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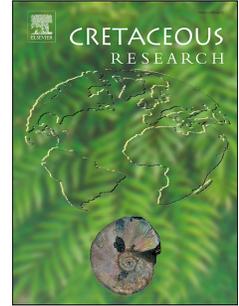
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A review of the Late Jurassic–Early Cretaceous charophytes from the northern Aquitaine Basin in south-west France

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

30

### 31 **Keywords**

32

33 Charophyta; Freshwater; Tithonian; Berriasian; Charentes basin

34

### 35 **Introduction**

36

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

45 Deak and Combaz (1967) were the first to find palynological indicators of the  
46 "Wealden", i.e., Lower Cretaceous non-marine strata, in the southern part of the north  
47 Aquitaine Basin. These observations were also made in the north-western part by Lanceron  
48 (1976), Platel and Moreau (1977) and Platel (1978). Much later, a number of studies devoted  
49 to the biostratigraphy of the Cretaceous northern Aquitaine Basin showed the occurrence of  
50 the Berriasian based on the presence of ostracodes, charophytes and dinoflagellates (Colin et

51 al., 2004; El Albani et al., 2004), as well as the occurrence of the Albian and Cenomanian  
52 (Néraudeau et al., 2002) and the Turonian (Néraudeau et al., 2016) based on palynological  
53 evidence. Moreover, a recent study indicated the possible occurrence of Hauterivian-  
54 Barremian deposits in Angeac-Charente (Néraudeau et al., 2012).

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

61

62 ----- Please insert Fig. 1 near here -----

63

#### 64 **Geological setting and stratigraphy**

65

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

71 The northern part of the Aquitaine Basin, sometimes referred to as “Charentes Basin”,  
72 is limited by normal faults with a north-west-south-east direction (Platel, 1980). The Upper  
73 Jurassic and Lowermost Cretaceous deposits predominantly contain carbonates, with  
74 evaporites at its edges (Platel, 1980; Cubaynes et al., 1989) and clayey or conglomeratic bone  
75 beds (Néraudeau et al., 2012; Vullo et al., 2012, 2014). The Lower Cretaceous record is

76 extremely limited in the northern Aquitaine Basin, especially for the Berriasian to Aptian  
77 (Fig. 2), while the uppermost Albian deposits are better represented (Néraudeau et al., 2002).  
78 A more complete sedimentary record of marine facies is present for the Cenomanian  
79 transgression, starting with detrital beds followed by limestone deposits.

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

91

92 ----- Please insert Fig. 2 near here -----

93

94 From a palaeogeographical viewpoint, it is assumed that the Aquitaine Basin was a  
95 shallow and narrow gulf opening onto the Atlantic domain during the latest Jurassic and  
96 earliest Cretaceous (Cubaynes et al., 1989; Hantzpergue and Lafaurie, 1994; Schnyder et al.,  
97 2012). During the Kimmeridgian, the Aquitaine Basin was linked to the Paris Basin by the  
98 Poitou threshold in its north-eastern part, but this connection ceased before the Tithonian  
99 (Thierry, 2000; Schnyder et al., 2012) due to the regressive trend starting in the latest  
100 Kimmeridgian (Hantzpergue, 1989). According to Thierry (2000) and Blakey (2011), some

101 connections with the western Tethys persisted in the Early Cretaceous through the Corbières-  
102 Provence platform to the south-east and the Dauphiné Basin to the north-east.

103

104 The Jurassic and Cretaceous from northern Aquitaine have been studied as early as the  
105 beginning of the 19<sup>th</sup> century by Fleuriau de Bellevue (1801) and d'Archiac (1837), among  
106 others, who concluded that the Lower Cretaceous was not represented in that part of the basin,  
107 a hypothesis that had been widely accepted until recently (Platel, 1980; Néraudeau et al.,  
108 2012). In the two last decades, a number of studies have provided evidence that the Lower  
109 Cretaceous is indeed represented (Schnyder, 2003; Billon-Bruyat, 2003; Colin et al., 2004;  
110 Néraudeau et al., 2002, 2012; Vullo et al., 2014). Thus, the present study aimed to perform a  
111 detailed review of the Lower Cretaceous records in three different areas of the “Charentes  
112 Basin”, Chassiron (Oléron Island) in the western part, Cherves-de-Cognac in the central part  
113 and Angeac-Charente in the eastern part (Fig. 1).

114

115 Chassiron (Oléron Island)

116

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

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

133           The third member, with a thickness of 23 m, is composed of limestone beds at the base  
134 (6 m), followed by 4 m of alternating limestone and clay, with brackish bivalves (e.g.,  
135 *Mactra*) and diverse marine species (such as corals, brachiopods, echinoids, bivalves, benthic  
136 foraminifera, ostracods and *Rhizocorallium* burrows). This member corresponds to  
137 sedimentation occurring in a shallow lagoon and other coastal environments, with normal  
138 salinity that has been occasionally subjected to storms (Schnyder et al., 2012).

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

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

149 from the late Kimmeridgian (Autissiodorensis Zone) to late-early Tithonian or early  
150 Berriasian.

151

152 Cherves-de-Cognac

153

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

159 The second unit (U2) shows alternating marlstone laminites and gypsum that  
160 progressively gives way to fossiliferous marly limestones in the upper parts (Colin et al., 2004;  
161 El Albani et al., 2004). This unit indicates both marine and freshwater influences in an  
162 estuarine context (El Albani et al., 2004). It contains a 1-m-thick bone bed that bears a  
163 particularly rich vertebrate fauna including fish, crocodylians and chelonians (Colin et al.,  
164 2004). Charophyte specimens were found in beds C32 to C36, C38 and C41, including the  
165 bone bed (Fig. 3). Colin et al. (2004) undertook a preliminary study of these charophytes and  
166 here, we will review the flora in depth. The Cherves-de-Cognac study area lies directly over  
167 Tithonian marine limestone (El Albani et al., 2004).

168

169 Angeac-Charente

170

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

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

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

195

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

197

198 **Material and methods**

199

## 200 Sample collection

201

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

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

211 The Angeac-Charente samples were obtained from palaeontological excavations in  
212 2010. Samples from beds An1 (An1-SA), An2 (An2-SA) and An4 (An4-SA) were obtained  
213 from the first excavation (ANG1-02-2010), while samples from An3-4 (An3-4-SB) were  
214 collected from the second excavation (ANG2-02-2010), located about 20 m north of the site  
215 of the first excavation (Néraudeau et al., 2012).

216

## 217 Sample preparation

218

219 Samples were disaggregated in a solution of water and hydrogen peroxide (100  
220 volumes), washed and then sieved through 200, 500 and 1000  $\mu\text{m}$  mesh sieves. In some cases,  
221 anhydrous sodium carbonate was added to deflocculate the clay. Before sieving, sieves were  
222 submerged in a solution of methylene blue to mark the residues of previous samples and then  
223 washed. Charophyte remains (thalli, gyrogonites and utricles) were manually picked out under

224 a Wild M5A stereomicroscope at 40x magnification. When necessary, an ultrasonic cleaner  
225 was used. Measurements were performed with the software Motic Images Plus 2.0 ML in a  
226 Motic BA310 stereomicroscope. Selected fructifications were photographed with a Quanta  
227 200 scanning electron microscope at the Scientific and Technical Services of the Universitat  
228 de Barcelona (UB). The gyrogonite and utricle specimens were stored in the Universities of  
229 Rennes (France) and Barcelona (Catalonia, Spain). Specifically all figured specimens,  
230 labelled IGR-PAL are stored in the collections of the University of Rennes (France).

231

## 232 **Systematic palaeontology**

233

### 234 **Division Charophyta MIGULA, 1897**

#### 235 **Class Charophyceae SMITH, 1938**

#### 236 **Order Charales LINDLEY, 1836**

#### 237 **Family Porocharaceae GRAMBAST, 1962 emend. SCHUDACK, 1993**

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

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

240

Fig. 4 (A-E).

241

242 1952 *Aclistochara westerbeckensis* nov. spec. – Mädlér, p. 28-29, pl. B, fig. 20-25.

243 1955 *Porochara westerbeckensis* nov. comb. – Mädlér, p. 271.

244

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

247

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

255

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

261

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

268

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

270

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

272

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

273 Fig. 4 (F-I).

274 1937 *Aclistochara latitruncata* PECK, n. sp. – PECK, p. 89, pl. 14, figs 1-4

275 1955 *Latochara latitruncata* (PECK) nov. comb. – MÄDLER, p. 271

276 1957 *Latochara latitruncata* (PECK) – PECK, p. 32-33, pl. 5, figs. 7, 21-23

277 1957 *Latochara collina* PECK, n. sp. – PECK, p. 33, pl. 5, figs 1-4.

278 1957 *Latochara concinna* PECK, n. sp. – PECK, p. 34, pl. 5, figs. 5-6, 8-9

279

280

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

282

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

291

292 Remarks. Peck (1957) noticed some similarities between *L. latitruncata* and *L.*  
293 *concinna*, and suggested also that *L. collina* was a subspecies of *L. latitruncata*. Schudack  
294 (1993) and Martín-Closas et al. (2008) regarded the three species as synonymous.

295

296 Distribution. This species has been identified in the Morrison Formation  
297 (Kimmeridgian to Tithonian in age) in the United States of America (Peck, 1957), from the

298 lower Tithonian of north-west Germany (Schudack, 1990, 1993) and in the Tithonian from  
299 Ukraine (Shaikin, 1967). Martín-Closas et al. (2008) also described this species from the same  
300 area as that studied here.

301

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

304 **Genus *Mesochara* GRAMBAST, 1962**

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

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

307 Fig. 4 (J-P).

308 1952 *Tolypella harrisii* nov. spec. – Mädlér, p. 31-32, pl. B, fig.31-35

309 1952 *Tolypella amoena* nov. spec. – Mädlér, p. 34-35, pl. B, fig. 43-49

310 1952 *Tolypella minuta* nov. spec. – Mädlér, p. 35-36, pl. B, fig. 50-52

311 1967 *Mesochara harrisii* SHAÏKIN nov. comb. – Shaikin, p. 47

312

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

315

316 Description. The specimens from Chassiron provide the only abundant population of  
317 this species in the northern Aquitaine Basin. They present small gyrogonites ranging from 239  
318 to 341  $\mu\text{m}$  in height and 190 to 312  $\mu\text{m}$  in width, with a spheroidal to prolate shape (ISI  
319 ranging from 100 to 142). The spiral cells are concave to almost flat and join at the apex  
320 without any modification. The base and apex are generally rounded, but are slightly pointed in  
321 some cases. The number of convolutions in lateral view ranges between 8 and 11, generally 9,  
322 with a mean width of 36.75  $\mu\text{m}$  at the equator. Some of the specimens from Angeac are

323 slightly larger (353 to 403  $\mu\text{m}$  high and 303 to 361  $\mu\text{m}$  wide) and more spheroidal (ISI,  
324 108–127). A basal plate cannot be observed, but is probably unicellular, based on gyrogonites  
325 of the same species from other European areas.

326

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

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

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

347

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

359

360 **Family Clavatoraceae PIA, 1927**

360

361 **Subfamily Clavatoroidae GRAMBAST, 1969 emend. MARTÍN-CLOSAS 1989 ex**

361

362 **SCHUDACK, 1993**

362

363 **Genus *Nodosclavator* MASLOV, 1963 emend. GRAMBAST, 1966**

363

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

364

365 Fig. 5 (A-H).

365

366

367 1939 *Clavator bradleyi* sp. nov. – HARRIS, p. 53-54, pl. XVI, fig. 1, 3-5, 7.

367

368 1969 *Nodosclavator bradleyi* (HARRIS) nov. comb. – GRAMBAST, p. 881, pl. 33, fig. 5.

368

369

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

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

379

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

387

388 Distribution. This species has been identified by Colin et al. (2004) and El Albani et  
389 al. (2004) in Cherves-de-Cognac (dating back to the Berriasian) and by Néraudeau et al.  
390 (2012) in Angeac-Charente. Outside France, it has been observed in the Lower Saxony basin  
391 of Germany from the lower Tithonian (Schudack, 1993) and in the palustrine areas of the  
392 Iberian Chain in Spain from the Tithonian to Barremian (Martín-Closas, 2000). In the United  
393 States, *N. bradleyi* has been reported to occur in the Cedar Mountain Formation (Utah) from  
394 the upper Berriasian and lower Valanginian and more rarely in the Lakota Formation, South  
395 Dakota (Martín-Closas et al., 2013), where it had already been identified by Peck (1957).

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

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**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  $\mu\text{m}$  in height and 364 to 533  $\mu\text{m}$  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.

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

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

434  
435           Distribution. *Clavator grovesii* var. *grovesii* has been observed to occur in England  
436 from the Tithonian and Berriasian in the Dorset and Weald Basins (Harris, 1939; Feist et al.,  
437 1995), in France (Colin et al., 2004; El Albani et al., 2004; Néraudeau et al., 2012), in the  
438 Swiss Jura (Häfeli, 1966; Mojon and Strasser, 1987; Détraz and Mojon, 1989), Spain  
439 (Schudack, 1993; Martín-Closas, 2000) and north-west Germany (Schudack, 1993). It has  
440 also been found in China from the Berriasian or Valanginian (Wang et al., 1976; and Hao et  
441 al., 1983). Martín-Closas et al. (2013) reported on its occurrence in the Berriasian from North  
442 America, suggesting that this species was the first clavatoracean to reach a cosmopolitan  
443 distribution in a subtropical latitudinal area of the Northern Hemisphere (Martín-Closas,  
444 2015). *C. grovesii* var. *discordis* is also present in Berriasian strata from Spain, often together  
445 with *C. grovesii* var. *grovesii* (Schudack, 1993; Martín-Closas, 2000).

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447 ----- Please insert Fig. 6 near here -----

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449

450 **Discussion**

451

## 452 Taphonomy

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

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

468 The population from Angeac-Charente (An3-4-SB) presented significant similarities to  
469 that from Cherves-de-Cognac. *N. bradleyi* and *C. grovesii* utricles were well preserved and  
470 associated with the calcified parts of clavatoracean thalli. This observation is sufficient to  
471 justify the autochthony of the assemblage, in contrast to that proposed by Néraudeau et al.  
472 (2012). Characean and porocharacean gyrogonites were generally well preserved, but their

473 thalli were absent. The An2-SA samples contained relatively corroded porocharacean  
474 gyrogonites compared to An3-4-SB specimens. This corrosion, in the form of spiral cells with  
475 alveolar surfaces, has been attributed to epidiagenetic processes (Martín-Closas and  
476 Grambast-Fessard, 1986).

477

#### 478 Palaeoecology

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

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

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

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

512

### 513 Biostratigraphy

514 The three study sites enabled us to revisit the biostratigraphic implications of the latest  
515 Jurassic and Early Cretaceous charophyte assemblages in the northern part of the Aquitaine  
516 Basin (Fig. 7). The assemblages from Chassiron were represented by *L. latitruncata*, *M.*  
517 *harrisii* and rarely *N. bradleyi*. The occurrence of *L. latitruncata* suggests that the  
518 assemblages dated from the Kimmeridgian to the late Tithonian, which is consistent with the  
519 age obtained from the associated fauna. By contrast, the assemblages from Cherves-de-  
520 Cognac and Angeac-Charente consisted of *N. bradleyi* (which was the predominant species in  
521 An3-4-SB in Angeac-Charente), *M. harrisii* and *P. westerbeckensis* together with *Clavator*  
522 *grovesii* var. *grovesii* and *C. grovesii* var. *discordis*. The two latter clavatoracean taxa are of

523 biostratigraphic interest as they form part of the *Flabellochara-Clypeator* anagenetic lineage  
524 described by Grambast (1970, 1974). These taxa are typically found in the uppermost  
525 Tithonian and Berriasian strata in Europe (Schudack, 1993; Martín-Closas, 2000), within the  
526 Maillardi, Incrassatus and Nurrensis charophyte biozones (Riveline et al., 1996). Our findings  
527 agree with those of previous studies on samples from Cherves-de-Cognac (Colin et al., 2004;  
528 El Albani et al., 2004), but disagree with the date of the Angeac-Charente bone bed proposed  
529 by Néraudeau et al. (2012). Using a complex fossil assemblage of terrestrial, freshwater,  
530 brackish and marine organisms, Néraudeau et al. (2012) proposed a Hauterivian-Barremian  
531 age mainly based on a few specimens of the dinoflagellate *Odontochitina imparilis*  
532 (DUXBURY) JAIN and KHOWAJA-ATEEQUZZAMAN and the benthic foraminifer  
533 *Trocholina cf. odukpaniensis* DESSAUVAGIE. The other fossils were typical of older ages,  
534 such as the bryozoans and charophytes, and were considered partly or totally reworked. This  
535 dating of the bone bed is refuted here based on the charophyte taphonomic data mentioned  
536 above (Fig. 8).

537

538 ----- Please insert Fig. 7 near here -----

539 Implications for basin evolution

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

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

555

556 ----- Please insert Fig. 8 near here -----

557

## 558 **Conclusions**

559

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

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

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

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

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

590

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600

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867 **Figure legends**

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

870 **Figure 2.** Stratigraphic framework of the Charentes Basin.

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

874 **Figure 4.** Charophyte fructifications from the Upper Jurassic and Lower Cretaceous of the  
875 northern part of the Aquitaine Basin. A-E, *Porochara westerbeckensis* from the Berriasian of  
876 Angeac-Charente. (A) Lateral view of a gyrogonite from sample An2-SA, IGR-PAL-2779.12;  
877 (B) lateral view of a gyrogonite (sample An3-4-SB), IGR-PAL-2779.13; (C) a multipartite  
878 basal plate (sample An3-4-SB), IGR-PAL-2779.32; (D) basal view of a gyrogonite (sample  
879 An3-4-SB), IGR-PAL-2779.15; and (E) apical view of a gyrogonite (sample An3-4-SB),  
880 IGR-PAL-2779.16. F-I, *Latochara latitruncata* from the lower Tithonian of Chassiron (level  
881 148). (F,G) Lateral views, IGR-PAL-2779.3 and IGR-PAL-2779.5; (H) basal view, IGR-  
882 PAL-2779.6, (I) apical view, IGR-PAL-2779.4. J-P, *Mesochara harrisii* from level 148 of the  
883 lower Tithonian of Chassiron (J, M, O) and from level An3-4-SB of the Berriasian of Angeac-  
884 Charente (H-L,N,P) . (J) Lateral view of a gyrogonite, IGR-PAL-2779.7; (K) lateral view,  
885 IGR-PAL-2779.17; (L) lateral view, IGR-PAL-2779.18; (M) basal view, IGR-PAL-2779.10;  
886 (N) basal view, IGR-PAL-2779.20; (O) apical view, IGR-PAL-  
887 2779.9; and (P) apical view, IGR-PAL-2779.19.

888 **Figure 5.** Charophyte fructifications from the Upper Jurassic and Lower Cretaceous of the  
889 northern part of the Aquitaine Basin. A-H, *Nodosoclavator bradleyi* from level 148 of the  
890 lower Tithonian Chassiron (A) and from the Berriasian of Angeac, samples An4 (B) and An3-  
891 4-SB (C-F, H) and An2-SA (G). (A) Lateral view of two utricles still attached to the phylloid,

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

898 **Figure 6.** Charophyte fructifications from the Upper Jurassic and Lower Cretaceous of the  
899 northern part of the Aquitaine Basin. A-G, *Clavator grovesii* from the Berriasian of Angeac-  
900 Charente (sample An3-4-SB). (A) Lateral view of a utricle, IGR-PAL-2780.6, (B) lateral view  
901 of a utricle, IGR-PAL-2779.27, (C) lateral view of a poorly calcified gyrogonite, IGR-PAL-  
902 2780.7, (D) lateral view of a utricle, IGR-PAL-2779.28, (E), lateral view of a utricle, IGR-  
903 PAL-2780.11, (F) lateral view of a utricle, IGR-PAL-2780.12, and (G) lateral view of a  
904 utricle, IGR-PAL-2779.30.

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

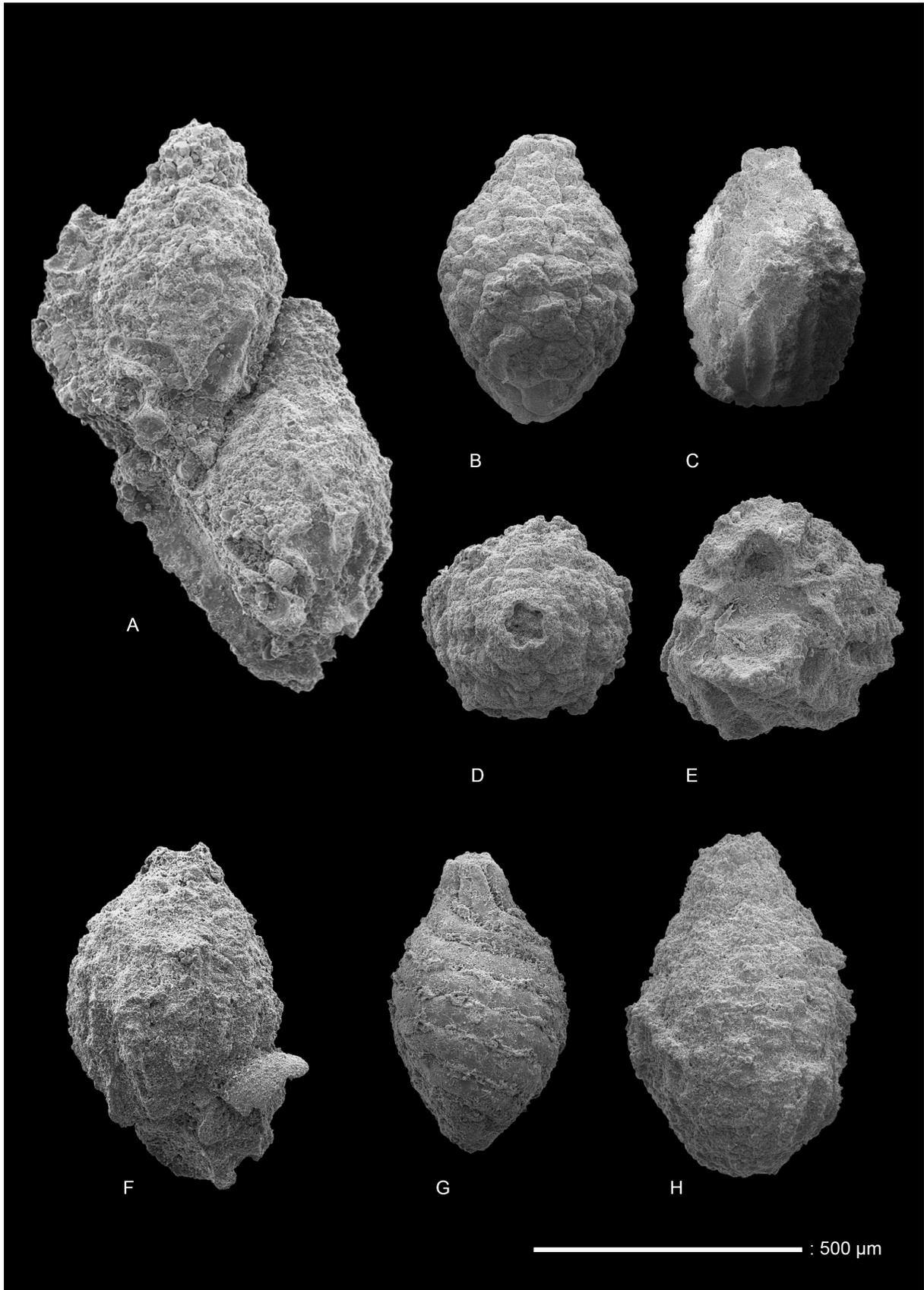
907 **Figure 8.** Palaeogeographic and structural map of the different rift systems between the  
908 European and the Iberian plates during the Late Jurassic-Early Cretaceous, showing the  
909 position of the Charentes basin (modified from Tugend et al., 2015). Study area in the  
910 Charentes marked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

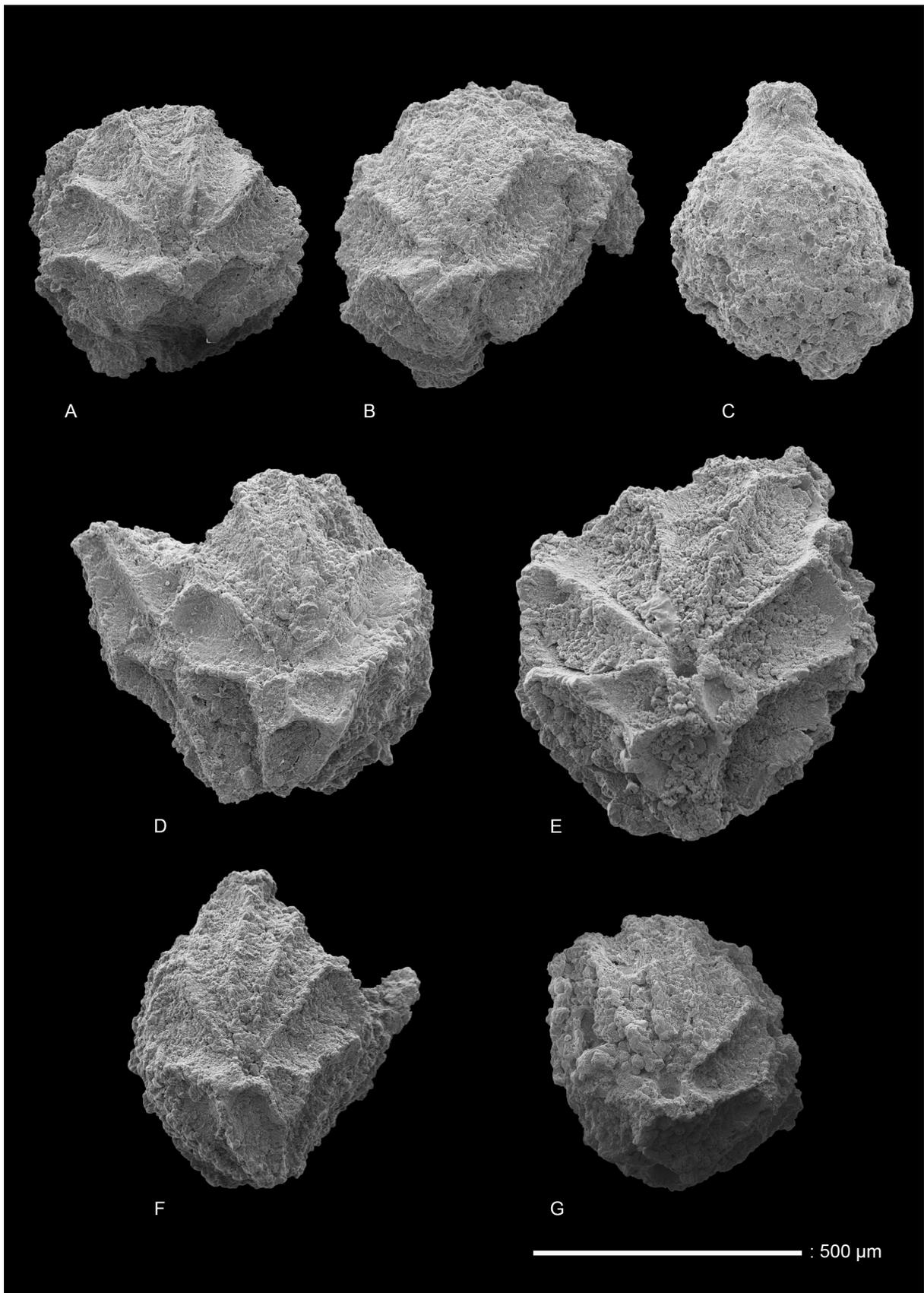
911 **Table 1.** Distribution of charophyte species and their abundance in the samples studied.

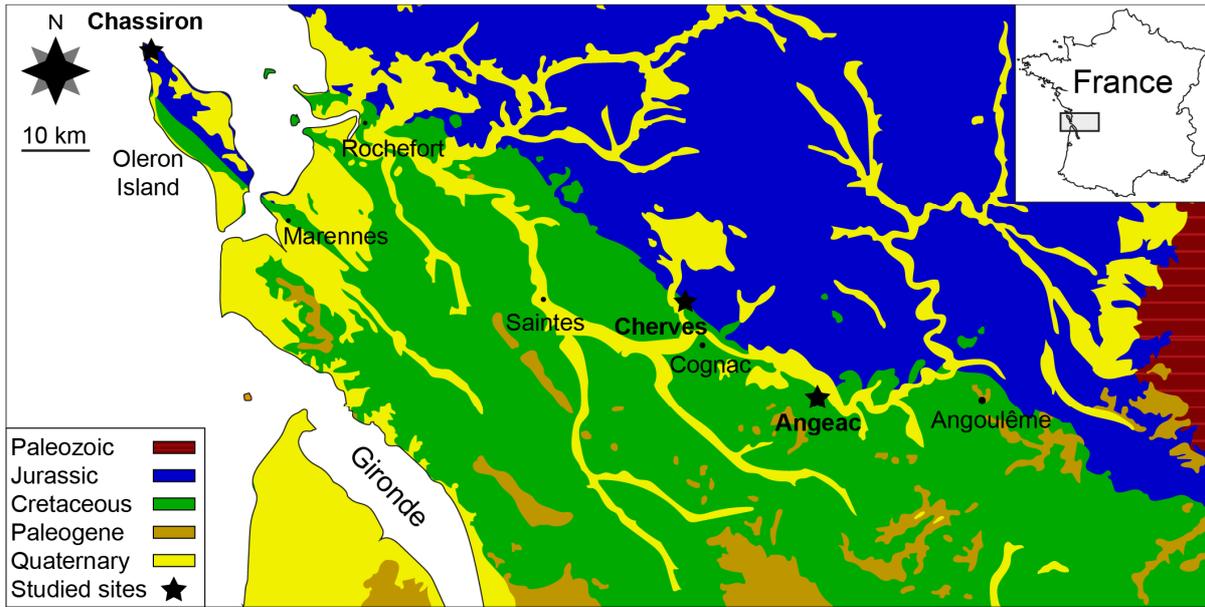
Lithostratigraphy Locality	Samples	Cherves-de-Cognac								Angeac-Charente				
		L148	C32	C33	C34	C35	C36	C38	C41	An1	An2	An3	An3-4	An4
<i>Porochara westerbeckensis</i>			•	•		●	•			•			●	
<i>Latochara latitruncata</i>		●												
<i>Mesochara harrisii</i>		•	•			•	•				•		•	
<i>Nodosoclavator bradleyi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

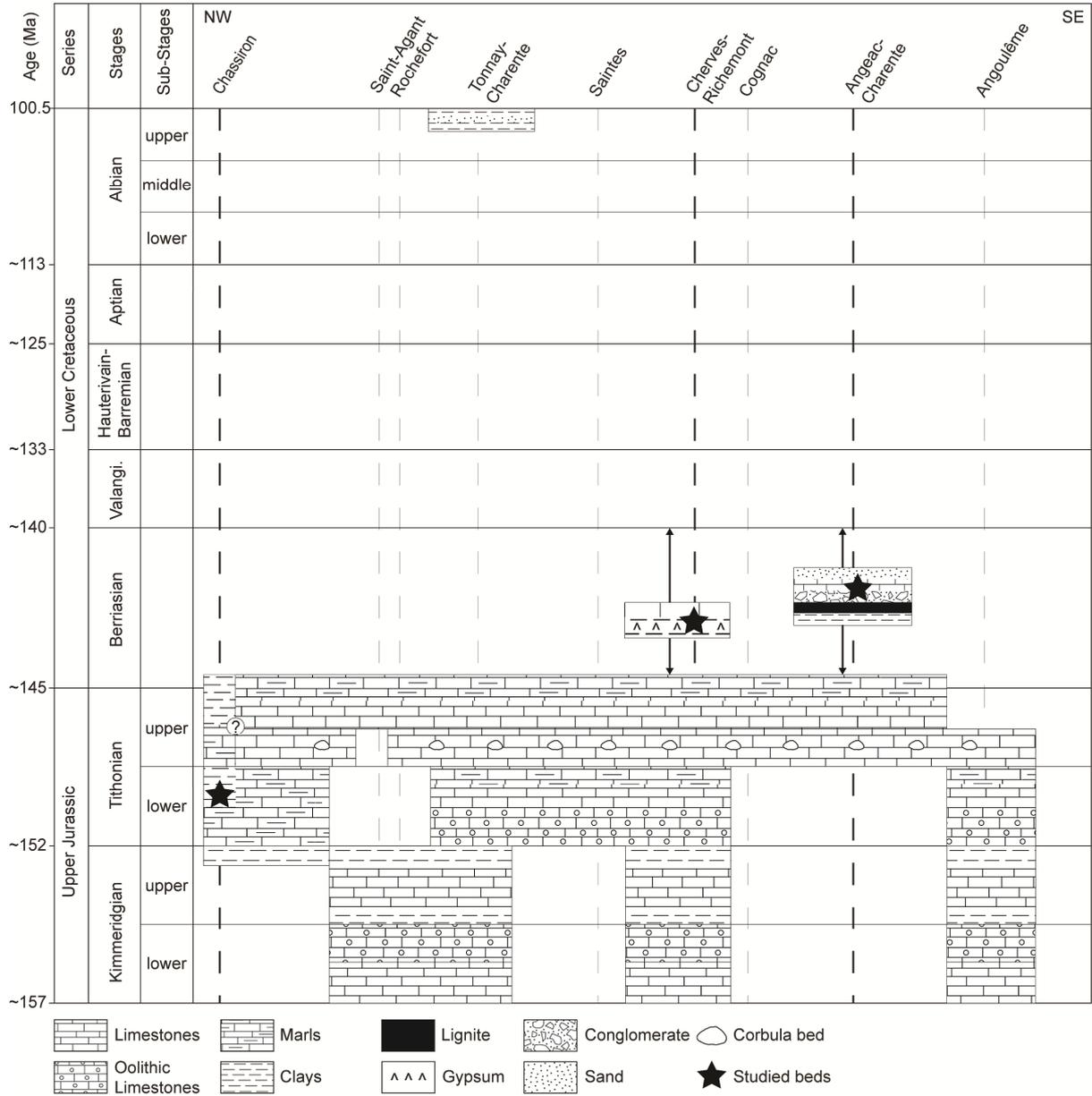
• 0-10    • 11-50    • 51-100    ● >100

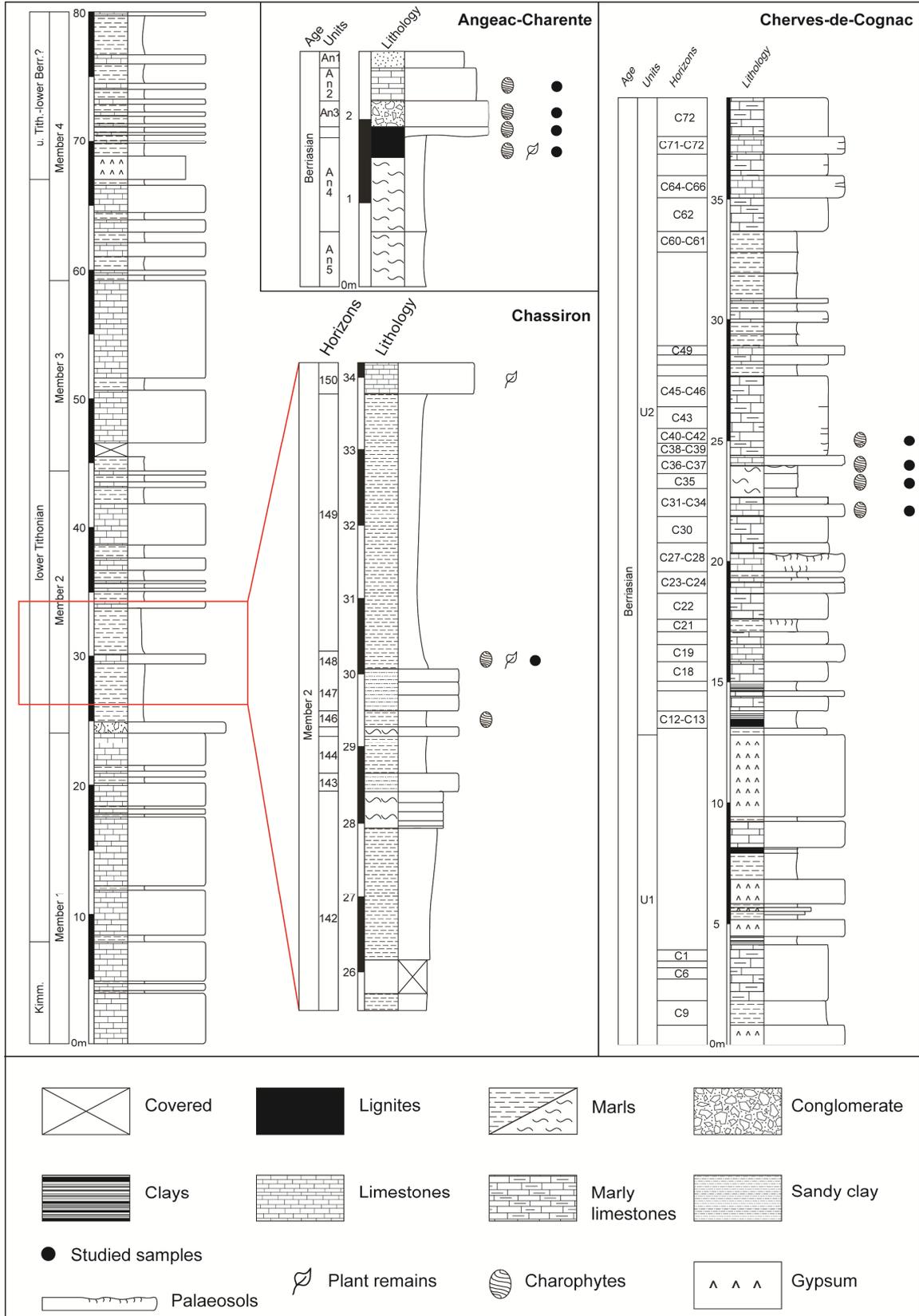
ACCEPTED MANUSCRIPT







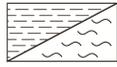




Covered



Lignites



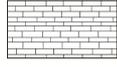
Marls



Conglomerate



Clays



Limestones



Marly limestones



Sandy clay

● Studied samples

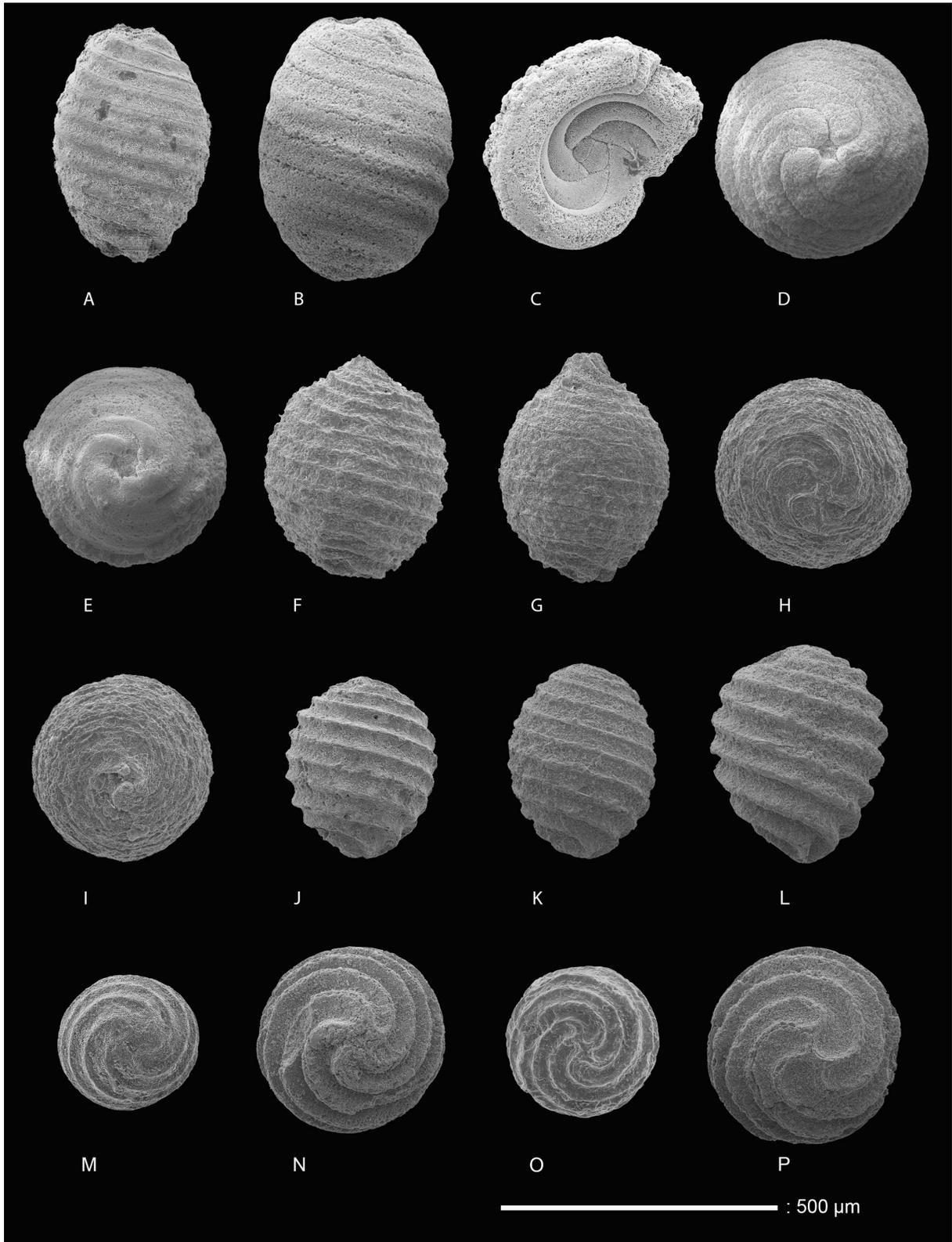


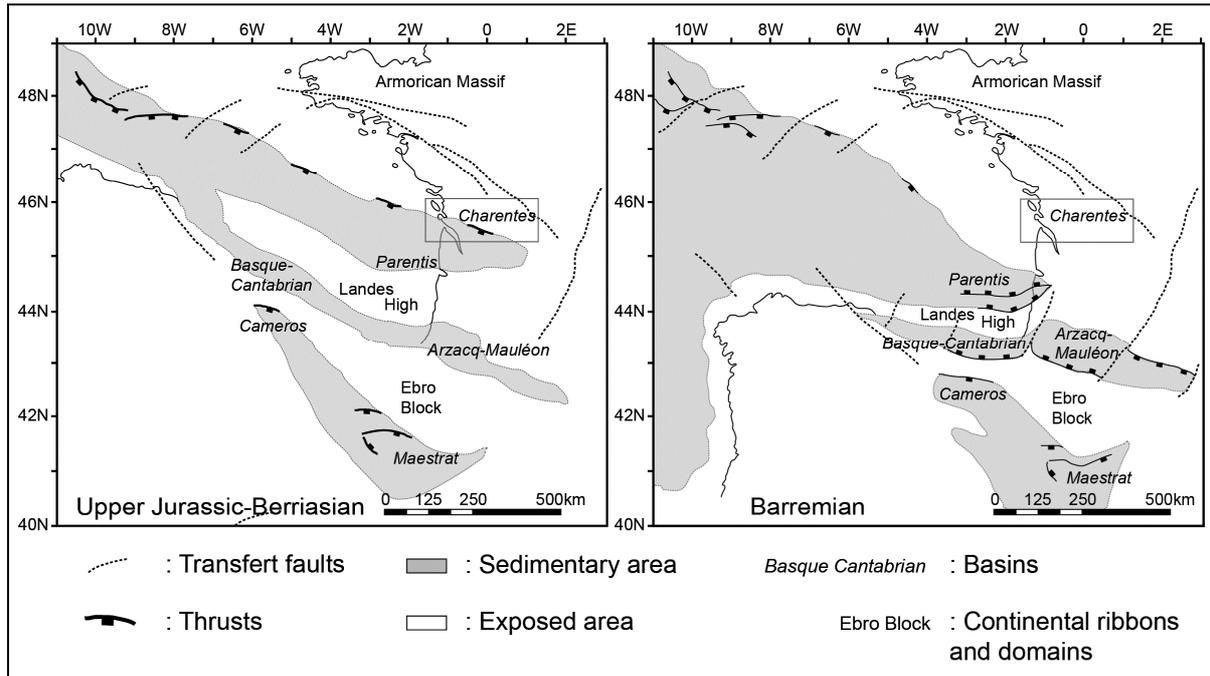
Palaeosols

🌿 Plant remains

🍄 Charophytes

△ △ △ Gypsum







## 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