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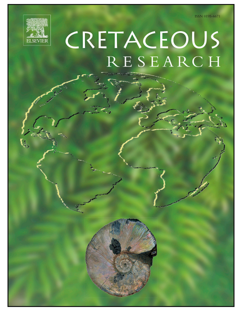

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A review of the Late Jurassic-Early Cretaceous charophytes from the northern Aquitaine Basin in south-west France

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Abstract

Late Jurassic and Early Cretaceous charophyte assemblages from the northern part of the Aquitaine Basin in south-west France are reviewed here to understand their palaeoecological, palaeobiogeographical and biostratigraphic features. Three sites were studied: the Tithonian-lower Berriasian of Chassiron, and the Berriasian of Cherves-de-Cognac and Angeac-Charente. Abundant porocharaceans, less abundant clavatoraceans and scarce characeans recorded in Cherves-de-Cognac and Angeac-Charente indicate that brackish water environments were substituted by freshwater environments eastwards. The occurrence of *Clavator grovesii* var. *grovesii* and morphotypes intermediate with *C. grovesii* var. *discordis* in the same areas is significant from a biostratigraphic viewpoint, since these species belong to the Maillardii, Incrassatus and Nurrensis European charophyte biozones, representing the Berriasian. This observation refutes a previous dating of the Angeac-Charente site and

highlights the absence of Hauterivian-Barremian records in northern Aquitaine, which is in contrast to the more complete Lower Cretaceous record in southern Aquitaine. These contrasting records could be due to differences in the available sedimentary space produced by the opening of the Bay of Biscay during the Barremian.

Keywords

Charophyta; Freshwater; Tithonian; Berriasian; Charentes basin

Introduction

The Aquitaine Basin in south-west France is among the lesser known European basins in terms of its Lower Cretaceous stratigraphic and palaeontological records. However, its location at the boundary between the Iberian and European plates makes it highly significant in understanding the rift processes that occurred in the Late Jurassic and Early Cretaceous during the opening of the North Atlantic Ocean and the Gulf of Biscay. In this sense, the biostratigraphy of the few Lower Cretaceous outcrops in the northern part of the Aquitaine Basin is fundamental in elucidating the basin's evolution and how it compares with the southern part of the Aquitaine Basin.

Deak and Combaz (1967) were the first to find palynological indicators of the "Wealden", i.e., Lower Cretaceous non-marine strata, in the southern part of the north Aquitaine Basin. These observations were also made in the north-western part by Lanceron (1976), Platel and Moreau (1977) and Platel (1978). Much later, a number of studies devoted to the biostratigraphy of the Cretaceous northern Aquitaine Basin showed the occurrence of the Berriasian based on the presence of ostracodes, charophytes and dinoflagellates (Colin et al., 2004; El Albani et al., 2004), as well as the occurrence of the Albian and Cenomanian (Néraudeau et al., 2002) and the Turonian (Néraudeau et al., 2016) based on palynological evidence. Moreover, a recent study indicated the possible occurrence of Hauterivian-Barremian deposits in Angeac-Charente (Néraudeau et al., 2012).

The present study is an in-depth review of the charophyte assemblages from three localities, Chassiron in the Oléron Island, Cherves-de-Cognac and Angeac-Charente (Fig. 1), which have been only partly studied in the past. The results significantly advance the biostratigraphic understanding of the Upper Jurassic and Lower Cretaceous of the northern Aquitaine Basin, refuting some of the previous biostratigraphic findings and improving the comparison with southern Aquitaine, the so-called Arzacq-Mauléon Basin.

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Geological setting and stratigraphy

The Aquitaine Basin was a rift basin during most of the Mesozoic. Its structure was affected by the formation of the oceanic crust between Europe and North America from the latest Callovian to the early Tithonian and the subsequent opening of the Gulf of Biscay during the Barremian, the basin forming along the transform plate boundary at the north of the Iberian plate (Schettino and Scotese, 2002; Schnyder et al., 2012; Tugend et al., 2015).

The northern part of the Aquitaine Basin, sometimes referred to as “Charentes Basin”, is limited by normal faults with a north-west-south-east direction (Platel, 1980). The Upper Jurassic and Lowermost Cretaceous deposits predominantly contain carbonates, with evaporites at its edges (Platel, 1980; Cubaynes et al., 1989) and clayey or conglomeratic bone beds (Néraudeau et al., 2012; Vullo et al., 2012, 2014). The Lower Cretaceous record is extremely limited in the northern Aquitaine Basin, especially for the Berriasian to Aptian (Fig. 2), while the uppermost Albian deposits are better represented (Néraudeau et al., 2002). A more complete sedimentary record of marine facies is present for the Cenomanian transgression, starting with detrital beds followed by limestone deposits.

In the southern part of the Aquitaine Basin (also called Arzacq-Mauléon Basin), a more complete Lower Cretaceous record provides information about the Berriasian, Hauterivian-Barremian and Aptian, such as the frequent marine deposits to the east and increasing non-marine influences to the west (Peybernès and Combes, 1994). An important transgression occurred during the Barremian that was interrupted by emersion episodes (Martín-Closas and Peybernès, 1987; Combes et al., 1998). Winnock (1973) explained the differences between the northern and southern parts of the Aquitaine Basin to be due to the reactivation of a Triassic fault structure ("flexure celtaquitaine") that separated the two areas and enhanced the subsidence to the south during the Early Cretaceous. Later, chalk sedimentation occurred until the end of the Late Cretaceous, representing the last occurrence of marine sediments.

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From a palaeogeographical viewpoint, it is assumed that the Aquitaine Basin was a shallow and narrow gulf opening onto the Atlantic domain during the latest Jurassic and earliest Cretaceous (Cubaynes et al., 1989; Hantzpergue and Lafaurie, 1994; Schnyder et al., 2012). During the Kimmeridgian, the Aquitaine Basin was linked to the Paris Basin by the Poitou threshold in its north-eastern part, but this connection ceased before the Tithonian (Thierry, 2000; Schnyder et al., 2012) due to the regressive trend starting in the latest Kimmeridgian (Hantzpergue, 1989). According to Thierry (2000) and Blakey (2011), some connections with the western Tethys persisted in the Early Cretaceous through the Corbières-Provence platform to the south-east and the Dauphiné Basin to the north-east.

The Jurassic and Cretaceous from northern Aquitaine have been studied as early as the beginning of the 19th century by Fleuriau de Bellevue (1801) and d'Archiac (1837), among others, who concluded that the Lower Cretaceous was not represented in that part of the basin, a hypothesis that had been widely accepted until recently (Platel, 1980; Néraudeau et al., 2012). In the two last decades, a number of studies have provided evidence that the Lower Cretaceous is indeed represented (Schnyder, 2003; Billon-Bruyat, 2003; Colin et al., 2004; Néraudeau et al., 2002, 2012; Vullo et al., 2014). Thus, the present study aimed to perform a detailed review of the Lower Cretaceous records in three different areas of the "Charentes Basin", Chassiron (Oléron Island) in the western part, Cherves-de-Cognac in the central part and Angeac-Charente in the eastern part (Fig. 1).

Chassiron (Oléron Island)

The stratigraphic section studied at Chassiron is composed of four informal members (Fig. 3). The first, up to 24.2 metres (m) thick, is composed of yellowish to grey irregular nodular limestone with thin marl intercalations. These are thought to represent open-marine platform facies (Schnyder et al., 2012). However, there is already evidence of episodic emersion (e.g., mudcracks) 18 m above the base. Furthermore, the presence of charophytes between 20 and 24.2 m from the base suggests increasing non-marine influences (Schnyder et al., 2012). This member is thought to range from the upper Kimmeridgian (Autissiodorensis Zone) to the lower Tithonian (Gigas Zone), according to Hantzpergue et al. (2004).

The second member, 20.5 m thick, begins with a conglomerate composed of a clay matrix and white calcareous clasts (bed 141). It is topped with 0.4-m-thick clay containing abundant conifer wood (Schnyder et al., 2012; Vullo et al., 2014). The upper part of the member is formed of 19 m of blue to black clay and marls, while the bottom part contains an important accumulation of vertebrate remains (Vullo et al., 2014). Charophyte gyrogonites were found in bed 148 (Fig. 3) and documented by Martín-Closas et al. (2008), who attributed them to the Tithonian. A previously unreported charophyte species from the same bed is described herein.

The third member, with a thickness of 23 m, is composed of limestone beds at the base (6 m), followed by 4 m of alternating limestone and clay, with brackish bivalves (e.g., *Mactra*) and diverse marine species (such as corals, brachiopods, echinoids, bivalves, benthic foraminifera, ostracods and *Rhizocorallium* burrows). This member corresponds to sedimentation occurring in a shallow lagoon and other coastal environments, with normal salinity that has been occasionally subjected to storms (Schnyder et al., 2012).

The fourth member of this series, which is 13 to 14 m thick, is composed of finely laminated and marly peloidal limestone, showing dinosaur footprints and numerous mudcrack-bearing surfaces (Moreau et al., submitted). Evaporitic beds (including calcite recrystallised after gypsum), halite pseudomorphs and fenestrae have been observed in some parts. These are the shallowest deposits in this stratigraphic section (Schnyder et al., 2012).

Members 2 to 4 have been assimilated into Purbeckian-type facies, with a strong terrestrial influence (Schnyder et al., 2012; Colombié et al., 2012; Vullo et al., 2014). The dating of the marine beds from this section was performed using calcareous nannofossils and dinoflagellates (Schnyder et al., 2012), ammonites (Hantzpergue et al., 2004), ostracods (Donze, 1960; Malz, 1966) and foraminifera (Bousquet, 1967), which gave a date ranging from the late Kimmeridgian (Autissiodorensis Zone) to late-early Tithonian or early Berriasian.

Cherves-de-Cognac

In the Champblanc quarry at Cherves-de-Cognac, two lithological units were identified, each with a thickness of 15 m (Colin et al., 2004). The basal unit (U1) is composed of alternating layers of fibrous gypsum and black clay laminites, sometimes with stromatolitic features (Colin et al., 2004; El Albani et al., 2004), corresponding to an environment of tidal flats in a restricted lagoon under an arid climate (El Albani et al., 2004).

The second unit (U2) shows alternating marlstone laminites and gypsum that progressively gives way to fossilerous marly limestones in the upper parts (Colin et al., 2004; El Albani et al., 2004). This unit indicates both marine and freshwater influences in an estuarine context (El Albani et al., 2004). It contains a 1-m-thick bone bed that bears a particularly rich vertebrate fauna including fish, crocodilians and chelonians (Colin et al., 2004). Charophyte specimens were found in beds C32 to C36, C38 and C41, including the bone bed (Fig. 3). Colin et al. (2004) undertook a preliminary study of these charophytes and here, we will review the flora in depth. The Cherves-de-Cognac study area lies directly over Tithonian marine limestone (El Albani et al., 2004).

Angeac-Charente

The Angeac-Charente study area is located between the cities of Cognac and Angoulême. It is composed of 7 characteristic beds, An7 to An1 from the base to the top. An7 and An6 are composed of red clay and irregularly stratified grey limestone, respectively

(Néraudeau et al., 2012). An5 does not crop out entirely, but is at least 0.7 m thick and contains green clay without macrofossils. Some grey-green sub-angular limestone blocks are observed in various places, suggesting reworking (Néraudeau et al., 2012). An4 is composed of blue-grey lignitic clay, which is generally 0.5 to 1 m thick and rich in plant remains (e.g., wood, cuticles and seeds). This bed yielded most of the large and well-preserved vertebrate remains, as well as woody axes, described in previous studies (Néraudeau, 2011; Néraudeau et al., 2012; Allain et al., 2014). Numerous calcareous clasts occur at the top of An4, and the delimitation with An3 is unclear (Néraudeau et al., 2012). An3 is 0.2 to 0.4 m thick, and composed of conglomeratic calcareous deposits with a blue-grey grainstone matrix and whitish limestone clasts. Diverse vertebrate remains (crocodiles, dinosaurs, turtles and fishes), plant debris (wood and cuticles), charophyte fructifications, ostracods and insect coprolites (termites) have been recorded in this bed (Colin et al., 2011; Néraudeau et al., 2012). An2 contains yellow to grey calcareous deposits with an irregular stratification that is perhaps linked to dinosaur trampling. It has a thickness ranging from 0.2 to 0.4 m, and grades from marlstone to limestone laterally and vertically (Néraudeau et al., 2012). This bed supplied some of the charophyte remains studied herein. Finally, An1 at the top of the section, with a thickness generally ranging from 0.1 to 0.2 m, is composed of white to greyish fine sand that is rich in fish remains such as scales, teeth and bones (Néraudeau et al., 2012).

Charophytes were found in bed An4, in the interbed between An4 and An3 (An3-4) and in An2 (Fig. 3). They were previously studied by Néraudeau et al. (2012) and here we will review the assemblage in depth.

--------------------------- Please insert Fig. 3 near here ---

Material and methods

Sample collection

The charophyte samples from Chassiron (Oléron Island) were collected and lent by D. Gendry (University of Rennes 1, France) and J.-P. Colin. The samples from Chassiron came from level 148 (Cha148-coll. D.G.) of member 2, as described by Schnyder et al. (2012) and Vullo et al. (2014). This also corresponds to the bed 1004-A in which Schnyder (2003) characterised a high concentration of vertebrate remains (Vullo et al., 2014).

The samples from Cherves-de-Cognac were collected by J.-P. Colin and lent to C. Martín-Closas for this study. They were collected from the beds C32 to C36, C38 and C41, as described in Rees et al. (2013) and Pouech et al. (2015), corresponding to the “bone bed” of the site (Colin et al., 2004; El Albani et al., 2004).

The Angeac-Charente samples were obtained from palaeontological excavations in 2010. Samples from beds An1 (An1-SA), An2 (An2-SA) and An4 (An4-SA) were obtained from the first excavation (ANG1-02-2010), while samples from An3-4 (An3-4-SB) were collected from the second excavation (ANG2-02-2010), located about 20 m north of the site of the first excavation (Néraudeau et al., 2012).

Sample preparation

Samples were disaggregated in a solution of water and hydrogen peroxide (100 volumes), washed and then sieved through 200, 500 and 1000 µm mesh sieves. In some cases, anhydrous sodium carbonate was added to deflocculate the clay. Before sieving, sieves were submerged in a solution of methylene blue to mark the residues of previous samples and then washed. Charophyte remains (thalli, gyrogonites and utricles) were manually picked out under a Wild M5A stereomicroscope at 40x magnification. When necessary, an ultrasonic cleaner was used. Measurements were performed with the software Motic Images Plus 2.0 ML in a Motic BA310 stereomicroscope. Selected fructifications were photographed with a Quanta 200 scanning electron microscope at the Scientific and Technical Services of the Universitat de Barcelona (UB). The gyrogonite and utricle specimens were stored in the Universities of Rennes (France) and Barcelona (Catalonia, Spain). Specifically all figured specimens, labelled IGR-PAL are stored in the collections of the University of Rennes (France).

Systematic palaeontology

Division Charophyta MIGULA, 1897

Class Charophyceae SMITH, 1938

Order Charales LINDLEY, 1836

Family Porocharaceae GRAMBAST, 1962 emend. SCHUDACK, 1993

Genus *Porochara* (MÄDLER, 1955) emend. SCHUDACK, 1986

***Porochara westerbeckensis* (MÄDLER, 1952) MÄDLER, 1955**

Fig. 4 (A-E).

1952 *Aclistochara westerbeckensis* nov. spec. – Mädler, p. 28-29, pl. B, fig. 20-25.

1955 *Porochara westerbeckensis* nov. comb. – Mädler, p. 271.

Material. About 250 specimens from An3-4-SB and around 120 specimens from Cherves-de-Cognac samples.

Description. Medium-sized gyrogonites, subprolate to prolate in shape. Specimens from Angeac (An3-4-SB) have a size ranging from 400 to 620 µm in height (mean: 505.7 µm) and 285 to 463 µm in width (mean: 385.3 µm). The isopolarity index (ISI) is above 120 for the majority of the gyrogonites (between 112 and 151, with a mean of 131.5). The number of convolutions (NC) is variable, generally 9 (8-10). The apical pore (mean: 48.34 µm) is wider than the basal pore (mean: 32.51 µm) and are very similar in shape, but the apical pore tends to be star shaped or circular and the basal pore pentagonal.

Remarks. Twelve smaller specimens were found in this population (height: 400-471 µm; width: 285-331 µm; ISI: 120-151; and NC: 8-12) that could be accommodated within *Porochara fusca* (MÄDLER, 1952) MÄDLER, 1955. However, Mojon (1989a) pointed out that the polymorphism of the porocharacean populations of the Upper Jurassic and Lower Cretaceous was high, and interpreted this in terms of palaeoecology.

Distribution. *Porochara westerbeckensis* has been found in north-west Germany from the upper Oxfordian to the lower Berriasian (Schudack, 1990, 1993), in south-east France and Switzerland from the Oxfordian/ Kimmeridgian (Mojon, 1989b), in Spain from the Kimmeridgian (Brenner, 1976) to the Barremian (Martín-Closas, 2000), in Portugal from the Kimmeridgian (Grambast-Fessard and Ramalho, 1985) and in Russia from the Kimmeridgian and Tithonian (Shaïkin, 1976).

--------------------------- Please insert Fig. 4 near here ---

Genus *Latochara* MÄDLER, 1955 emend. FEIST in FEIST and CUBAYNES, 1984

***Latochara latitruncata* (PECK, 1937) MÄDLER, 1955**

Fig. 4 (F-I).

1937 *Aclistochara latitruncata* PECK, n. sp. – PECK, p. 89, pl. 14, figs 1-4

1955 *Latochara latitruncata* (PECK) nov. comb. – MÄDLER, p. 271

1957 *Latochara latitruncata* (PECK) – PECK, p. 32-33, pl. 5, figs. 7, 21-23

1957 *Latochara collina* PECK, n. sp. – PECK, p. 33, pl. 5, figs 1-4.

1957 *Latochara concinna* PECK, n. sp. – PECK, p. 34, pl. 5, figs. 5-6, 8-9

Material. About 200 specimens from the Chassiron samples (Level 148b).

Description. Small- to medium-sized gyrogonites, 326-424 µm high (mean: 388.65 µm) and 254-330 µm wide, with an ISI from 115 to 142 (mean: 128.77). These gyrogonites are subspheroidal to ellipsoidal in shape with an apical neck. The number of convolutions varies from 10 to 13. The spiral cells are flat to concave, with a carinated suture. When approaching the apical part, the spiral cells are wider in the periapical zone and then narrow up to the apical neck. In a few specimens, a periapical depression is present. The apical pore is very small (hardly visible under the stereomicroscope) and the basal plate cannot be observed, but is thought to be multipartite like in the other species of this genus.

Remarks. Peck (1957) noticed some similarities between *L. latitruncata* and *L. concinna*, and suggested also that *L. collina* was a subspecies of *L. latitruncata*. Schudack (1993) and Martín-Closas et al. (2008) regarded the three species as synonymous.

Distribution. This species has been identified in the Morrison Formation (Kimmeridgian to Tithonian in age) in the United States of America (Peck, 1957), from the lower Tithonian of north-west Germany (Schudack, 1990, 1993) and in the Tithonian from Ukraine (Shaïkin, 1967). Martín-Closas et al. (2008) also described this species from the same area as that studied here.

Family Characeae (RICHARD. ex C.A. AGARDH, 1824) emend. MARTÍN-CLOSAS and SCHUDACK, 1991

Genus *Mesochara* GRAMBAST, 1962

Mesochara* gr. *voluta sensu Martín-Closas (2000)

***Mesochara harrisii* (MÄDLER, 1952) SHAÏKIN, 1967**

Fig. 4 (J-P).

1952 *Tolypella harrisii* nov. spec. – Mädler, p. 31-32, pl. B, fig.31-35

1952 *Tolypella amoena* nov. spec. – Mädler, p. 34-35, pl. B, fig. 43-49

1952 *Tolypella minuta* nov. spec. – Mädler, p. 35-36, pl. B, fig. 50-52

1967 *Mesochara harrisii* SHAÏKIN nov. comb. – Shaïkin, p. 47

Material. 100 gyrogonites from Chassiron (level 148), 25 specimens from An3-4-SB and a few from An2 from Angeac-Charente, and 15 specimens from Cherves-de-Cognac.

Description. The specimens from Chassiron provide the only abundant population of this species in the northern Aquitaine Basin. They present small gyrogonites ranging from 239 to 341 µm in height and 190 to 312 µm in width, with a spheroidal to prolate shape (ISI ranging from 100 to 142). The spiral cells are concave to almost flat and join at the apex without any modification. The base and apex are generally rounded, but are slightly pointed in some cases. The number of convolutions in lateral view ranges between 8 and 11, generally 9, with a mean width of 36.75 µm at the equator. Some of the specimens from Angeac are slightly larger (353 to 403 µm high and 303 to 361 µm wide) and more spheroidal (ISI, 108–127). A basal plate cannot be observed, but is probably unicellular, based on gyrogonites of the same species from other European areas.

Remarks. Peck (1957), when describing some specimens of "*Mesochara*" *voluta* that are similar to those found in Charentes, did not separate the specimens with a slightly pointed apex and/or base from those with a rounded apex and/or base. He also noticed a strong similarity with another species, *Tolypella minuta* MÄDLER, 1952 from Germany dating to the Kimmeridgian, which now corresponds to *Mesochara harrisii* (MÄDLER, 1952) SHAÏKIN, 1967. Martín-Closas (2000) assigned *M. harrisii* and *M. voluta* to the same morphogroup (*M.* gr. *voluta)* and remarked that the type population of *M. voluta*, included only 3 gyrogonites, which is an insufficient number to properly characterise a fossil charophyte species.

The difference in size between the two morphotypes present in the An3-4 samples could be the result of ecological variations. Vicente et al. (2016) observed that the different genera of Mesozoic characeans, including *Mesochara*, *Tolypella* and *Microchara*, present the smallest morphotypes in shallow, temporary and turbid ponds of floodplains. Recent data indicate that this might be due to the short life cycles adopted in temporary ponds in response to the very warm and exceedingly well illuminated growth conditions (Sanjuan et al., 2017).

It is important to note here that the basal plate is required to distinguish between the gyrogonites of genus *Mesochara* and the genus *Tolypella* (Martín-Closas et al., 2009). The basal plate is formed by three cells (only two are calcified) in *Tolypella* and is unicellular in *Mesochara*. Therefore, the attribution of the specimens to the correct genera was subject to uncertainty in this study.

Distribution. This species has been observed in north-west Germany, from the Upper Oxfordian to the Berriasian-Valanginian? (Schudack, 1990, 1993), in Spain, from the Kimmeridgian (Brenner, 1976; Schudack, 1987), and Berriasian to Barremian (Martín-Closas and Grambast-Fessard, 1986; Schudack, 1989; Martín-Closas, 2000), in Russia from the Kimmeridgian and Tithonian (Shaïkin, 1967, 1976) and in China from the Lower and Upper Cretaceous (Wang, 1965; Hao et al., 1983; Liu and Wu, 1985). In France, the species has been recorded from the Tithonian (Martín-Closas et al., 2008) and the Berriasian in the Aquitaine Basin (Colin et al., 2004; El Albani et al., 2004; Néraudeau et al., 2012), and in the lowermost Aptian of the Northern Subalpine Chains (Martín-Closas et al., 2009). In Japan, *M. harrisii* has been reported in the lower part of the Kitadani Formation that is thought to date back to the Barremian (Kubota, 2005).

Family Clavatoraceae PIA, 1927

Subfamily Clavatoroidae GRAMBAST, 1969 emend. MARTÍN-CLOSAS 1989 ex SCHUDACK, 1993

Genus *Nodosoclavator* MASLOV, 1963 emend. GRAMBAST, 1966

***Nodosoclavator bradleyi* (HARRIS, 1939) comb. nov. GRAMBAST, 1969**

Fig. 5 (A-H).

1939 *Clavator bradleyi* sp. nov. – HARRIS, p. 53-54, pl. XVI, fig. 1, 3-5, 7.

1969 *Nodosoclavator bradleyi* (HARRIS) nov. comb. – GRAMBAST, p. 881, pl. 33, fig. 5.

Material. About 300 specimens in sample An3-4-SB and a few in sample An2 from Angeac-Charente, 1 from Cherves-de-Cognac and 4 specimens from the Chassiron samples.

Description. Medium-sized gyrogonites, often 500 to 650 µm in height and 300 to 415 µm in width, bottle-shaped with a long apical neck and subprolate to prolate (ISI, 124-180). The basal plate has not been observed. The utricle is mostly formed by the nodular layer, with the nodules located on the spiral cell suture. The nodular layer is sometimes partially covered by 5 to 7 individual bract cells, digitated in shape, which are not organised in any particular symmetry and vary in height (from one-third to two-thirds of the gyrogonite).

Remarks. Although the basal plate could not be observed in this species, it has been found to be single celled in several other related species from Clavatoraceae (Clavatoroideae: *Hemiclavator adnatus* (MARTÍN-CLOSAS and GRAMBAST-FESSARD, 1986) SCHUDACK, 1993 and *Clavator harrisii* PECK, 1941; Atopocharoideae: *Atopochara trivolvis* var. *trivolvis* PECK, 1938), as shown by Martín-Closas (1988, 2000). Some of the specimens from Chassiron and Angeac-Charente are well preserved and enabled us to see the features of the outer layer, which is really rare.

Distribution. This species has been identified by Colin et al. (2004) and El Albani et al. (2004) in Cherves-de-Cognac (dating back to the Berriasian) and by Néraudeau et al. (2012) in Angeac-Charente. Outside France, it has been observed in the Lower Saxony basin of Germany from the lower Tithonian (Schudack, 1993) and in the palustrine areas of the Iberian Chain in Spain from the Tithonian to Barremian (Martín-Closas, 2000). In the United States, *N. bradleyi* has been reported to occur in the Cedar Mountain Formation (Utah) from the upper Berriasian and lower Valanginian and more rarely in the Lakota Formation, South Dakota (Martín-Closas et al., 2013), where it had already been identified by Peck (1957).

---------------------------- Please insert Fig. 5 near here --

Genus *Clavator* REID and GROVES, 1916 emend. MARTÍN-CLOSAS, 1989 ex SCHUDACK, 1993

***Clavator grovesii* var. *grovesii* (HARRIS, 1939) nov. comb. MARTIN-CLOSAS, 1996**

Fig. 6 (A-G).

1939 *Clavator grovesii* sp. nov. – Harris, p. 46-53, pl. 10 fig. 1-12, pl.11-12, pl. 17, fig. 8-13.

1962 *Flabellochara grovesii* (HARRIS) nov. comb. – Grambast, p. 69.

1993 *Clavator grovesii grovesii* (HARRIS, 1939) n. comb. – Schudack, p. 76-77, fig. 35; pl. 9, figs 8-14.

1996 *Clavator grovesii* var. *grovesii* (HARRIS, 1939) n. comb. – Martín-Closas, p. 278.

Material. Seven specimens from Angeac-Charente (An3-4-SB) and 33 specimens from Cherves-de-Cognac.

Description. Medium-sized utricles, 475 to 650 µm in height and 364 to 533 µm in width, with a bilateral symmetry. They are composed of a structured layer of 3 primary bract cells, one large cell that is opposite the phylloid and two shorter cells in a lateral position and bearing a fan of secondary bract cells. The three primary bract cells are connected to a basal pore. The tips of the lateral bract cells appear as a pore in section. Some utricles (variety 1) show 2 basal cells surrounding the lateral bract cells, while the fan is composed of 5 to 6 flattened cells in the direction of the apex. These cells are fused and ellipsoidal. Other utricles (variety 2) show a small basal cell covering the lateral bract cells, while the fans are similar in structure to the former variety. It is important to note that intermediate forms between these two varieties occur in the same population.

Remarks. The two varieties are part of the *Flabellochara-Clypeator* lineage described by Grambast (1974), later considered by Martín-Closas (1989, 1996,) and Schudack (1993) to represent anagenetic forms of the same evolutionary species *Clavator grovesii*. The first form described above corresponds to *Clavator grovesii* var. *grovesii* (HARRIS, 1939) comb. nov. MARTÍN-CLOSAS, 1996, while the second represents transitional forms between *C. grovesii* var. *grovesii* and *C. grovesii* var. *discordis* (SHAÏKIN, 1976) comb. nov. MARTÍN-CLOSAS, 1996.

It is important to point out the small size of the specimens studied. The utricle size in this species normally ranges from 400 to 850 µm in height and from 350 to 750 µm in width. The small size may be due to ecological variations, as explained previously for *Mesochara harrisii* gyrogonites by Vicente et al. (2016) and for extant *Chara* by Sanjuan et al.(2017).

Distribution. *Clavator grovesii* var. *grovesii* has been observed to occur in England from the Tithonian and Berriasian in the Dorset and Weald Basins (Harris, 1939; Feist et al., 1995), in France (Colin et al., 2004; El Albani et al., 2004; Néraudeau et al., 2012), in the Swiss Jura (Häfeli, 1966; Mojon and Strasser, 1987; Détraz and Mojon, 1989), Spain (Schudack, 1993; Martín-Closas, 2000) and north-west Germany (Schudack, 1993). It has also been found in China from the Berriasian or Valanginian (Wang et al., 1976; and Hao et al., 1983). Martín-Closas et al. (2013) reported on its occurrence in the Berriasian from North America, suggesting that this species was the first clavatoracean to reach a cosmopolitan distribution in a subtropical latitudinal area of the Northern Hemisphere (Martín-Closas, 2015). *C. grovesii* var. *discordis* is also present in Berriasian strata from Spain, often together with *C. grovesii* var. *grovesii* (Schudack, 1993; Martín-Closas, 2000).

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Discussion

Taphonomy

The charophyte remains from Chassiron generally displayed good preservation. The most significant observation was the occurrence of a number of utricles attached to the same phylloid in *N. bradleyi* (Fig. 5A). In some cases, these specimens still showed parts of the external layer of their utricles. Some calcified parts of clavatoracean axes were also found. These features are indicative of autochthony (El Albani et al., 2004). One part of the charophyte assemblage from Chassiron, especially *M. harrisii* and *L. latitruncata*, is laterally compressed due to diagenetic deformation.

In Cherves-de-Cognac, the clavatoracean utricles (*N. bradleyi* and *C. grovesii*) were well preserved and, like the utricles from Chassiron, some displayed an anatomical connection to the phylloid. Calcified parts of clavatoracean thalli were also found. As above, these features suggest autochthony of the assemblage (El Albani et al., 2004). Characean and porocharacean gyrogonites from Cherves-de-Cognac were also well preserved, but not associated with vegetative remains, indicating that these gyrogonites were gently transported from an adjacent growing area, forming a parautochthonous assemblage, or that the thalli of these species did not calcify (El Albani et al., 2004).

The population from Angeac-Charente (An3-4-SB) presented significant similarities to that from Cherves-de-Cognac. *N. bradleyi* and *C. grovesii* utricles were well preserved and associated with the calcified parts of clavatoracean thalli. This observation is sufficient to justify the autochthony of the assemblage, in contrast to that proposed by Néraudeau et al. (2012). Characean and porocharacean gyrogonites were generally well preserved, but their thalli were absent. The An2-SA samples contained relatively corroded porocharacean gyrogonites compared to An3-4-SB specimens. This corrosion, in the form of spiral cells with alveolar surfaces, has been attributed to epidiagenetic processes (Martín-Closas and Grambast-Fessard, 1986).

Palaeoecology

During the Late Jurassic and Early Cretaceous, the occurrence of the genus *Latochara* was restricted to a latitudinal area of the boreal realm (Schudack, 1996). Thus, its occurrence in Chassiron represents its southernmost biogeographical distribution of that time (Martín-Closas et al., 2008). Generally, the abundance of porocharaceans in the Upper Jurassic and Cretaceous, particularly that of *Latochara*, indicates brackish water environments such as coastal marshes (Martín-Closas et al., 2008), which is consistent with the data obtained from member 2 of the Chassiron stratigraphic section (Schnyder et al., 2012).

Similarly, assemblages dominated by porocharaceans in the Cretaceous are thought to be indicative of brackish water environments (Martín-Closas and Grambast-Fessard, 1986; Mojon, 1989a, b; El Albani et al., 2004; Villalba-Breva and Martín-Closas, 2013), while clavatoraceans are more abundant and diverse in freshwater facies (Schudack, 1993; El Albani, 2004, Climent et al., 2009). The occurrence of both taxa in Cherves-de-Cognac and Angeac-Charente, with porocharaceans dominating in the former and clavatoraceans in the latter (especially in An3-4 samples), suggests deposition in an increasingly freshwater environment occurring eastwards within the northern Aquitaine Basin. The environment of Angeac-Charente has been postulated to have been a swamp that had occasionally been connected to the sea (Néraudeau et al., 2012); however, the marine influence would have been greater higher up in the stratigraphic section. Villalba-Breva et al. (2012) and Villalba and Martín-Closas (2013) described the occurrence of abundant porocharaceans in the

Maastrichtian of the Vallcebre and Tremp Basins (Catalonia), corresponding to the progradation of a deltaic-estuarine system. The lignite and limestone facies of this unit display some similarities with An3-4 in Angeac-Charente, such as the coal macerals of the vitrinite group, the abundance of conifer remains and the absence of root traces at the base of the coal beds, indicating a parautochthonous accumulation of organic matter rather than a deposit in peat mires or swamps (Villalba-Breva et al. 2012; Villalba-Breva and Martín-Closas, 2013).

Another reason for the occasional marine influence and variation in salinity is the relatively important polymorphism of porocharaceans in the assemblages from Cherves-de-Cognac and Angeac-Charente. Mojon (1989a) highlighted the occurrence of a number of morphotypes within the Berriasian *Porochara* populations found in the Swiss and French Jura mountains. By comparing to the extant species *Lamprothamnium papulosum* (WALLROTH) GROVES, Mojon (1989a) postulated that this variation was linked to seasonal fluctuations of ecological parameters such as salinity and hydrodynamism, with the morphotypes corresponding to different ecophenotypes rather than to different species.

Biostratigraphy

The three study sites enabled us to revisit the biostratigraphic implications of the latest Jurassic and Early Cretaceous charophyte assemblages in the northern part of the Aquitaine Basin (Fig. 7). The assemblages from Chassiron were represented by *L. latitruncata*, *M. harrisii* and rarely *N. bradleyi*. The occurrence of *L. latitruncata* suggests that the assemblages dated from the Kimmeridgian to the late Tithonian, which is consistent with the age obtained from the associated fauna. By contrast, the assemblages from Cherves-de-Cognac and Angeac-Charente consisted of *N. bradleyi* (which was the predominant species in An3-4-SB in Angeac-Charente), *M. harrisii* and *P. westerbeckensis* together with *Clavator grovesii* var. *grovesii* and *C. grovesii* var. *discordis*. The two latter clavatoracean taxa are of biostratigraphic interest as they form part of the *Flabellochara-Clypeator* anagenetic lineage described by Grambast (1970, 1974). These taxa are typically found in the uppermost Tithonian and Berriasian strata in Europe (Schudack, 1993; Martín-Closas, 2000), within the Maillardi, Incrassatus and Nurrensis charophyte biozones (Riveline et al., 1996). Our findings agree with those of previous studies on samples from Cherves-de-Cognac (Colin et al., 2004; El Albani et al., 2004), but disagree with the date of the Angeac-Charente bone bed proposed by Néraudeau et al. (2012). Using a complex fossil assemblage of terrestrial, freshwater, brackish and marine organisms, Néraudeau et al. (2012) proposed a Hauterivian-Barremian age mainly based on a few specimens of the dinoflagellate *Odontochitina imparilis* (DUXBURY) JAIN and KHOWAJA-ATEEQUZZAMAN and the benthic foraminifer *Trocholina* cf. *odukpaniensis* DESSAUVAGIE. The other fossils were typical of older ages, such as the bryozoans and charophytes, and were considered partly or totally reworked. This dating of the bone bed is refuted here based on the charophyte taphonomic data mentioned above (Fig. 8).

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Implications for basin evolution

The absence of any Hauterivian-Barremian stratigraphic record in northern Aquitaine compared to the much more complete record of that period in southern Aquitaine, which forms part of the Arzacq-Mauléon Basin, is relevant for analysing the basin's evolution. The creation of sedimentary space in the Iberian and south-eastern French basins has been linked to the "hyperextension" of the continental crust associated with the opening of the Bay of Biscay (Tugend et al., 2015). This process started during the Barremian and lasted until the Early Albian, leading to an increase in the tectonic subsidence of neighbouring basins such as the Maestrat and Cameros Basins in the Iberian Chain, the Arzacq-Mauléon and Organyà

Basin in the Pyrenees, the Basque-Cantabrian Range, and the Bay of Biscay-Parentis Basin, including part of Aquitaine (Tugend et al., 2015). However, while this "hyperextension" had a significant effect within the Iberian Plate, reaching up to a thousand kilometres far away from the main rift axis, its influence was comparatively very limited within the European Plate. Our biostratigraphic results confirm that this hyperextension was limited exclusively to the southern part of Aquitaine, its influence disappearing completely around a hundred kilometres north of the main rift zone and thus, failing to reach the Charentes Basin (Fig. 8).

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Conclusions

The charophyte remains studied in Chassiron, Cherves-de-Cognac and Angeac-Charente provide new data that improve the current knowledge on the Late Jurassic and Early Cretaceous charophyte flora of the northern part of the Aquitaine Basin, yielding further information on the basin's evolution.

The Upper Jurassic and Lower Cretaceous northern Aquitaine Basin are uniquely composed of three intervals with freshwater to brackish facies, the Tithonian (in part) from Chassiron, the Berriasian from Cherves-de-Cognac and Angeac-Charente, and the Uppermost Albian from Charente-Maritime. Only the first three areas were studied here. The Tithonian deposits of Chassiron contain a purely brackish water assemblage of charophytes, as reported by Martín-Closas et al. (2008). The assemblage is predominantly composed of *Latochara latitruncata*, also containing the rare *Mesochara harrisii* and the newly reported *Nodosoclavator bradleyi*

The assemblages of Cherves-de-Cognac and Angeac-Charente are quite similar. The presence of *Porochara westerbeckensis*, *Nodosoclavator bradleyi*, *Clavator grovesii* and *Mesochara harrisii* at different levels, together with sedimentological, taphonomical and palaeontological data, indicate that the environment became increasingly composed of freshwater eastwards during the Berriasian from Cherves-de-Cognac to Angeac-Charente.

The association of the clavatoraceans *Clavator grovesii* var. *grovesii* and *Clavator grovesii* var. *discordis* in both Cherves-de-Cognac and Angeac-Charente suggests a Berriasian age for the latter area, which disagrees with the Hauterivian-Barremian age proposed by Néraudeau et al. (2012). Indeed, no other Hauterivian-Barremian records have been obtained to date in the northern Aquitaine Basin, which is in contrast to the many found in the southern Aquitaine, i.e., the Arzacq-Mauléon Basin.

In terms of basin evolution, the absence of any Hauterivian-Barremian record in northern Aquitaine suggests that the sedimentary space produced as a result of the crustal extension during the opening of the Gulf of Biscay was limited to the southern part of Aquitaine (Arzacq-Mauléon Basin), which was palaeogeographically located close to the main extensional structures. In this sense, northern Aquitaine only represents a minor part of the same basin containing only the Upper Jurassic and Berriasian records linked to the opening of the North Atlantic Ocean.

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Figure legends

Figure 1. Geological map of the Charentes Basin and locations of the studied sites (modified from Géoportail.fr).

Figure 2. Stratigraphic framework of the Charentes Basin.

Figure 3. Stratigraphic columns of Chassiron, Cherves-de-Cognac and Angeac-Charente (modified from Schnyder et al. (2012), Rees et al. (2013) and Néraudeau et al. (2012), respectively).

Figure 4. Charophyte fructifications from the Upper Jurassic and Lower Cretaceous of the northern part of the Aquitaine Basin. A-E, *Porochara westerbeckensis* from the Berriasian of Angeac-Charente. (A) Lateral view of a gyrogonite from sample An2-SA, IGR-PAL-2779.12; (B) lateral view of a gyrogonite (sample An3-4-SB), IGR-PAL-2779.13; (C) a multipartite basal plate (sample An3-4-SB), IGR-PAL-2779.32; (D) basal view of a gyrogonite (sample An3-4-SB), IGR-PAL-2779.15; and (E) apical view of a gyrogonite (sample An3-4-SB), IGR-PAL-2779.16. F-I, *Latochara latitruncata* from the lower Tithonian of Chassiron (level 148). (F,G) Lateral views, IGR-PAL-2779.3 and IGR-PAL-2779.5; (H) basal view, IGR-PAL-2779.6, (I) apical view, IGR-PAL-2779.4. J-P, *Mesochara harrisii* from level 148 of the lower Tithonian of Chassiron (J, M, O) and from level An3-4-SB of the Berriasian of Angeac-Charente (H-L,N,P) . (J) Lateral view of a gyrogonite, IGR-PAL-2779.7; (K) lateral view, IGR-PAL-2779.17; (L) lateral view, IGR-PAL-2779.18; (M) basal view, IGR-PAL-2779.10; (N) basal view, IGR-PAL-2779.20; (O) apical view, IGR-PAL-2779.9; and (P) apical view, IGR-PAL-2779.19.

Figure 5. Charophyte fructifications from the Upper Jurassic and Lower Cretaceous of the northern part of the Aquitaine Basin. A-H, *Nodosoclavator bradleyi* from level 148 of the lower Tithonian Chassiron (A) and from the Berriasian of Angeac, samples An4 (B) and An3-4-SB (C-F, H) and An2-SA (G). (A) Lateral view of two utricles still attached to the phylloid,

with small bract cells of the structured layer visible, IGR-PAL-2779.1; (B) lateral view of a utricle, with the nodular layer visible, IGR-PAL-2780.5; (C) lateral view of a utricle with the structured layer visible, IGR-PAL-2780.13; (D) apical view of a utricle, IGR-PAL-2779.26; (E) basal view of a utricle, IGR-PAL-2779.21; (F) lateral view of a utricle with the structured layer visible, IGR-PAL-2779.25; (G) lateral view of a gyrogonite with remains of the nodular layer attached to it, IGR-PAL-2779.11; and (H) lateral view of a utricle, IGR-PAL-2779.22.

Figure 6. Charophyte fructifications from the Upper Jurassic and Lower Cretaceous of the northern part of the Aquitaine Basin. A-G, *Clavator grovesii* from the Berriasian of Angeac-Charente (sample An3-4-SB). (A) Lateral view of a utricle, IGR-PAL-2780.6, (B) lateral view of a utricle, IGR-PAL-2779.27, (C) lateral view of a poorly calcified gyrogonite, IGR-PAL-2780.7, (D) lateral view of a utricle, IGR-PAL-2779.28, (E), lateral view of a utricle, IGR-PAL-2780.11, (F) lateral view of a utricle, IGR-PAL-2780.12, and (G) lateral view of a utricle, IGR-PAL-2779.30.

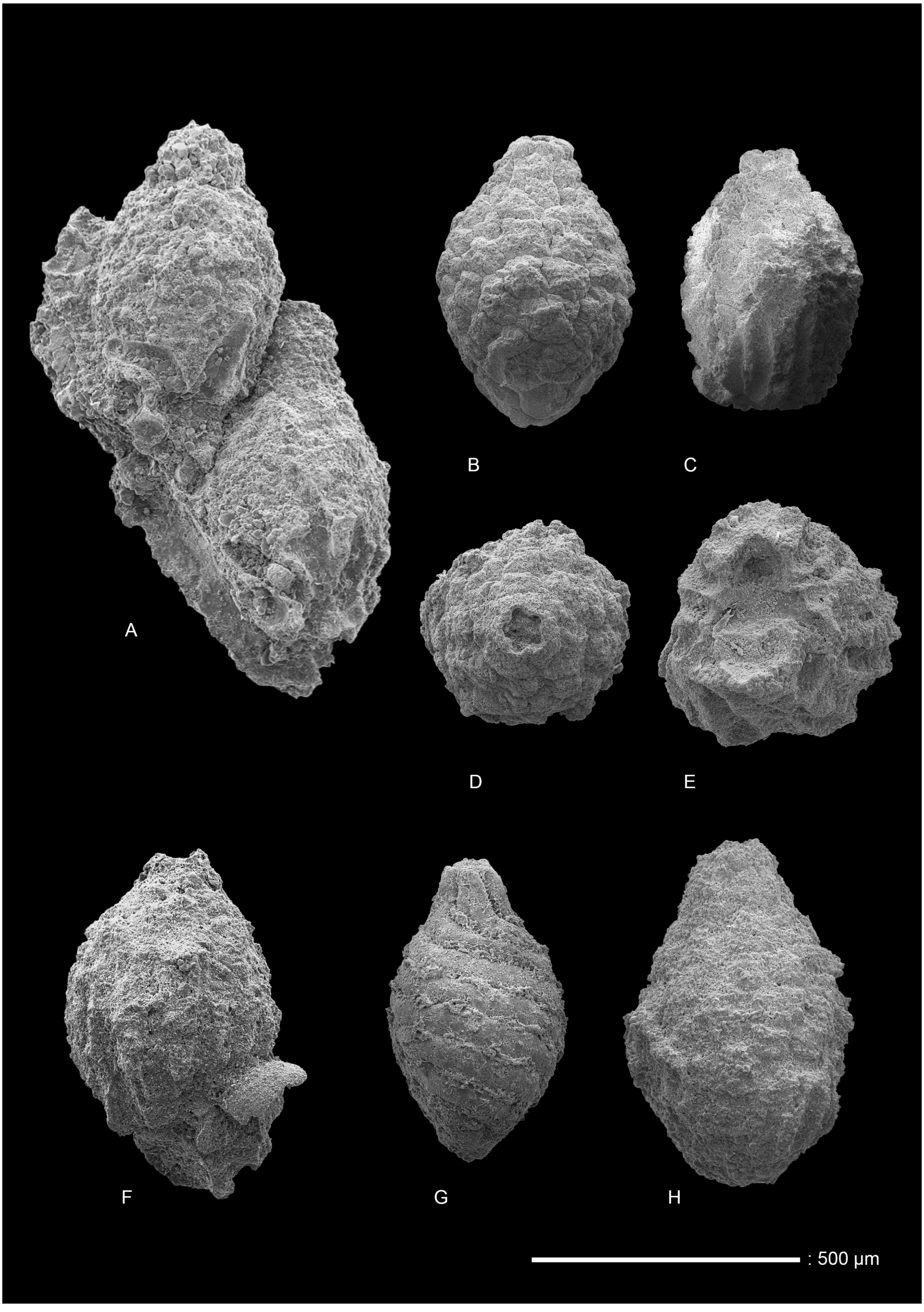
Figure 7. Stratigraphic distribution of species in Chassiron, Cherves-de-Cognac and Angeac-Charente.

Figure 8. Palaeogeographic and structural map of the different rift systems between the European and the Iberian plates during the Late Jurassic-Early Cretaceous, showing the position of the Charentes basin (modified from Tugend et al., 2015). Study area in the Charentes marked with a rectangle.

Table 1. Distribution of charophyte species and their abundance in the samples studied.

Lithostratigraphy / Locality / Samples / Species	Chassiron	Cherves-de-Cognac							Angeac-Charente				
	L148	C32	C33	C34	C35	C36	C38	C41	An1	An2	An3	An3-4	An4
Porochara westerbeckensis		•	•		⬤	•			·			⬤	
Latochara latitruncata	⬤												
Mesochara harrisii	●	·			·	·				·		●	
Nodosoclavator bradleyi	·	·								·		⬤	
Clavator grovesii		●		·	·	·						·	

· 0-10 • 11-50 ● 51-100 ⬤ >100


A
B
C
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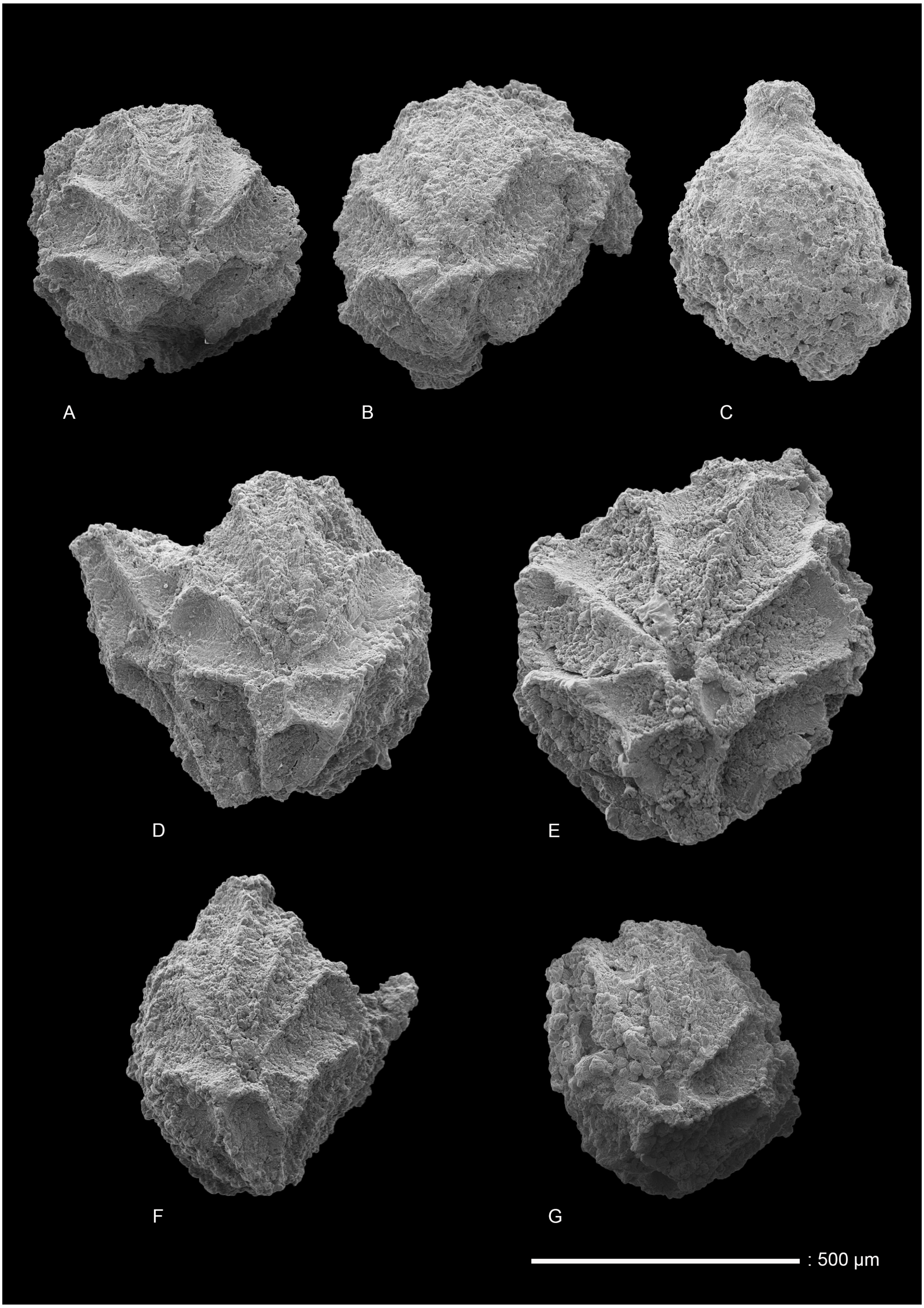
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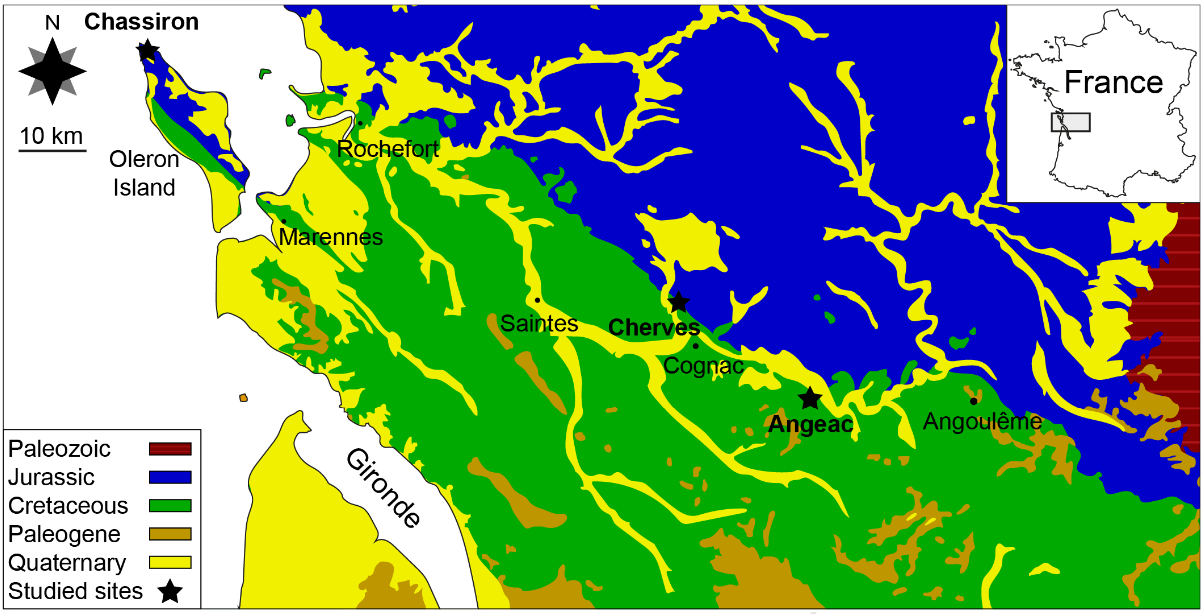
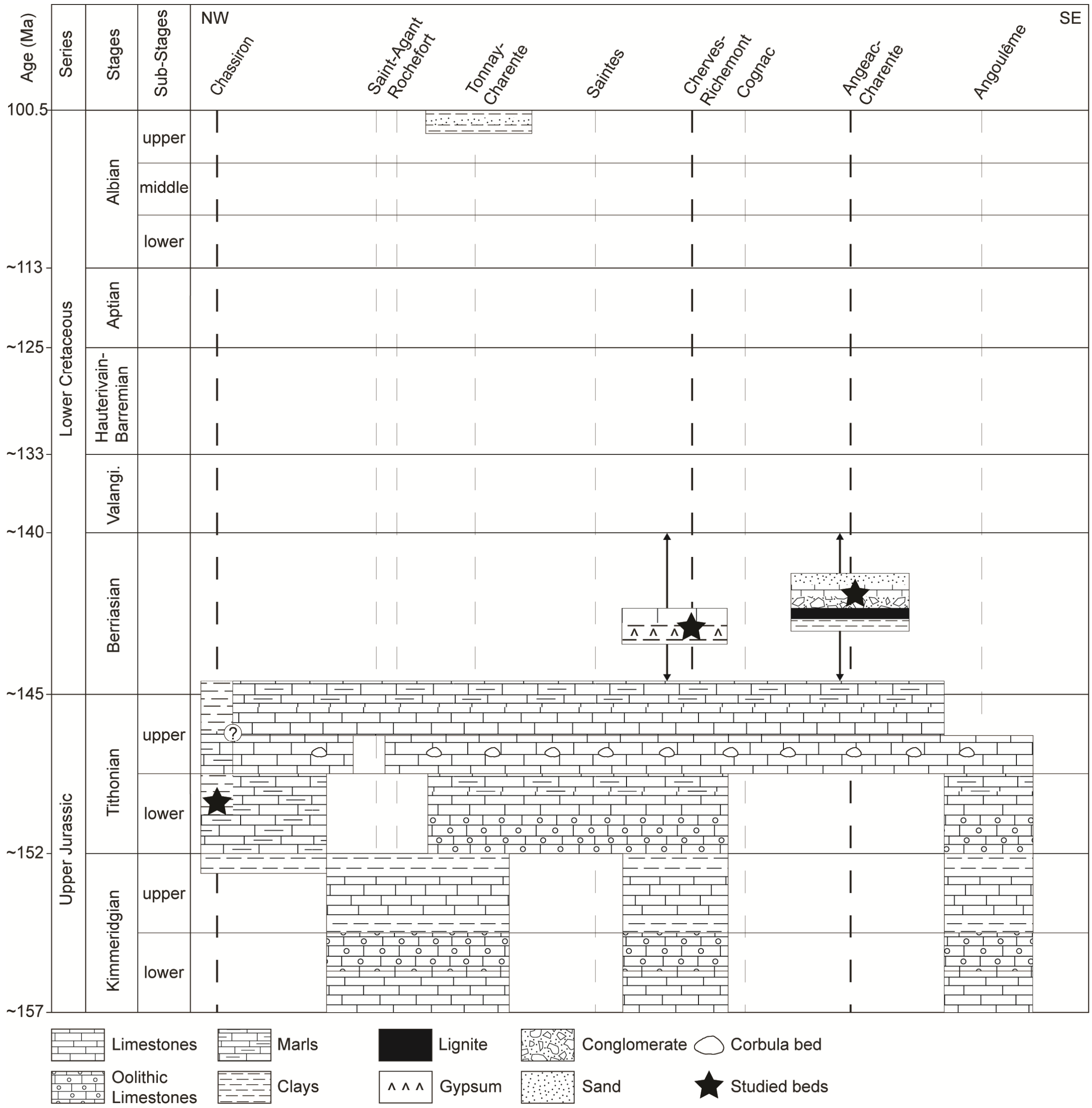
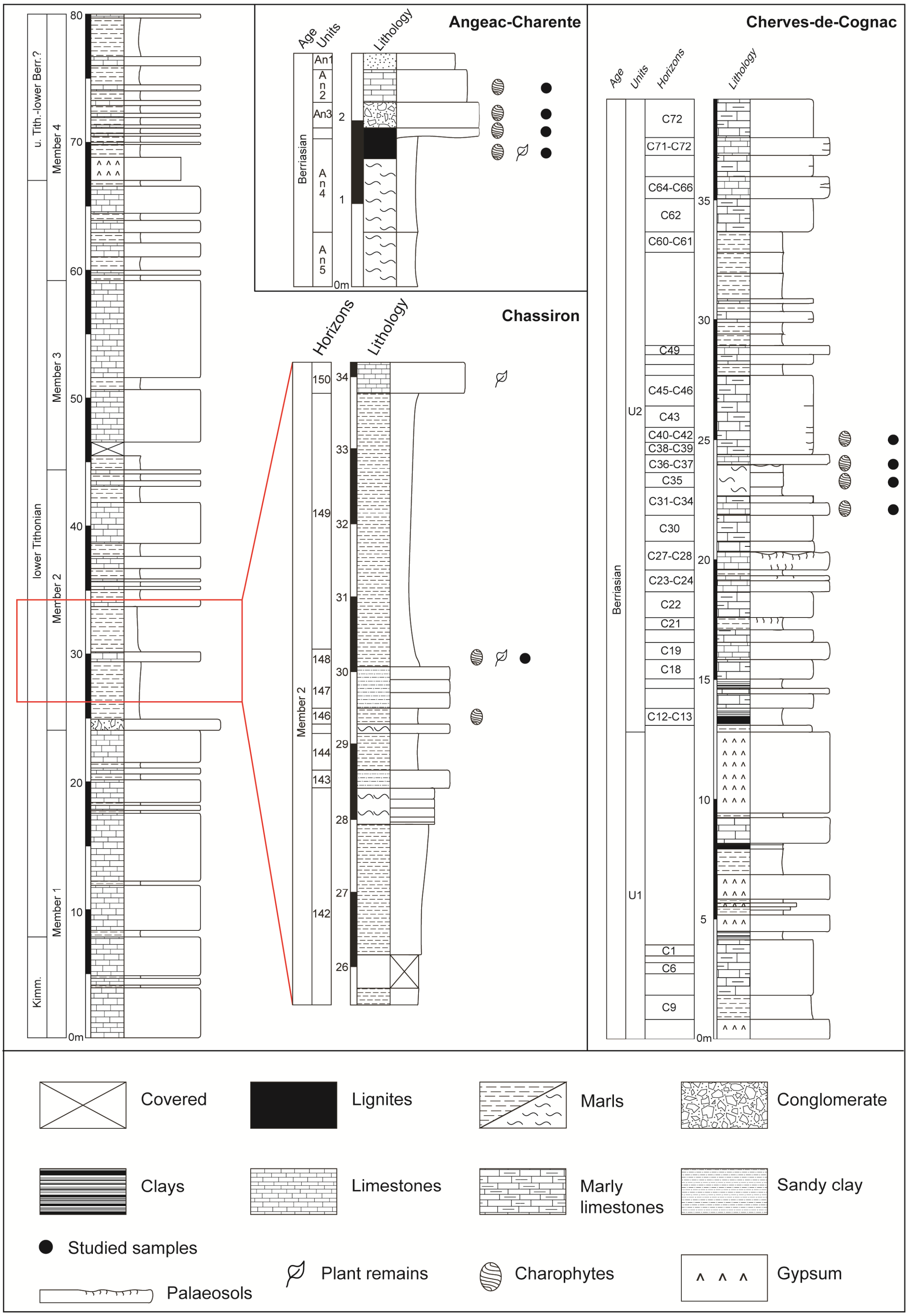
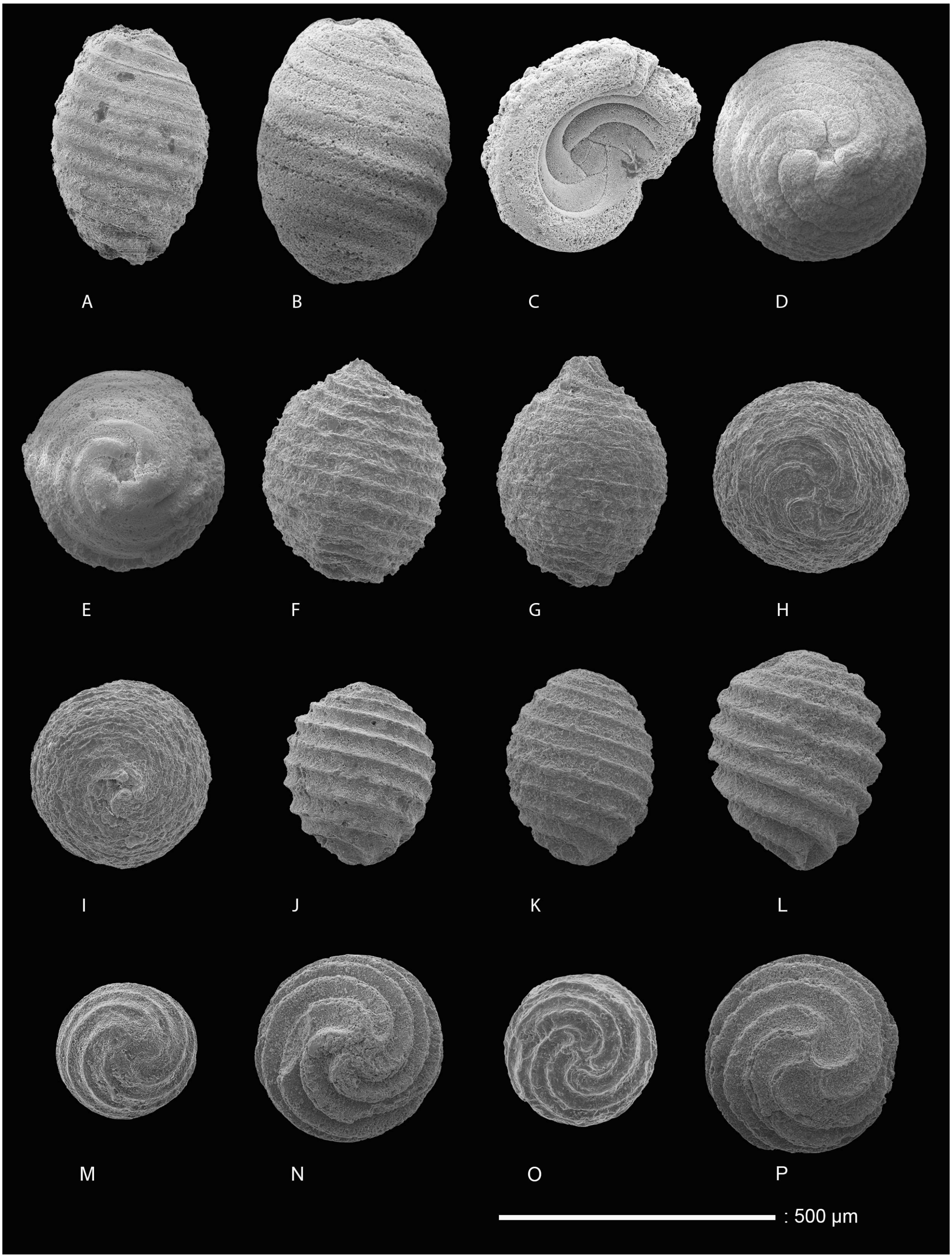

N
Chassiron
10 km
Oleron
Island
Rochefort
Marennes
Saintes
Cherves
Cognac
Angeac
Angoulême
Gironde
France
Paleozoic
Jurassic
Cretaceous
Paleogene
Quaternary
Studied sites



Age (Ma)
Series
Stages
Sub-Stages
NW
SE
Chassiron
Saint-Agant
Rochefort
Tonnay-
Charente
Saintes
Cherves-
Richemont
Cognac
Angeac-
Charente
Angoulême
100.5
~113
~125
~133
~140
~145
~152
~157
Lower Cretaceous
Upper Jurassic
Albian
Aptian
Hauterivain-
Barremian
Valangi.
Berriasian
Tithonian
Kimmeridgian
upper
middle
lower
upper
lower
upper
lower
?
Limestones
Oolithic
Limestones
Marls
Clays
Lignite
Gypsum
Conglomerate
Sand
Corbula bed
Studied beds



Angeac-Charente
Age
Units
Lithology
Berriasian
An1
An2
An3
An4
An5
0m
1
2
Chassiron
Horizons
Lithology
Member 2
150
149
148
147
146
144
143
142
26
27
28
29
30
31
32
33
34
Cherves-de-Cognac
Age
Units
Horizons
Lithology
Berriasian
U1
U2
C72
C71-C72
C64-C66
C62
C60-C61
C49
C45-C46
C43
C40-C42
C38-C39
C36-C37
C35
C31-C34
C30
C27-C28
C23-C24
C22
C21
C19
C18
C12-C13
C1
C6
C9
0m
5
10
15
20
25
30
35
Kimm.
lower Tithonian
u. Tith.-lower Berr.?
Member 1
Member 2
Member 3
Member 4
0m
10
20
30
40
50
60
70
80
Covered
Lignites
Marls
Conglomerate
Clays
Limestones
Marly limestones
Sandy clay
Studied samples
Palaeosols
Plant remains
Charophytes
Gypsum


A
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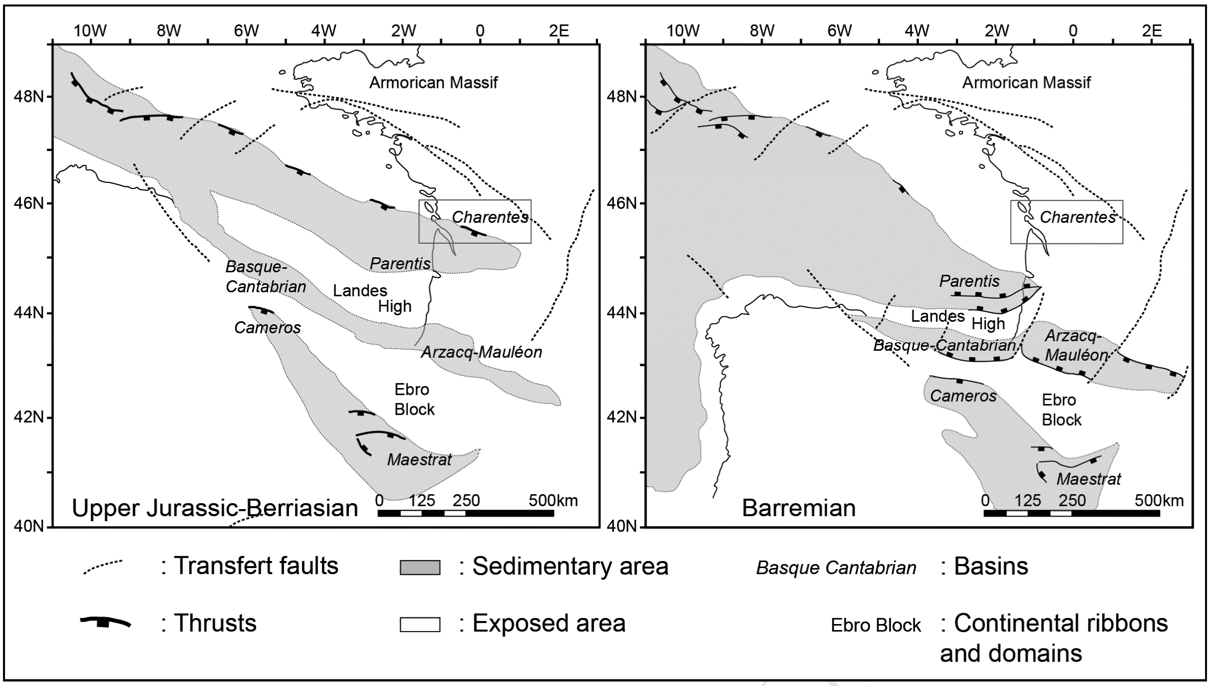
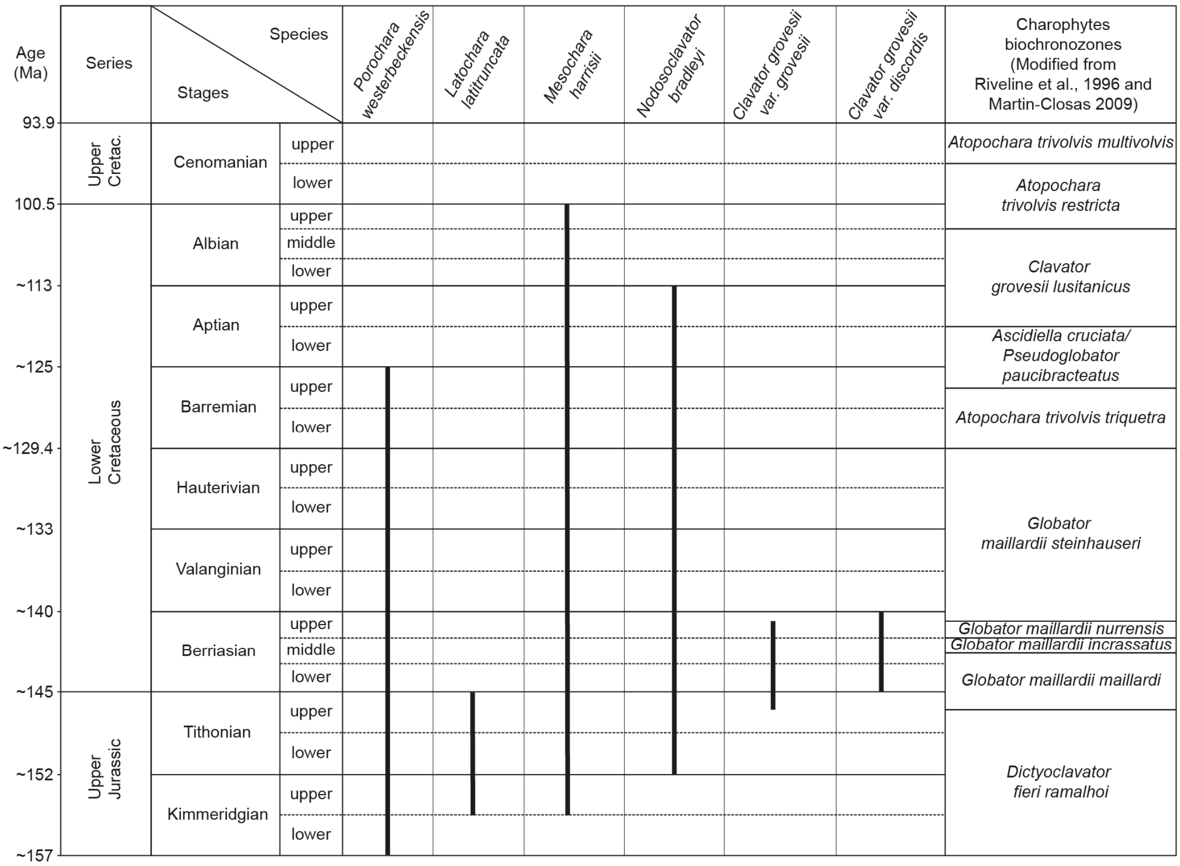
H
I
J
K
L
M
N
O
P
: 500 µm


10W
8W
6W
4W
2W
0
2E
48N
46N
44N
42N
40N
Armorican Massif
Charentes
Parentis
Basque-
Cantabrian
Landes
High
Cameros
Arzacq-Mauléon
Ebro
Block
Maestrat
Upper Jurassic-Berriasian
0
125
250
500km
Barremian
Parentis
Landes
High
Basque-Cantabrian
Arzacq-
Mauléon
Cameros
Ebro
Block
Maestrat
: Transfert faults
: Sedimentary area
Basque Cantabrian
: Basins
: Thrusts
: Exposed area
Ebro Block
: Continental ribbons and domains


Age (Ma)
Series
Species
Stages
Porochara westerbeckensis
Latochara latitruncata
Mesochara harrisii
Nodosoclavator bradleyi
Clavator grovesii var. grovesii
Clavator grovesii var. discordis
Charophytes biochronozones (Modified from Riveline et al., 1996 and Martin-Closas 2009)
93.9
100.5
~113
~125
~129.4
~133
~140
~145
~152
~157
Upper Cretac.
Lower Cretaceous
Upper Jurassic
Cenomanian
Albian
Aptian
Barremian
Hauterivian
Valanginian
Berriasian
Tithonian
Kimmeridgian
upper
middle
lower
Atopochara trivolvis multivolvis
Atopochara trivolvis restricta
Clavator grovesii lusitanicus
Ascidiella cruciata/ Pseudoglobator paucibracteatus
Atopochara trivolvis triquetra
Globator maillardii steinhauseri
Globator maillardii nurrensis
Globator maillardii incrassatus
Globator maillardii maillardi
Dictyoclavator fieri ramalhoi

Highlights

Charophytes from Charente are exclusively Tithonian-Berriasian in age

Former claims of Hauterivian-Barremian records are not confirmed in the Charente basin

The opening of the Biscay basin left no sedimentary record in the Charente basin.

Clavatoraceans dominated Berriasian assemblages over characeans and porocharaceans

Charophyte assemblages show increasing freshwater influence eastwards in the basin