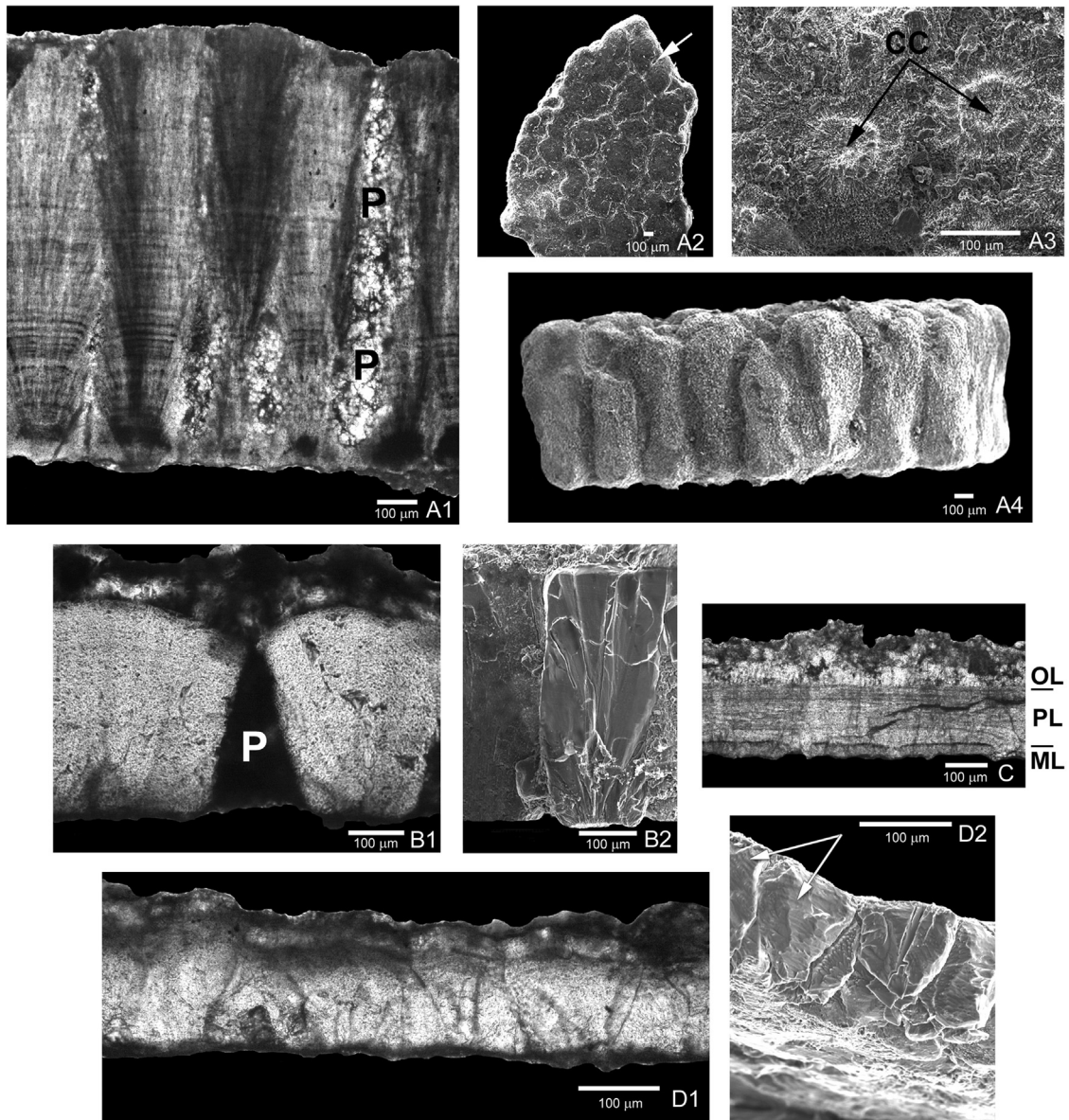


Fig. 21. Eggshells. A, Megaloolithid eggshells: A1, radial thin section in non-polarized light showing the tubocanalicular pore canal (P), widened by the recrystallization; A2, outer typical ornamentation consisting of bulbous nodes, sometimes flattened by erosion; the white arrow indicates the presence of a pore opening; A3, inner surface under SEM with well-preserved mamillae with central cores (CC); A4, radial view under SEM. B, testudoïd eggshells: B1, thin section in polarized light showing two adjacent crystalline units with a canal pore (P); B2, unit detail under SEM; note the organisation originating from a central core. C, prismatic eggshells: three-layered structures with an external recrystallized layer (OL); the black arrow marks the approximate limit between the mammillary (ML) and prismatic (PL) layers. D, crocodiloïd eggshells: D1, polarized light microscopic view of radial thin section with a typical microstructure; D2, units under SEM showing the tabular structure (white arrows).

Fig. 21. Coquilles d'œufs. A, Coquille de mégaloolithid : A1, lame mince en vue radiale sous lumière non polarisée montrant le canal aérifère de type tubocanaliculé (P), élargi par la recrystallisation; A2, ornementation externe typique formée de mamelons bulbeux, parfois aplanis par l'érosion; la flèche blanche indique la présence d'une ouverture de pore; A3, surface interne au MEB avec des mamilles préservées avec leurs cœurs centraux (CC); A4, vue radiale au MEB. B, coquille testudoïde : B1, lame mince sous lumière polarisée montrant deux unités cristallines adjacentes avec un canal aérifère (P); B2, détail de l'unité au MEB; noter l'organisation des cristaux autour du cœur central. C, coquille prismatique : trois niveaux structuraux avec présence d'un niveau externe recrystallisé (OL); la flèche noire marque la limite approximative entre les niveaux mamillaire (ML) et prismatique (PL). D, coquille crocodiloïde : D1, lame mince vue au microscope polarisant montrant la microstructure caractéristique des coquilles d'œufs de crocodile; D2, unités au MEB montrant la structure tabulaire (flèches blanches).

4. Conclusion

The locality of Chassiron has yielded abundant and diverse fossil remains of plants and animals of a Latest

Jurassic ecosystem. This assemblage mainly consists of terrestrial and freshwater aquatic organisms (e.g., charophytes, planorbids, lissamphibians), besides a few euryhaline and coastal marine taxa (e.g., neomiodontids,

plesiochelyids, hybodontids). The latter testify to sporadic marine inputs in a freshwater environment close to the sea shore. The salinity variations were probably one of the causes of mass mortality of stenohaline aquatic invertebrates and small tetrapods. In the Charentes region, similar fluctuations of salinity have been recorded in the Berriasian vertebrate-bearing beds of Cherves-de-Cognac (El Albani et al., 2004), while the Hauterivian–Barremian bonebed of Angeac shows less fluctuating conditions and indications (e.g., bivalve assemblage consisting exclusively of one unionoid taxon) of a more stable freshwater environment (Néraudeau et al., 2012).

Mammals are reported for the first time from the Jurassic of France, and the observed diversity of some other groups (e.g., pterosaurs) is noteworthy. Several rich localities from the northern part of the Aquitaine Basin have recently provided numerous data on the Early Cretaceous continental biota of this area (Adl et al., 2011; Mazin et al., 2008; Néraudeau et al., 2012). There, this kind of data has not been available for the end of the Jurassic, mainly because of the predominance of marine strata of this age in that region. The Chassiron locality extends this window back to the Latest Jurassic (Tithonian), complements the regional vertebrate-bearing series, and thus gives new insights into the Jurassic–Cretaceous transition in western Europe. Comparisons with the well-known Purbeck Group of southern England show numerous similarities in terms of palaeobiodiversity and depositional environment. As in southern England, the Charentes region offers a remarkable opportunity to study biological changes that occurred during this crucial part of the Mesozoic. Further detailed studies (systematics, taphonomy, palaeoecology) are now needed for a deeper understanding of the Chassiron assemblage.

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