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► To cite this version:

Delphine Desmares, Marc Testé, Bérengère Broche, Maxime Tremblin, Silvia Gardin, et al.. High-resolution biostratigraphy and chemostratigraphy of the Cenomanian stratotype area (Le Mans, France). *Cretaceous Research*, 2020, 10.1016/j.cretres.2019.104198 . hal-02328773

HAL Id: hal-02328773

<https://hal.science/hal-02328773>

Submitted on 23 Oct 2019

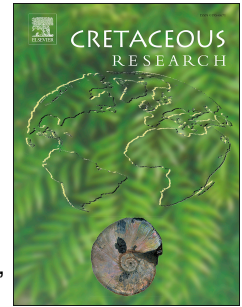
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Journal Pre-proof

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PII: S0195-6671(19)30086-2

DOI: <https://doi.org/10.1016/j.cretres.2019.104198>

Reference: YCRES 104198

To appear in: *Cretaceous Research*

Received Date: 1 March 2019

Revised Date: 12 July 2019

Accepted Date: 31 July 2019

Please cite this article as: Desmares, D., Testé, M., Broche, B., Tremblin, M., Gardin, S., Villier, L., Masure, E., Grosheny, D., Morel, N., Raboeuf, P., High-resolution biostratigraphy and chemostratigraphy of the Cenomanian stratotype area (Le Mans, France), *Cretaceous Research*, <https://doi.org/10.1016/j.cretres.2019.104198>.

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1 High-resolution biostratigraphy and chemostratigraphy of the Cenomanian stratotype area (Le
2 Mans, France)

3

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21 Highlights

22

23 - Biostratigraphy and chemostratigraphy of the Cenomanian stratotype area

24 - Description of *Praeglobotruncana rillella* nov. sp. and of *Dicarinella falsohelvetica* nov. sp.

25 - Change in coiling direction among *Muricohedbergella delrioensis* during the OAE2

26 - $\delta^{18}\text{O}$ offset between left- and right-coiled *M. delrioensis*

27 - Correlation between Pueblo (GSSP) and Le Mans area (area of historical type section for the
28 Cenomanian stage)

29

30

31 Abstract

32

33 The definition of the Cenomanian stage was based on the description of several type
34 sections scattered in the vicinity of Le Mans (Sarthe, France). Despite limited exposures
35 nowadays, the area remains a reference for the palaeontology of the Cenomanian due to its
36 outstanding richness in marine macrofossils, especially molluscs, bryozoans, brachiopods and
37 echinoderms. The publication in 2015 of the volume dedicated to the Cenomanian stratotype
38 yielded the opportunity to restudy the last accessible outcrops. This paper provides a high-
39 resolution stratigraphic scheme and palaeoenvironmental reconstruction for the middle and
40 late Cenomanian interval in its type area. La Garenne Quarry is a window on the middle
41 Cenomanian, where *Praeglobotruncana rillella* nov. sp. has been identified. The $\delta^{13}\text{C}_{\text{carb}}$ and
42 $\delta^{18}\text{O}_{\text{carb}}$ record of a Cenomanian–Turonian succession close to Le Mans is correlated with the
43 type section of Pueblo (Colorado). Isotopic and biotic events highlight the presence of several
44 hiatuses in the sedimentary record of Le Mans especially around the Cenomanian–Turonian
45 boundary with a dramatic truncation of the plateau of high $\delta^{13}\text{C}_{\text{carb}}$ values. Coiling reversal
46 events among the surface dwellers *Muricohedbergella delrioensis*, indicate sea surface
47 temperature changes with transient coolings, including the *Plenus* cold event, and warm
48 conditions at the Cenomanian–Turonian boundary. Sandy to chalky facies have yielded
49 empty, well-preserved shells of foraminifera allowing the description of *Dicarinella*
50 *falsohelvetica* nov. sp. Oxygen isotopic analyses performed on right- and left-coiled *M.*

51 *delrioensis* reveal a systematic offset during cold events which lead to discuss about the
52 potential occurrence of cryptic species in the Mesozoic.

53

54 Keywords Planktonic foraminifera, Middle Cenomanian, Cenomanian–Turonian stage
55 boundary, Oceanic Anoxic Event 2, Anglo-Paris Basin, shell coiling direction

56

57 1. Introduction

58

59 "*Stratotype Cénomancien*" (Morel, 2015) is a book of the series *Patrimoine géologique*
60 (Geological Heritage) published by the *Muséum national d'Histoire naturelle* of Paris to
61 facilitate access of French historical stratotypes to the scientific community and to a wider
62 audience. The editing of this volume led to the reinvestigation of two historical sections
63 (Saint-Ulphace and Mézières-sur-Ponthouin) close to Le Mans in the Department of Sarthe
64 (Figs. 1, 2, 3).

65 The Cenomanian stage was originally defined by d'Orbigny in 1847 in his book
66 *Paléontologie Française* and numerous fossils were collected and described during the 19th
67 century, by d'Orbigny himself as well as by local naturalists such as Guéranger (1850). Most
68 available outcrops around Le Mans became degraded or disappeared at the beginning of the
69 20th century. Few researchers have reinvestigated the stratigraphy of the Cenomanian type
70 area employing modern standards (Hancock, 1959; Marks, 1967b, a; Juignet, 1973; Juignet et
71 al., 1973; Juignet et al., 1978; Juignet et al., 1983; Ferré, 1995; Robaszynski et al., 1998;
72 Lasseur, 2007; Gaspard, 2014; Gaspard and Loubry, 2017; Kočí et al., 2017). In comparison,
73 hundreds of papers are devoted to the Pueblo GSSP section (Colorado, USA), that
74 encompasses the Cenomanian–Turonian stage boundary. The lack of interest in the historical
75 stratotype area can be explained by the proximal environments it represents and the numerous

76 erosional surfaces and non-deposition intervals interrupting the sedimentary series. The facies
77 are partly sandy (Fig. 1) and several hardgrounds and erosional surfaces indicate the presence
78 of hiatuses (Juignet, 1973). Another difficulty is that the type Cenomanian cannot be
79 described at one main site but only from a series of sections. Most of the outcrops are now
80 vegetated or urbanized. For example, two of the fourteen formations, which comprise the
81 Cenomanian are no longer accessible (Morel, 2015).

82 Nevertheless, the stratotype area is a pertinent site, especially because planktonic
83 foraminifera, nannofossil and ammonite biostratigraphic schemes can be coupled with
84 chemostratigraphic analysis. Planktonic foraminifera are particularly well-preserved, although
85 they are quite rare except in the upper Cenomanian – lower Turonian chalky facies. Scanning
86 electron photomicrographs (Figs. 4, 5, 6) show the excellent preservation of detailed surface
87 ornament and test ultrastructure. The test chambers are mostly free of secondary calcite,
88 allowing precise geochemical analyses.

89

90 2. Geological setting

91

92 Transgressive Albian deposits overlie Jurassic sediments East of Le Mans and
93 Armorican basement to the west (Fig. 1). During the early and middle Cenomanian, the
94 stratotype area was characterized by nearshore sedimentary environments close to Le Mans
95 and by more open marine environments a few tens of kilometres eastwards. Sandy detrital
96 facies alternate with calcareous marls and occasionally chalky deposits; the calcareous
97 formations increasing eastwards of Le Mans (Fig. 1). With the late Cenomanian transgression,
98 chalky facies accumulated through a large part of the Paris Basin (Fig. 1).

99 La Garenne Quarry at Saint-Ulphace exposes the Sables et Grès de Lamnay and the
100 overlying Craie de Théligny. The site remains one of the last two outcrops of the stratotype

101 area where the Middle Cenomanian can be accessed (Fig. 2). To conform to regulation, the
102 quarries will be restored to a natural landscape after the end of sand mining (Morel, 2015).
103 The Courgenard borehole, drilled less than three kilometres west of Saint-Ulphace in the 80's,
104 pierced the entire Craie de Théligny and indicates that this formation has a thickness of about
105 twenty metres (Juignet et al., 1983). At La Garenne Quarry, only the basal three metres of the
106 chalky formation are accessible. Above the Théligny hardground, the base of the Craie de
107 Théligny comprises 30 centimetres of a glauconite-rich chalk layer. This basal level contains
108 an abundant fauna of molluscs (bivalves and ammonites). In the Craie de Théligny,
109 ammonites are quite common and diversified; the whole formation is assigned to the middle
110 Cenomanian *Acanthoceras rhotomagense* Zone (Juignet et al., 1978; Morel, 2015).

111 The Cenomanian–Turonian stage boundary crops out on the banks of the Chemin de la
112 Crêle close to Mézières-sur-Ponthouin village. The section does not present any lithologic
113 evidence (i.e., black shales) of the Oceanic Anoxic Event (OAE2). The section begins in the
114 upper part of the Sables du Perche and ranges up to the Craie à *Inoceramus labiatus* (Fig. 3).
115 However, only about 10 centimetres of the Craie à *I. labiatus* can be sampled in the bank of
116 La Crêle path. The formation is more clearly visible in an outcrop facing the path but
117 estimating how much is missing between the two sites is unclear. As the banks are covered in
118 vegetation, trenches were dug to sample properly the basal part of the section; the chalky
119 facies being the only parts visible on the upper part of the path. Even though this section is
120 one of the most documented ones in the area (Juignet, 1973; Kennedy and Juignet, 1994a;
121 Ferré, 1995; Morel, 2015), it has yielded few ammonites. Most of the ammonites reported
122 from the vicinity of Le Mans have been described from other regional localities. Among rare
123 ammonites collected in Mézières-sur-Ponthouin, *Metoicoceras geslinianum* indicates that the
124 Sables à *Catopygus obtusus* belong to the *M. geslinianum* Zone (Kennedy and Juignet,
125 1994a). The fauna of the Marnes à *Ostrea biauriculata* in the Sarthe indicates that this

126 formation belongs to the *Calycoceras guerangeri* Zone (Juignet et al., 1978; Kennedy and
127 Juignet, 1994b; Morel, 2015). According to Kennedy and Juignet (1994a), the basal part of
128 the Craie à *Terebratella carantonensis* can be assigned to the uppermost Cenomanian
129 *Neocardioceras juddii* Zone with one specimen of the nominate species found in Saint-Calais
130 in the eastern part of the Sarthe. In the western part of the Paris Basin, the Turonian is
131 indicated in the Craie à *I. labiatus* by the occurrence of the ammonite *Mammites nodosoides*
132 that is so far not recorded in the stratotype area (Juignet et al., 1973). The Cenomanian–
133 Turonian boundary (CTB) is supposed to be on the upper 2/3 of the Craie à *T. carantonensis*
134 (Juignet, 1973; Robaszynski et al., 1998), a few centimetres below the base of the Craie à *I.*
135 *labiatus*. The boundary between the two chalky formations is characterized by the
136 disappearance of glauconite.

137

138 3. Material and methods

139

140 15 samples (with a sampling interval of 20 centimetres) and 40 samples (with a
141 sampling interval varying from 10 to 30 centimetres) were respectively collected at La
142 Garenne Quarry (Fig. 2) and at the Chemin de la Crêle (Fig. 3) for stable isotope analyses and
143 detailed biostratigraphic survey (planktonic foraminifera and nannofossils).

144 Following standard procedures, sediments were soaked in a peroxide solution and
145 subsequently washed over 63 μm and 1 mm sieves. The planktonic foraminifera have been
146 extracted from this fraction (63 μm -1mm). Particular attention has been given to the
147 *Muricohedbergella delrioensis* population. Due to the low abundance of planktonic
148 foraminifera in the assemblage, only between 50 and 100 specimens of *M. delrioensis* could
149 be counted per sample. Presenting a low trochospiral test with 4.5 to 5.5 globular chambers
150 on the last whorl, the specimens of *M. delrioensis* have been observed from the spiral side.

151 Right-coiling refers to those specimens that are coiled in a clockwise direction and left-coiling
152 to those that show an anticlockwise coiling. This published work and the nomenclatural acts it
153 contains have been registered in ZooBank. The LSID (Life Science Identifier) for this
154 publication is: urn:lsid:zoobank.org:pub:047E90B9-1CA9-4B02-8165-3865E98AF928. Type
155 and figured specimens of planktonic foraminifera are deposited in the collections of the
156 Sorbonne Université, Paris.

157 For study of the nannofossil assemblages, 14 samples from La Garenne Quarry at
158 Saint-Ulphace and 30 samples from the Chemin de la Crêle at Mézières were selected and
159 processed in simple smear slides using ammoniac distilled water (pH = 8.5). Three traverses of
160 each slide were thoroughly examined using a Zeiss Axioscope imaging at 1500X (cross-
161 polarized and plane light) to locate and quantify key biostratigraphic species. Some samples
162 were also analysed with the SEM in order to check for the preservation state.

163 Bulk rock carbonate and *M. delrioensis* were analysed for oxygen and carbon stable
164 isotope composition with a Kiel IV mass spectrometer. Organic matter was removed from the
165 carbonates by soaking the sample overnight in 5% sodium hypochlorite solution. For *M.*
166 *delrioensis* isotope analysis, about 5 to 6 empty individuals were selected, cleaned in an
167 ultrasonic bath and analysed. Stable isotope values were calibrated relative to the Vienna Pee
168 Dee Belemnite (‰VPDB) via the NBS-19 international standard. The reproducibility of
169 measurements is $\pm 0.1\text{‰}$ for $\delta^{18}\text{O}_{\text{carb}}$ and $\pm 0.05\text{‰}$ for $\delta^{13}\text{C}_{\text{carb}}$. All analytical results are listed
170 in Appendix A.

171

172 4. Results

173

174 4.1. La Garenne Quarry at Saint-Ulphace

175

176 Planktonic foraminifera are abundant in the first centimetres of Craie de Théligny. The
177 basal glauconitic beds yielded only small triserial *Guembelitra cretacea* (Fig. 2). The
178 assemblage becomes more diversified above the glauconitic levels. Almost all the samples of
179 the assemblage contain rare *Rotalipora cushmani* (Figs. 2, 4). Most specimens of this index
180 species are small with 4 to 5.5 chambers on the last whorl (Fig. 4). Some of them present a
181 highly convex spiral side and are close to *Rotalipora cushmani* var. *expansa* described by
182 Carbonnier (1952). Other rotaliporids such as *Thalmaninella brotzeni* and *Thalmaninella*
183 *globotruncanoides* are rare. *Praeglobotruncana* are particularly abundant and diversified
184 (Figs. 5, 6) with *Praeglobotruncana aumalensis*, *Praeglobotruncana* aff. *oraviensis*,
185 *Praeglobotruncana gibba*, *Praeglobotruncana rillella* Desmares nov. sp., *Praeglobotruncana*
186 *stephani*, and *Praeglobotruncana* aff. *Dicarinella hagni*. Some medium-sized to large
187 *Praeglobotruncana* with a distinctive lobate periphery and a thick row of pustules (at least at
188 the beginning of the last whorl) are quite similar to *P. oraviensis* (Fig. 5). According to
189 Falzoni et al. (2016) the first occurrence of this species should be close to the Cenomanian–
190 Turonian boundary. Specimens from the middle Cenomanian of Saint-Ulphace present more
191 pustulose tests than the specimens illustrated and described by Falzoni et al. (2016). *P.* aff.
192 *oraviensis* could be considered as earlier occurrences of *P. oraviensis*. However, the presence
193 of specimens morphologically intermediate between *P. aumalensis* and *P.* aff. *oraviensis* raise
194 the question of an eventual test alteration linked to some sort of environmental pressure.
195 Those forms could also be interpreted as transitional forms between *Praeglobotruncana* and
196 first *P.* aff. *D. hagni* (Fig. 5) recorded in the upper part of the section (Fig. 2). *P.* aff.
197 *Dicarinella hagni* present a typical profile of *D. hagni* but have not yet acquired two keels.
198 These morphotypes with a pustulose band were already described by Robaszynski et al.
199 (1993) in the uppermost lower Cenomanian of Central Tunisia.

200 The globular forms *Whiteinella aprica* and *M. delrioensis* (Fig. 4) are also well-represented.
201 Contrary to the assumption of the Time Scale 2012 (Anthonissen and Ogg, 2012), *W. aprica*
202 cannot be an objective marker of the upper Cenomanian base, as this species is already
203 recorded in the middle Cenomanian.

204 The percentages of left-coiled morphotypes among *M. delrioensis* are quite high with
205 values ranging between 35% and 55%.

206 Calcareous nannofossils are relatively common to abundant and moderately to well-
207 preserved in the Saint-Ulphace assemblages. No specific biohorizons
208 (appearance/disappearance) were highlighted through this section, but the common
209 occurrence of *Litraphidites acutus*, *Axopodorhabdus albianus*, *Helenea chiastia*,
210 *Cretharhabdus striatus*, and the absence of *Gartnerago theta*, seems to indicate an age not
211 older than the middle Cenomanian, roughly corresponding to biozones CC10 (Sissingh, 1977;
212 Perch-Nielsen, 1985) UC3 (Burnett, 1998).

213 The $\delta^{13}\text{C}_{\text{carb}}$ curve does not present any positive isotopic excursion (Fig. 2); values are
214 relatively constant (comprise between 1‰ and 2‰).

215

216 4.2. Mézières-sur-Ponthouin

217

218 The lower and middle parts of Marnes à *O. biauriculata* did not yield any calcareous
219 microfossils. The planktonic foraminifera occur first in this formation just below the Bousse
220 hardground within the last 50 centimetres of the Marnes à *O. biauriculata* (Fig. 3). Among
221 them several specimens of the index species *R. cushmani* have been found in association with
222 other keeled forms, including *Thalmanninella greenhornensis* and *Dicarinella hagni*. It
223 should be noticed that maybe related to the shallow-water settings, all the specimens of *Th.*
224 *greenhornensis* (Fig. 4) are smaller than usual, and they do not exceed 300 μm at Mézières-

225 sur-Ponthouin. Two morphotypes of *D. hagni* are commonly found, the classical biconvex
226 forms and more planoconvex morphotypes, with a flat spiral side, that were already described
227 and figured in Robaszynski et al. (1979) and in the upper Cenomanian Sables du Perche
228 Formation in the Civray-de-Touraine borehole (Amédéo et al., 2018) (Fig. 7). As previously
229 recorded by Ferré (1995), the last specimens of *R. cushmani* were identified just below the
230 Bousse hardground. In the PhD memoir of Ferré (1995), several occurrences of index species
231 *Helvetoglobotruncana helvetica* are mentioned, but not figured, in the Craie à *I. labiatus* one
232 metre above the disappearance of the glauconitic chalk (Fig. 3). But we did not find any
233 specimen of this latter species. However, several vaulted *Dicarinella* occurred within the
234 Craie à *T. carantonensis* (Figs. 3, 4, 7). These morphotypes are similar in shape to *Dicarinella*
235 *concovata* with their distinctive bowl-shaped profiles but with discrete staircase-like imbricate
236 structures on spiral side (Fig. 7). It was particularly surprising assuming that the lowest record
237 of *D. concavata* was in the Upper Turonian of Tunisia, on the southern Tethyan margin
238 (Robaszynski et al., 1990). These double-keeled planoconvex variants are quite common and
239 have already been observed in the Upper Cenomanian in different paleogeographic domains.
240 In particular, similar forms were also recognized at Hot Springs in the Western Interior Basin
241 (Fig. 7). We considered that this upper Cenomanian form represent a new species *Dicarinella*
242 *falsohelvetica* Desmares nov. sp. Evolution of similar planoconvex morphotypes could be
243 iterative or could be linked with environmental conditions. The phylogenetic relationships
244 between *D. hagni* planoconvex morphotypes, *Dicarinella falsohelvetica* and *D. concavata*
245 have yet to be clarified. The lowest occurrence (LO) of *D. concavata* has been considered to
246 be a reliable biomarker for placement of the base of the upper Turonian–lower Coniacian *D.*
247 *concovata* Zone (Sigal, 1955; Robaszynski et al., 1990; Premoli Silva and Sliter, 1995;
248 Robaszynski and Caron, 1995) but several studies have already illustrated the diachronous
249 nature of this marker (Robaszynski et al., 1990; Petrizzo, 2000).

250 The chalky facies in the upper part of the Mézières-sur-Ponthouin section contain
251 abundant and well-preserved nannofossils while in the lower part assemblages are sparse and
252 sediments often barren. A succession of key nannofossil biohorizons, (disappearances of *C.*
253 *striatus*, *L. acutus*, *A. albianus*, *H. chiastia* and appearance of *Quadrum intermedium*,
254 *Eprolithus octopetalus*, *E. moratus*, *Q. gartneri*) has been recorded at Mézières-sur-Ponthouin
255 (Figs. 3, 8) which constrains the CTB interval (Fig. 3), in agreement with published literature
256 (Tsikos et al., 2004; Desmares et al., 2007; Fernando et al., 2010; Linnert et al., 2011; Corbett
257 et al., 2014) and the planktonic foraminifera data.

258 *Whiteinella* and *Muricohedbergella* are common and well-represented at Mézières-
259 sur-Ponthouin. The population of *M. delrioensis* exhibits major changes from the Marnes à *O.*
260 *biauriculata* to the Craie à *T. carantonensis* formations. In the last 50 centimetres of the
261 Marnes à *O. biauriculata*, the percentage of the left-coiled morphotype (Fig. 9) drops
262 significantly from 36% to 16%. Above the Bousse hardground, the percentage of sinistral
263 specimens is again greater than 20%. In the Sables à *C. obtusus*, a general progressive
264 decrease of the number of left-coiled morphotype is observed, and only right-coiled forms are
265 present at the base of the Craie à *T. carantonensis*. In the glauconitic chalk, the percentages of
266 sinistral forms increase again but never exceed 15%.

267 Due to the outcrop conditions and to the low carbonate percentage, only two values of
268 $\delta^{13}\text{C}_{\text{carb}}$ were acquired in the Marnes à *O. biauriculata* (Fig. 9). The Sables à *C. obtusus* are
269 characterized by strong $\delta^{13}\text{C}$ values (greater than 3,5 ‰) in its lower half (Fig. 9) and by
270 lighter values on its upper half (between 0 and 1‰). The Craie à *T. carantonensis* exhibits a
271 single moderate peak of $\delta^{13}\text{C}$ values (Fig. 9).

272 $\delta^{18}\text{O}_{\text{carb}}$ presents heavier values above the Bousse hardground in the basal part of the
273 Sables à *C. obtusus* before a change to lighter values in the upper part of the formation (Fig.

274 9). The values remain within the same range up to the basal part of the Craie à *I. labiatus*.
275 $\delta^{18}\text{O}$ performed on dextral and sinistral *M. delrioensis* follow a similar overall trend (Fig. 10).

276

277 5. Discussion

278

279 5.1. Stratigraphic framework

280

281 The Mid-Cenomanian Event I is defined by double $\delta^{13}\text{C}_{\text{carb}}$ peaks (Ia and Ib) within
282 the middle Cenomanian (Jenkyns et al., 1994; Paul et al., 1994). In the English Chalk, high-
283 resolution chemostratigraphy integrated with ammonite biostratigraphy (Paul et al., 1994;
284 Mitchell et al., 1996; Jarvis et al., 2006) indicated that the two positive $\delta^{13}\text{C}_{\text{carb}}$ excursions Ia
285 and Ib respectively occur in the *Cunningtoniceras inerme* Zone and in the lower part of the *A.*
286 *rhotomagense* Zone. If the *C. inerme* Zone is not represented in the north-eastern part of
287 Sarthe (Morel, 2015), we have investigated the possibility of recording Ib in the basal part of
288 the Craie de Théligny. However, the $\delta^{13}\text{C}_{\text{carb}}$ curve does not present any noticeable variation
289 (Fig. 2). As previously reported in the Courgenard borehole (Juignet et al., 1983), data on
290 planktonic foraminifera indicated that the basal part of the Craie de Théligny in Saint-Ulphace
291 area already belongs to the *R. cushmani* total range Zone that begins in the middle
292 Cenomanian and extends upwards to the Upper Cenomanian in the Anglo-Paris Basin, an age
293 which is also confirmed by nannofossil assemblages. In England, the first *R. cushmani*
294 appears just after a sharp increase in the proportion of planktonic foraminifera: the
295 Planktonic/Benthic event (P/B event). Rotaliporidae become a significant element of the
296 planktonic assemblage in the Anglo-Paris Basin after the P/B event (Paul et al., 1994; Jarvis
297 et al., 2006). In the Théligny area, due to the facies change between the Sables and Grès de
298 Lamnay and the Craie de Théligny, the recognition of a P/B event is not possible. However,

299 as observed by Juignet et al. (1983), Rotaliporidae are already common in the first metres of
300 the Craie de Théligny. Close to the P/B break, isotopic $\delta^{13}\text{C}_{\text{carb}}$ values are quite low and stable
301 even if on longer time series (Jarvis et al., 2006), the P/B break corresponds to an inflection
302 point to more rapidly rising $\delta^{13}\text{C}_{\text{carb}}$ values. Such a trend is not visible in La Garenne Quarry.
303 Considering the ammonite biostratigraphic data, foraminiferal assemblages and the stable low
304 $\delta^{13}\text{C}_{\text{carb}}$ values, it can be assumed that the basal part of the Craie de Théligny is post Mid-
305 Cenomanian Event I and coeval with the P/B event. Consequently, the base of the A.
306 *rhotomagense* Zone is probably not recorded in the Théligny area suggesting a hiatus. It is in
307 accordance with the presence of an often phosphatised macrofauna at the base of the Craie de
308 Théligny indicating low sedimentation rate and reworking.

309
310 The Cenomanian–Turonian stage boundary coincided worldwide with an increase in
311 marine productivity and with the burial of organic carbon (Jenkyns, 1980). Consequently,
312 OAE2 is characterised by a major $\delta^{13}\text{C}_{\text{carb}}$ positive excursion (Fig. 9). This isotopic shift,
313 composed of high frequency events, is synchronous and allows high-resolution correlations
314 between distant sites (Tsikos et al., 2004; Kuhnt et al., 2005; Grosheny et al., 2006; Desmares
315 et al., 2007; Takashima et al., 2009; Westermann et al., 2010). The initial increase of the
316 $\delta^{13}\text{C}_{\text{carb}}$ and peak of values (A) is particularly well recorded at Mézières-sur-Ponthouin in the
317 sandy facies above the Bousse hardground. By contrast, the second increase and plateau (B)
318 within the Craie à *T. carantonensis* appears to be particularly reduced (Fig. 9). This weak
319 expression could be related to presence of one or several hiatuses. Juignet (1973)
320 characterised an erosional surface between the Sables à *C. obtusus* and the Craie à *T.*
321 *carantonensis*.

322 The extension of this (these) hiatus(es) needs to be constrained with an integrative
323 stratigraphic approach. As surface dwellers, muricohedbergellids were not affected by OAE2

324 and provide a continuous signal throughout the Cenomanian–Turonian boundary interval
325 (Desmares et al., 2016). Several reversals in coiling direction have been characterised in mid-
326 latitude sections of the Western Interior Seaway and of the Umbria-Marche and Vocontian
327 basins (Desmares et al., 2016; Grosheny et al., 2016). The recognition of these events at
328 Mézières-sur-Ponthouin provides stratigraphic markers.

329

330 5.2. Coiling reversal events among *M. delrioensis*

331

332 Among some modern and recent fossil species of planktonic foraminifera, the
333 proportion of left- to right-coiled shells in a population appears to be temperature-dependent;
334 the relative abundance of each morphotype reflecting ecological preferences (Ericson, 1959;
335 Bandy, 1960; Boltovskoy, 1973; Bauch et al., 2003; Darling et al., 2006; Darling and Wade,
336 2008; Ujiie et al., 2010). A similar relationship has been identified among *M. delrioensis* at
337 the Cenomanian–Turonian stage boundary in several mid-latitude sites (Desmares et al.,
338 2016; Grosheny et al., 2016), including the Pueblo type section (Fig. 9). As an example, at
339 Pueblo, the increase of left-coiled *M. delrioensis* in the assemblage is clearly related to higher
340 $\delta^{18}\text{O}_{\text{carb}}$ values suggesting that changes in the coiling direction in this surface dweller
341 represent a new proxy for constraining Sea Surface Temperature (SST) variations (Desmares
342 et al., 2016; Grosheny et al., 2016). At Pueblo, several events were previously identified in
343 the pattern of *M. delrioensis* shell coiling (Fig. 9):

344 (S1) An important rise in the relative percentage of sinistral *M. delrioensis* begins in the upper
345 part of the *Metoicoceras mosbyense* Zone. Associated with heavier $\delta^{18}\text{O}_{\text{carb}}$ values, this event
346 indicates a cooling episode (Desmares et al., 2016). S1 persists into the lower part of the
347 *Sciponoceras gracile* Zone (*M. geslinianum* equivalent) before a stepwise decline. A brief

348 drop subdivides this event into two episodes: S1a and S1b. Temporally, the base of S1b is
349 coincident with the first peak (A) of the $\delta^{13}\text{C}_{\text{carb}}$ curve.

350 (S2) Of lesser amplitude, S2 occurs in the upper part of the *S. gracile* Zone and pertains to
351 the general progressive decrease in frequency of sinistral forms. The end of S2, at the base of
352 the *N. juddii* Zone, coincides with the onset of the $\delta^{13}\text{C}_{\text{carb}}$ plateau of values (B) and with the
353 beginning of the *Heterohelix* shift (Leckie et al., 1998; Caron et al., 2006; Desmares et al.,
354 2007)

355 (D) Close to the CTB, right-coiled *M. delrioensis* become dominant. This event is coeval with
356 the $\delta^{13}\text{C}_{\text{carb}}$ plateau of values (B). In accordance with $\delta^{18}\text{O}_{\text{carb}}$ values, the dominance of right-
357 coiling forms records a thermal maximum.

358 Based on the ammonite biostratigraphy and $\delta^{13}\text{C}_{\text{carb}}$ excursions, most of the events
359 among *M. delrioensis* can be recognized at Mézières-sur-Ponthouin (Fig. 9).

360 The high proportion of sinistral forms recorded in the upper part of the Marnes à *O.*
361 *biauriculata* can correspond to the base of S1. However, as the contact between the Sables à
362 *C. obtusus* and the Marnes à *O. biauriculata* is erosive, it cannot be excluded that this sinistral
363 event records an earlier cooling event (Fig. 9). Indeed, new data from the Hartland Shale in
364 the Pueblo section indicated other major coiling reversals within the *M. mosbyense* Zone (Fig.
365 9).

366 The high abundance of sinistral morphotypes above the Bousse hardground, coeval
367 with the first peak (A) of $\delta^{13}\text{C}_{\text{carb}}$ pertains to the S1b event. As for the Pueblo section, S1b is
368 associated with heavier $\delta^{18}\text{O}_{\text{carb}}$ values and thus clearly reflects a cooling event. This cooling
369 episode is particularly well-expressed in southern England where the positive $\delta^{18}\text{O}_{\text{carb}}$
370 excursion (Jarvis et al., 2011) within the mid-*M. geslinianum* Zone is recognizable and
371 coincides with the *Plenus* Cold Event, a temporary influx of Boreal fauna throughout Europe
372 (Jefferies, 1962; Gale and Christensen, 1996). However, at Mézières-sur-Ponthouin, the

373 percentage of sinistral *M. delrioensis* during S1 is significantly lower (Fig. 9). Such a
374 discrepancy could indicate higher SST in the Anglo-Paris Basin even if the two reference
375 sites, historical stratotype and GSSP, are both located within an epicontinental seaway at a
376 similar palaeolatitude of about 40°N (Torsvik et al., 2012; van Hinsbergen et al., 2015).

377 With very few left-coiled specimens, the D event is clearly identified within the basal
378 part of the Craie à *T. carantonensis*. In more detail, in Pueblo, the D event exhibits three
379 successive lows; the first one, the lowest, belonging to the *N. juddii* Zone. In accordance with
380 the ammonite biostratigraphy (Kennedy and Juignet, 1994a), the low records at Mézières-sur-
381 Ponthouin could correspond to the first low of Pueblo. Then, the progressive increase of
382 sinistral forms could be correlated to the same trend observed in the lower Turonian of
383 Pueblo, coeval with the end of the $\delta^{13}\text{C}_{\text{carb}}$ plateau of values.

384 S2 seems to be incompletely recorded but the boundary between the Sables à *C.*
385 *obtusus* and the Craie à *T. carantonensis* corresponds to an erosion surface (Juignet, 1973).
386 This incomplete pattern can therefore be explained by a hiatus that includes the onset of the
387 $\delta^{13}\text{C}_{\text{carb}}$ plateau of values (B).

388

389 5.3. Significance of the $\delta^{18}\text{O}$ offset between dextral and sinistral morphotypes of *M.*
390 *delrioensis*

391

392 When sinistral *M. delrioensis* exceeds a threshold of 12%, a significant isotopic
393 difference of at least 0.5‰ (up to 1.3‰) between left-coiled *M. delrioensis* and right-coiled
394 *M. delrioensis* is observed (Fig. 10); dextral *M. delrioensis* being systematically lighter and
395 presumably warmer. Such results are particularly surprising because they are similar to what
396 has been published for the *Neogloboquadrina pachyderma* isotopic signature (Bauch et al.,
397 2003; Nyland et al., 2006). An isotopic difference of about 0.5‰ has been highlighted

398 between left- and right-coiling *N. pachyderma*, since 10 Ka (Bauch et al., 2003). Recent
399 advances in molecular analysis provide new insights concerning the diversity of planktonic
400 foraminifera which has been underestimated while focusing only on the morphological
401 features of the test (Bauch et al., 2003; Darling et al., 2006; Darling and Wade, 2008);
402 morphospecies as previously understood, being in fact composed of several cryptic species.
403 Among the extant *N. pachyderma* s.l., the dextral forms now named *Neogloboquadrina*
404 *incompta* and the left-coiled *N. pachyderma*. They are in fact different species with distinct
405 ecologies and biogeographic distributions (Darling et al., 2006). Thus, the Holocene $\delta^{18}\text{O}$
406 offset between left-coiled *N. pachyderma* and right-coiled *N. incompta* may 1) represent a
407 genotype-specific vital effect (Bauch et al., 2003) or 2) be related to hydrological factors such
408 as different calcification depths (Bauch et al., 2003; Nyland et al., 2006). Similar assumptions
409 might arise for the *M. delrioensis* population. Does the systematic $\delta^{18}\text{O}$ difference reflect a
410 vital effect and/or correspond to any hydrological factor?

411 Genetic evidence (Bauch et al., 2003; Darling et al., 2006) among *N. pachyderma* s.l.
412 show that the morphological distinction of coiling directions is not sufficient to distinguish
413 two morphotypes; low level (<3%) of aberrant coiling being associated with both
414 morphotypes (Bauch et al., 2003). As an example, a small percentage of tests with a right
415 coiling morphology (1–3%) are found in planktonic assemblages and persist in the
416 sedimentary record even in the most extreme polar conditions. Despite their right coiling
417 morphology, such forms have a sinistral isotopic composition (Bauch et al., 2003). Similarly,
418 it could be argued that during the latest Cenomanian warming and the early Turonian thermal
419 maximum, the rare left-coiled *M. delrioensis* are aberrant forms of the right-coiled variety. It
420 could explain why in this interval, sinistral *M. delrioensis* and dextral *M. delrioensis* have a
421 similar isotopic signature. Interestingly, while the $\delta^{18}\text{O}$ reveals a systematic offset, there is no
422 marked difference in $\delta^{13}\text{C}$ either between sinistral *N. pachyderma* and dextral *N. incompta*

423 (Bauch et al., 2003) neither between sinistral *M. delrioensis* and dextral *M. delrioensis* over
424 the entire time interval (Fig. 10). Since $\delta^{13}\text{C}$ values of foraminifers are thought to record
425 specific environmental conditions, the similar $\delta^{13}\text{C}$ signatures between sinistral and dextral
426 forms could mean that the $\delta^{18}\text{O}$ offset represents a genotype-specific vital effect rather than
427 reflecting hydrological factors. As an example, Wang (2000) and Numberger et al. (2009)
428 showed that different $\delta^{13}\text{C}$ values in distinct morphotypes of *Globigerinoides ruber* reflect
429 their depth habitat within the water column. Regardless, such a conclusion must be taken with
430 caution as the $\delta^{13}\text{C}$ of left-coiled *N. pachyderma* is about constant with water depth (Bauch et
431 al., 2002) meaning that the influence of $\delta^{13}\text{C}$ of the dissolved inorganic carbon in the
432 foraminiferal shell can be masked by other effects.

433 In conclusion, as for sinistral *N. pachyderma* and dextral *N. incompta*, it remains
434 difficult to determine whether the coiling-dependent $\delta^{18}\text{O}$ offset among *M. delrioensis*
435 represents annual, seasonal or water-depth hydrological differences rather than a vital effect
436 signature.

437

438 6. Systematic Palaeontology

439

440 Order FORAMINIFERIDA Eichwald, 1830

441 Suborder GLOBIGERININA Delage and Hérouard, 1896

442 Family HEDBERGELLIDAE Loeblich & Tappan, 1961

443

444 Genus *Dicarinella* Porthault, 1970

445

446 *Dicarinella falsohelvetica* Desmares, nov. sp.

447 LSID urn:lsid:zoobank.org:act:7C728E33-B64C-4A03-A1AF-1FE5FDE95C20

448

449 Description. Typical forms included in this species have a large (> 400 µm) planoconvex test
450 with 5 to 6 chambers on the final whorl. Equatorial periphery is lobate. On the spiral side,
451 chambers are petaloid in shape and present a discrete staircase-like imbricated chamber. The
452 species presents a bowl-shaped profile with two well-expressed keels. Its umbilicus is narrow.
453 Umbilical sutures are radial and depressed.

454

455 Remarks. This species is distinguished from *H. helvetica* by having two keels. It differs from
456 *Dicarinella marianosi* by its smaller size, a fewer number of chambers on the last whorl and
457 its narrower umbilicus. The spiral side of *D. falsohelvetica* is less depressed than *D.*
458 *concovata*.

459

460 Test size. Maximum test diameter: holotype 430 µm, illustrated paratypes 450 µm-500 µm.

461

462 Type locality. Chemin de la Crêle, Mézières sur Ponthouin, Cenomanian stratotype area
463 (Sarthe, France).

464

465 Type horizon. Cenomanian-Turonian stage boundary, Craie à *Carantonensis* Fm.

466

467 Repository. Holotype (collection number MEZ Craie 1, P6M4365, Fig. 7, 5a-c) and paratypes
468 (collection numbers P6M4364, P6M4366, P6M4367, P6M4368, Fig. 7., 4a-c, 6a-b, 7a-b 8a-b)
469 are deposited in the collections of the Sorbonne Université, Paris, France.

470

471 Derivation of the name. Due to the shape of its lateral view, this species could be
472 misidentified as a specimen of *H. helvetica* but with two keels.

473

474 Genus *Praeglobotruncana* Bermudez, 1952

475

476 *Praeglobotruncana rillella* Desmares, nov. sp.

477 LSID urn:lsid:zoobank.org:act:D8BAB6CC-27CB-4CC1-874F-0FA2F9F28FBD

478

479 Description. Typical forms included in this species have a large (> 350 µm) planoconvex test
480 with 5 to 6 chambers on the final whorl. Equatorial periphery is lobate. On the spiral side,
481 chambers are petaloid in shape and have a coarsely porous aspect, at least on the last whorl,
482 whereas in the inner whorl, porosity is partly hidden by large pustules. Sutures on the spiral
483 side are curved and slightly raised except between the last chambers where it becomes
484 depressed. This species is seemingly “double-keeled” but in detail it presents umbilical well-
485 developed pustules but the last chamber is entirely smooth. On the umbilical side, sutures are
486 radial and depressed; chambers are inflated and triangular in shape. Principal aperture is
487 umbilical and is protected by a narrow lip. The species presents a prominent nonporous
488 carinal band composed of numerous pustules in the earlier part of the last whorl. This band
489 can be less distinct on the final chamber. Even if this species was not abundant enough in the
490 samples to realise a representative count, both dextral and sinistral forms have been found.

491

492 Remarks. This species is distinguished from *Whiteinella praehelvetica* (Trujillo, 1960) by a
493 quadratic edge on the last chambers, by a non-pustulose test on the spiral side of the last
494 chamber, by slowly expanding chambers and by a pustulose carinal band in the earlier part of
495 the last whorl. Moreover, 95% of *W. praehelvetica* are dextral forms whereas *P. rillella*
496 exhibits both dextral and sinistral morphotypes. This species differs from the Turonian

497 species *Helvetoglobotruncana microhelvetica* Huber and Petrizzo, 2017 by its larger size and
498 the absence of keel.

499

500 Test size. Maximum test diameter: holotype 370 μm , illustrated paratype 480 μm ; maximum
501 breadth: holotype 300 μm , illustrated paratype 400 μm .

502

503 Type locality. La Garenne Quarry at Saint-Ulphace, Cenomanian stratotype area (Sarthe,
504 France).

505

506 Type horizon. Middle Cenomanian (*A. rhotomagense* Zone and *R. cushmani* Zone), Craie de
507 Théligny Fm., within the three metres above the contact between the formations of "Sables
508 and Grès de Lamnay" and "Craie de Théligny".

509

510 Repository. Holotype (collection number UP15, P6M4360, Fig. 6, 3a-c) and paratypes
511 (collection numbers UP15, P6M4358, P6M4359, Figs. 1a-c, 2a-c) are deposited in the
512 collections of the Sorbonne Université, Paris, France.

513

514 Derivation of the name. Derived from the Middle French: "rillé" (piece of pork) and dedicated
515 to the local "pâté" of Le Mans area.

516

517 7. Conclusions

518

519 Samples of middle Cenomanian from Saint-Ulphace yield diverse and well-preserved
520 planktonic foraminifera assigned to the *R. cushmani* Zone in accordance with nannofossil
521 data. Among planktonic foraminifera, *Praeglobotruncana* are particularly well-represented.

522 Their excellent preservation allows the description of a new species *P. rillella* and the
523 opening of discussion on some transitional morphotypes between *Praeglobotruncana* and
524 *Dicarinella*.

525 At Mézières-sur-Ponthouin, several biohorizons among nannofossils and planktonic
526 foraminifera are identified including the disappearance of *T. greenhornensis* and *R. cushmani*
527 below the Bousse hardground. Sinistral event S1b is recognised in the lower part of the Sable
528 à *C. obtusus*. Bio- and chemostratigraphic correlations with the type section of Pueblo
529 highlight the presence of small hiatuses in the stratotype area. While the first peak (A) of $\delta^{13}\text{C}$
530 values is clearly recognized in the sandy facies above the Bousse hardground, the plateau (B)
531 is limited to the Craie à *T. carantonensis*. This plateau is coeval with the Dextral event (D)
532 encompassing the CTB at Pueblo. In the almost complete absence of specimens of ammonite
533 in this section, this integrated stratigraphic study supports the regional age calibration of the
534 series proposed from ammonite biozonation and suggests that CTB is placed in the middle
535 part of the condensed Craie à *T. carantonensis*.

536

537

538 Acknowledgments

539

540 The authors thank Nathalie Labourdette for running the mass spectrometer, Alexandre
541 Lethiers for the drawings. The authors acknowledge funding of the ASM Patrimoine
542 (Muséum national d'Histoire naturelle, Paris). Martin Pickford is thanked for checking the
543 English. The authors wish to emphasize the contributions of Francis Robaszynski to this work
544 with numerous discussions and helpful comments. The authors are especially grateful to
545 Eduardo Koutsoukos and Mark Leckie whose corrections and suggestions improved this
546 manuscript significantly. The authors also thank the anonymous reviewer.

547

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757 **Figure Captions**

758

759 Figure 1. A. Palaeogeographic setting of the Anglo-Paris Basin, modified after Juignet and
760 Kennedy (1976). B. Lithostratigraphy of the Cenomanian stratotype area with the location of
761 Mézières-sur-Ponthouin and Saint-Ulphace, modified after Juignet et al. (1978).

762

763 Figure 2. Distribution of planktonic foraminifera in the basal part of the Craie de Théligny
764 Fm. at La Garenne Quarry (Saint-Ulphace) set against $\delta^{13}\text{C}_{\text{carb}}$ and $\delta^{18}\text{O}_{\text{carb}}$.

765

766 Figure 3. Distribution of planktonic nannofossils at the Chemin de la Crêle (Mézières-sur-
767 Ponthouin). The base of the *H. helvetica* Zone is placed after Ferré (1995).

768

769 Figure 4. 1a-c. *Rotalipora cushmani* (Morrow, 1934), UP15, P6M4339. 2a-c. *R. cushmani*,
770 MEZ10, P6M4340. 3a-c. *Thalmaninella globotruncanoides* (Sigal, 1948), UP18, P6M4341.
771 4a-c. *R. cushmani* var. *expansa*, UP15, P6M4342. 5a-b. *Thalmaninella brotzeni* Sigal, 1948,
772 UP18, P6M4343. 6a-b. *Thalmaninella greenhornensis* (Morrow, 1934), MEZ11, P6M4344.

- 773 7a-c. *Whiteinella aprica* (Loeblich and Tappan, 1961), MEZ Craie 1, P6M4345. 8a-b.
774 *Globigerinelloides bentonensis* (Morrow, 1934), MEZ10, P6M4346. 9a-c. *Muricohedbergella*
775 *delrioensis* (Carsey, 1926), MEZ Craie 1, P6M4347. 10a-c. *W. aprica* (Loeblich and Tappan,
776 1961), UP15, P6M4348. 11a-c. *M. delrioensis*, UP15, P6M4349.
777
778 Figure 5. 1a-c. *Praeglobotruncana aumalensis* (Sigal, 1952), UP15, P6M4350. 2a-c. *P.*
779 *aumalensis*, UP15, P6M4351. 3a-c. *Praeglobotruncana stephani* (Gandolfi, 1942), UP12,
780 P6M4352. 4a-c. *P. stephani*, UP12, P6M4353. 5a-c. *Praeglobotruncana gibba* (Klaus, 1942),
781 UP18, P6M4354. 6a-c. *Praeglobotruncana* sp. aff. *Dicarinella hagni* (Scheibnerova, 1962),
782 UP15, P6M4355. 7a-c. Intermediate between *P. aumalensis* and *Praeglobotruncana* aff.
783 *oraviensis* Scheibnerova 1960, UP15, P6M4356. 8a-c. *Praeglobotruncana* aff. *oraviensis*,
784 UP15, P6M4357.
785
786 Figure 6. 1a-c, 2a-c. *Praeglobotruncana rillella*, n. sp., paratype, UP15, P6M4358, P6M4359.
787 3a-c. *Praeglobotruncana rillella*, n. sp., holotype, UP15, P6M4360.
788
789 Figure 7. 1a-c. *D. hagni*, biconvex morphotype, MEZ Craie 1, P6M4361. 2a-c. *D. hagni*,
790 intermediate morphotype between planoconvex and biconvex forms, MEZ Craie 1, P6M4362.
791 3a-c. *D. hagni*, planoconvex morphotype, Civray (France), upper Cenomanian (Turonian
792 stratotypic area), P6M4363. 4a-c. *Dicarinella falsohelvetica* n. sp., paratype, MEZ Craie 1,
793 P6M4364. 5a-c. *D. falsohelvetica* n. sp., holotype, MEZ Craie 1, P6M4365. 6a-b. *D.*
794 *falsohelvetica* n. sp., paratype, MEZ Craie 1, P6M4366. 7a-b., 8a-c. *D. falsohelvetica* n. sp.,
795 paratype, HS9, Hot Springs (South-Dakota, US), upper Cenomanian (*S. gracile* Zone),
796 P6M4367, P6M4368.
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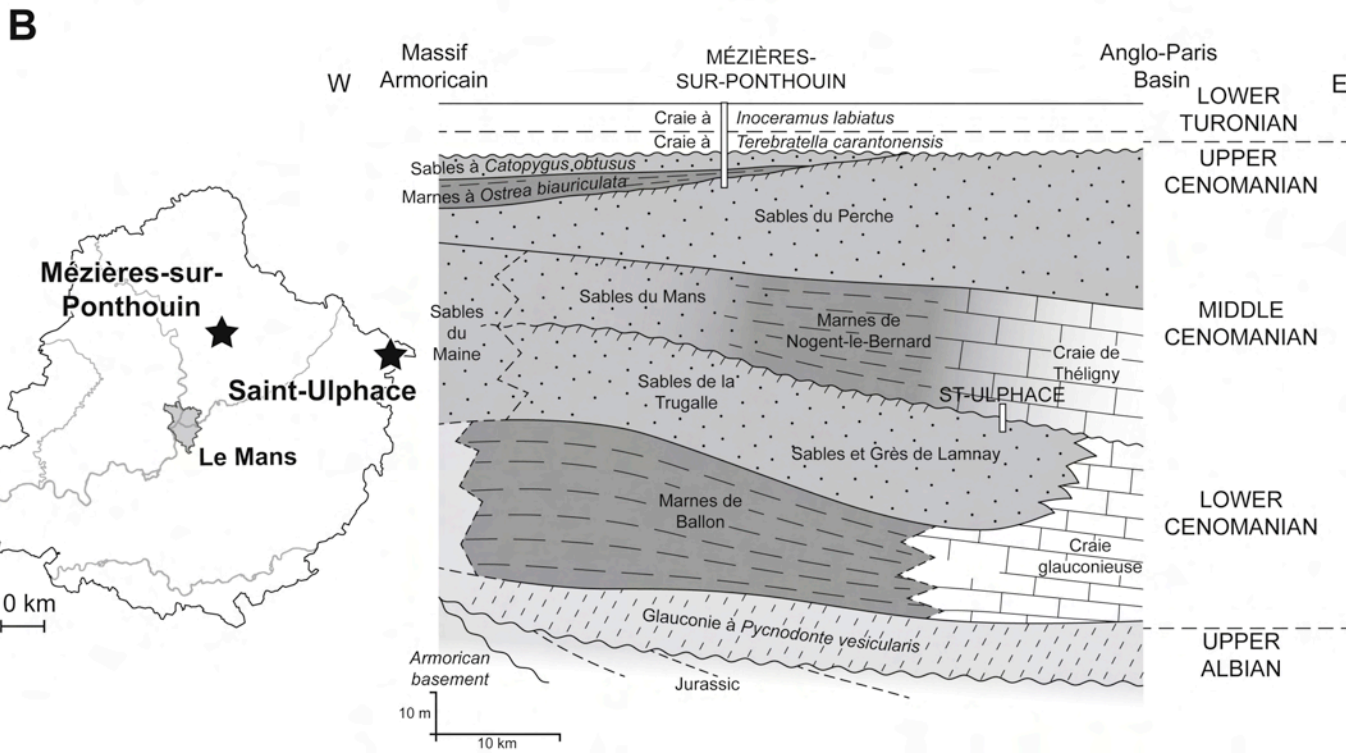
798 Figure 8. 1. *Cretarhabdus striatus* (Stradner 1963) Black, 1973; sample MEZ 12. 2.
799 *Eiffelithus* cf *E. eximius* (Stover, 1966) Perch-Nielsen 1968; sample MEZ 29. 3.
800 *Axopodorhabdus albianus* (Black, 1967) Wind & Wise in Wise & Wind, 1977; sample MEZ
801 12. 4. *Eprolithus octopetalus* Varol, 1992; sample MEZ 34. *Eprolithus moratus* (Stover,
802 1966) Burnett, 1998; sample MEZ 39. *Gartnerago segmentatum* (Stradner, 1966) Thierstein,
803 1974; sample MEZ 12. 7. *Quadrum intermedium* Varol, 1992; sample MEZ 28. 8. *Quadrum*
804 *gartneri* Prins and Perch-Nielsen 1977; sample MEZ 37. 9. *Lithraphidites acutus* Verbeek &
805 Manivit, 1977; sample MEZ 12. Scale bar = 5 μ m.

806

807 Figure 9. $\delta^{18}\text{O}_{\text{carb}}$ and $\delta^{13}\text{C}_{\text{carb}}$ records compared to the changes in the percentage of sinistral
808 *M. delrioensis* in the sections at Pueblo (Desmares et al., 2016) and at Mézières-sur-
809 Ponthouin. Isotopic $\delta^{13}\text{C}$ events A: initial increase in values and first peak; B: second increase
810 and plateau.

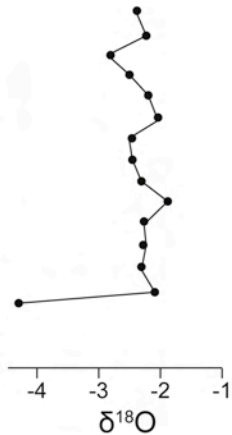
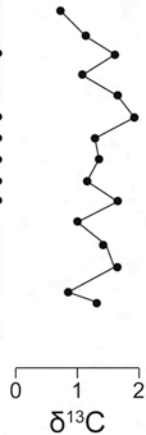
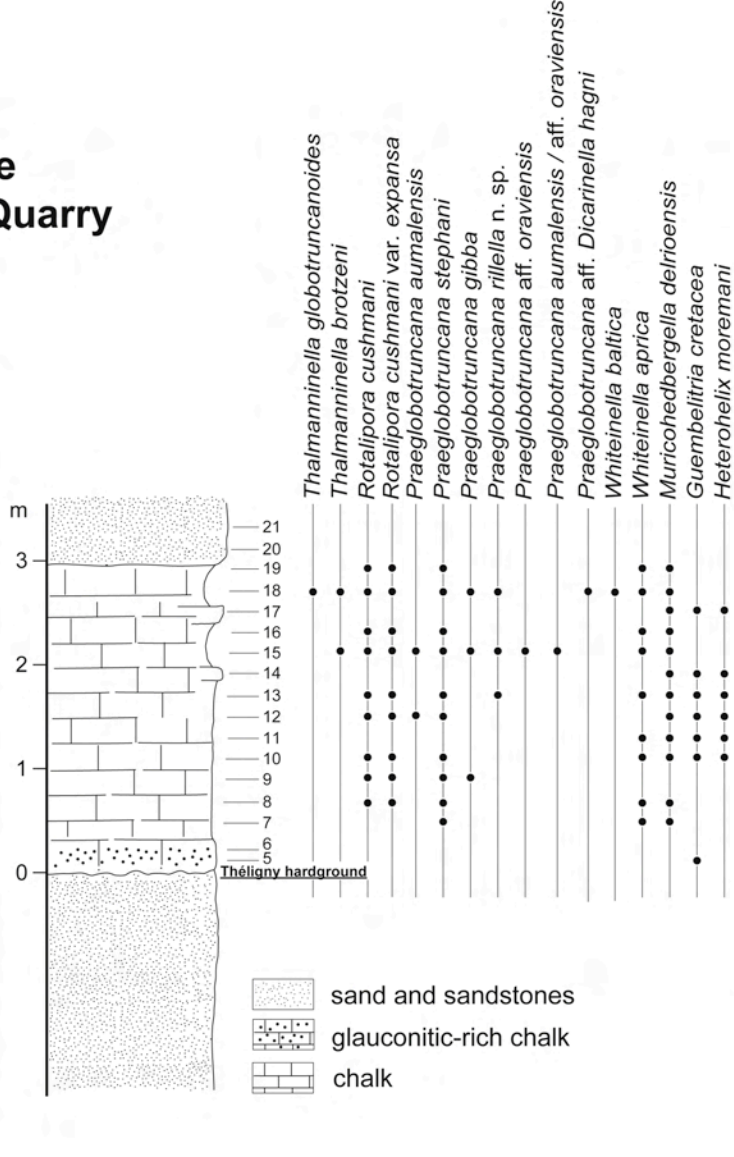
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812 Figure 10. Carbon and oxygen isotopic compositions for left-coiled (white dots) and right-
813 coiled *M. delrioensis* (black dots) at Mézières-sur-Ponthouin. Data are compared with bulk
814 isotopic composition and with the percentage of sinistral morphotypes.

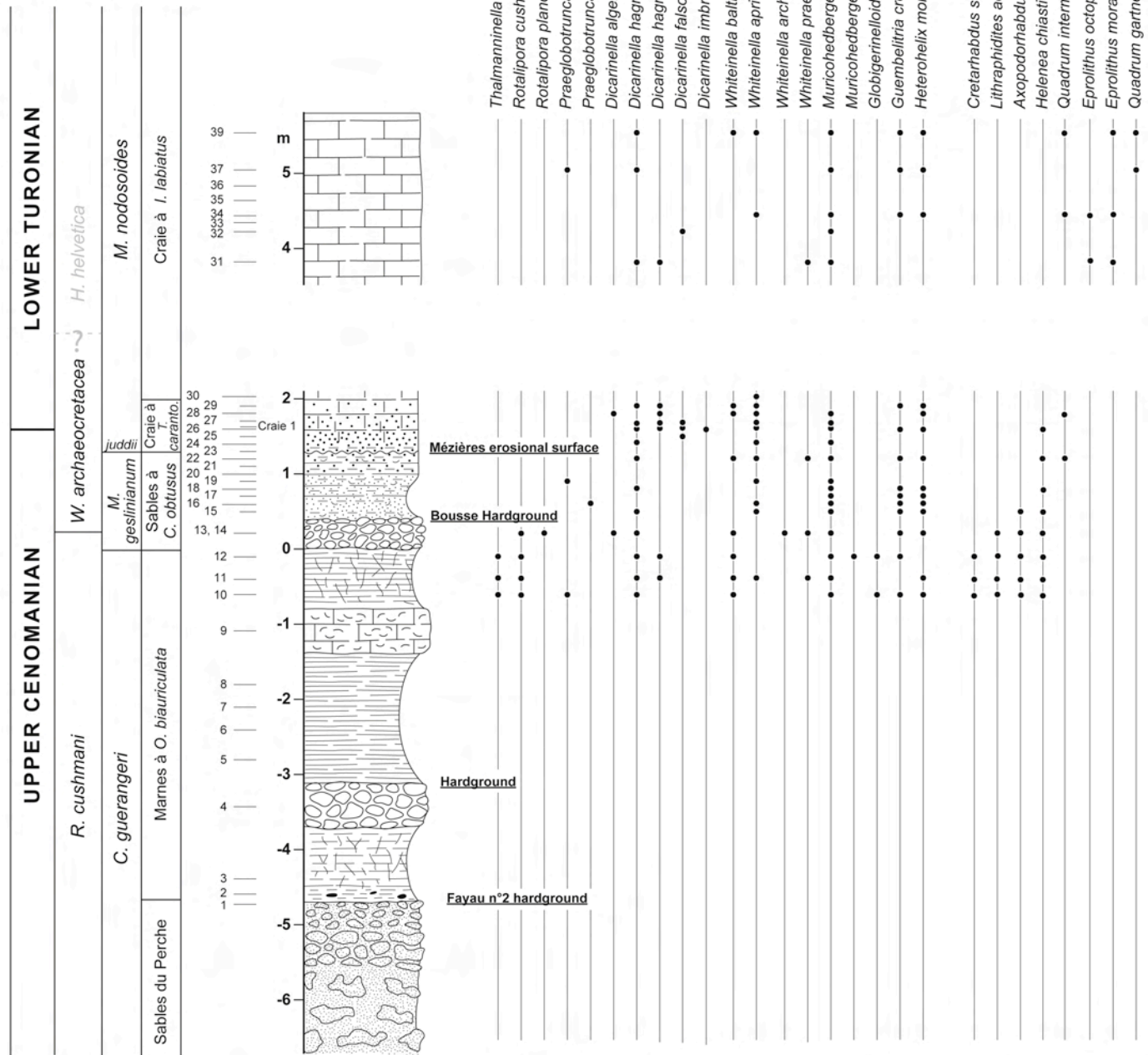





Saint-Ulphace La Garenne Quarry




LOWER CENOMANIAN	MIDDLE CENOMANIAN
<i>M. dixoni</i>	<i>A. rhotomagense</i>
Sables et Grès de Lamnay	Craie de Théligny

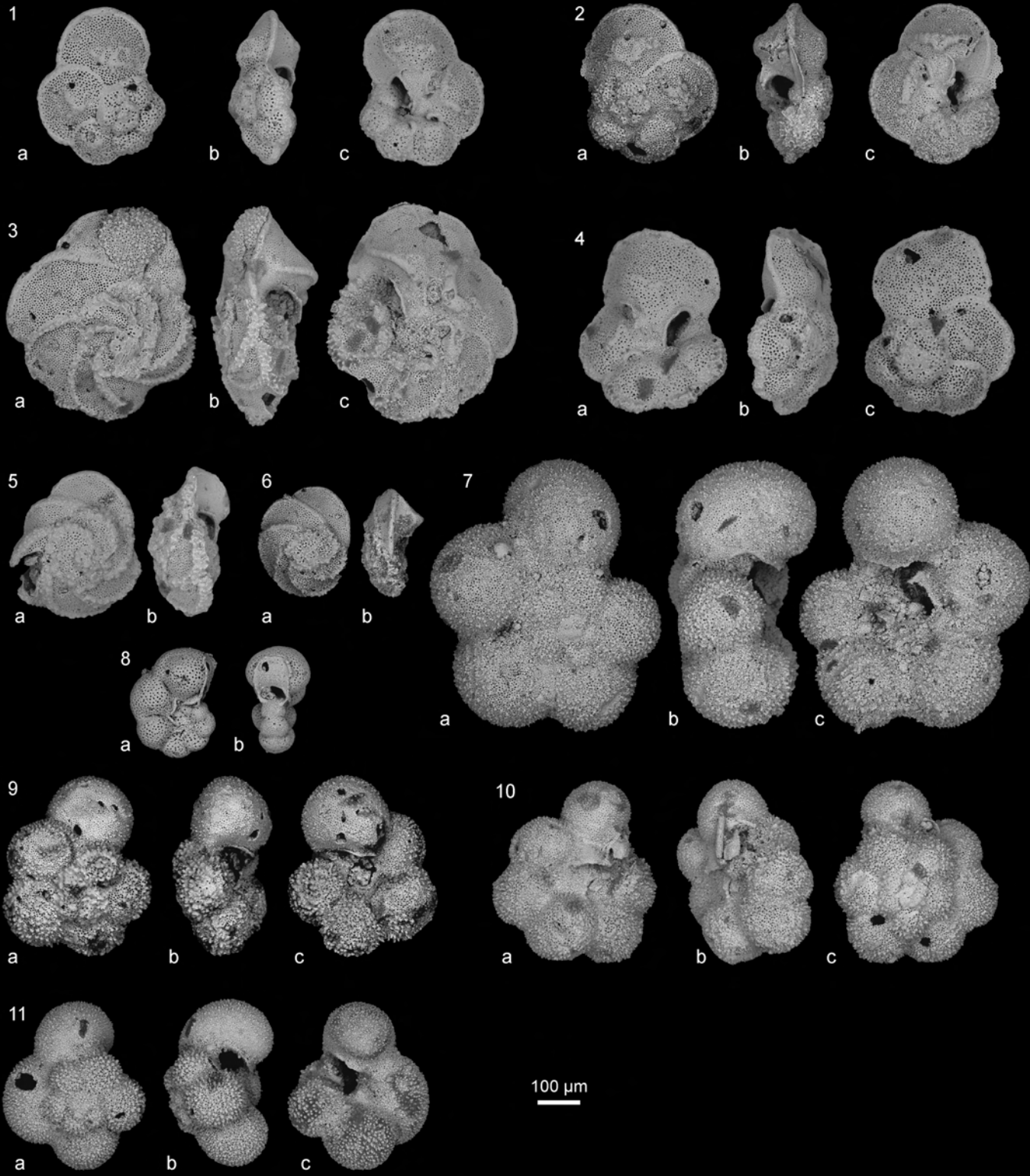


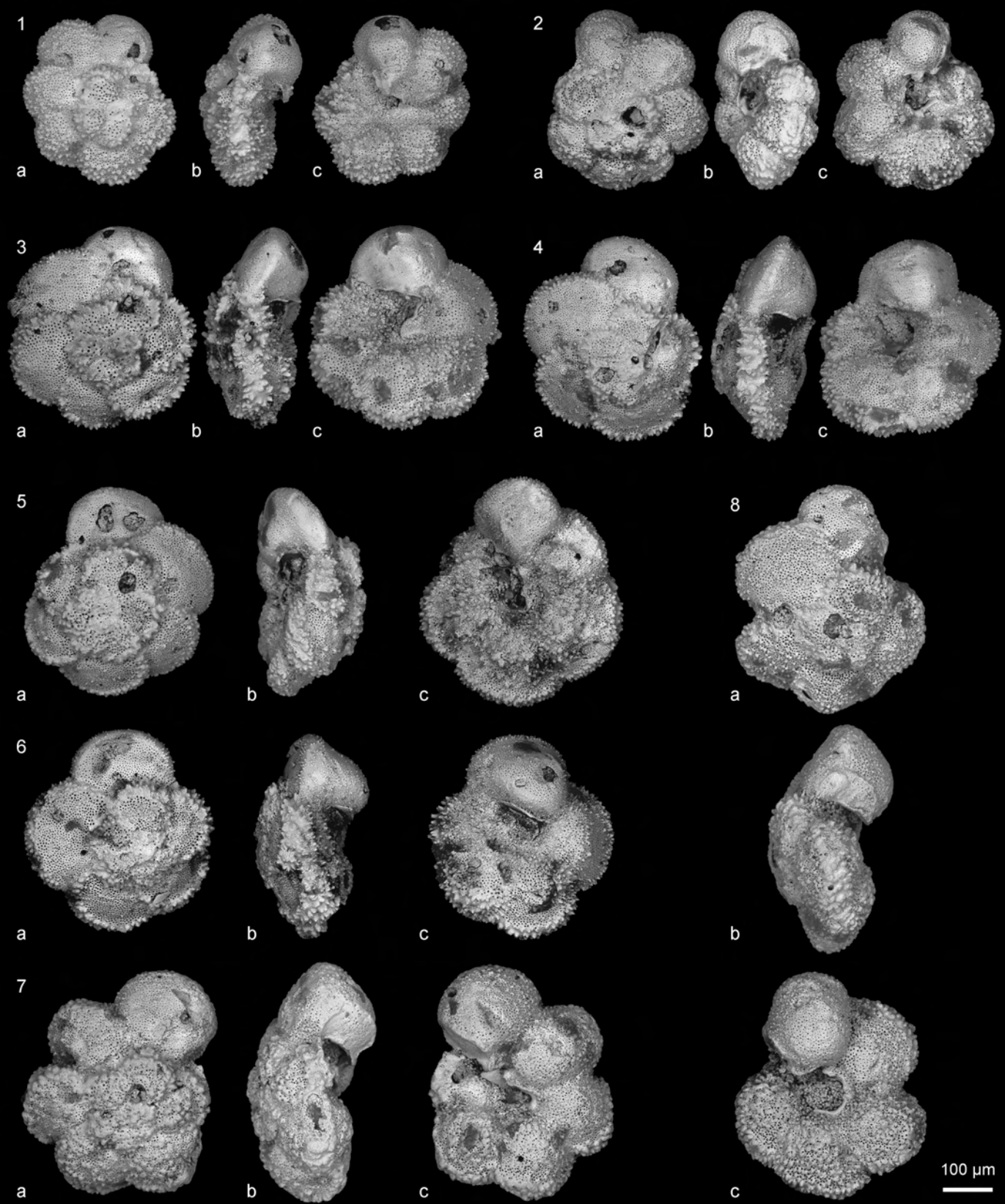
Mézières-sur-Ponthoïn

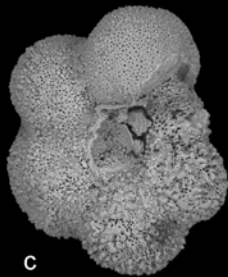
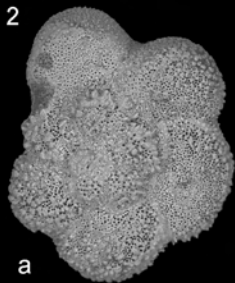
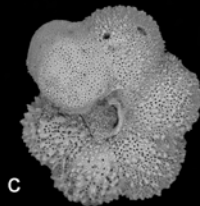
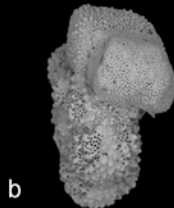
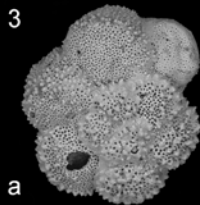
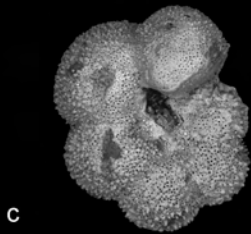
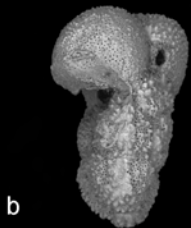
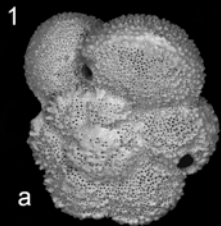


-  sand and sandstones
-  glauconitic-rich chalk
-  chalk

-  bioclastic limestones
-  nodular limestones
-  calcareous rich claystone

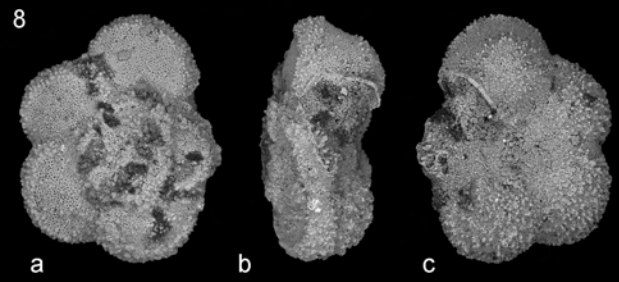
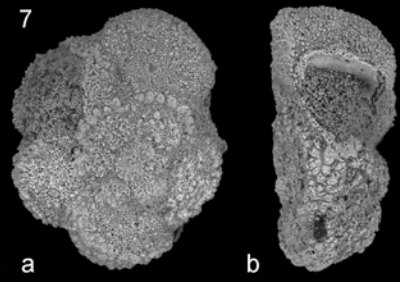
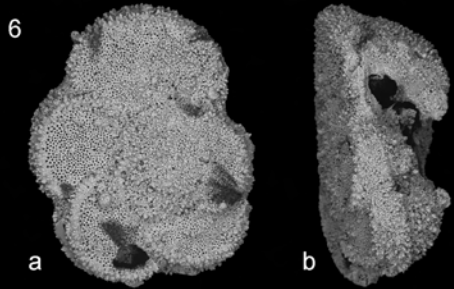
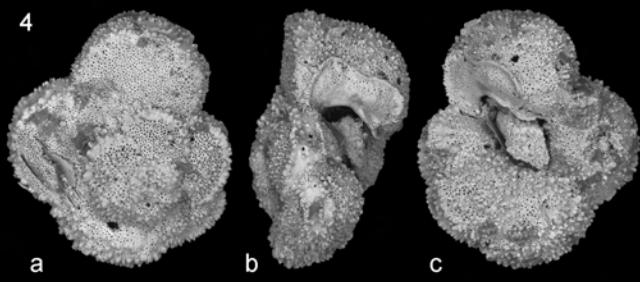
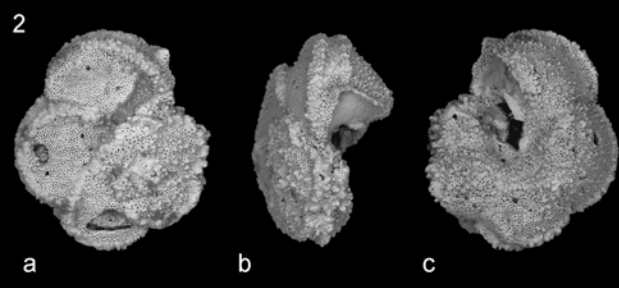
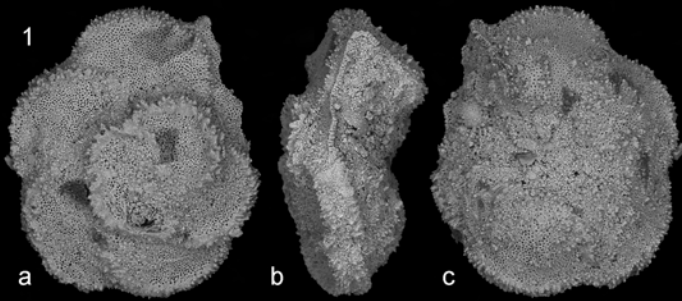




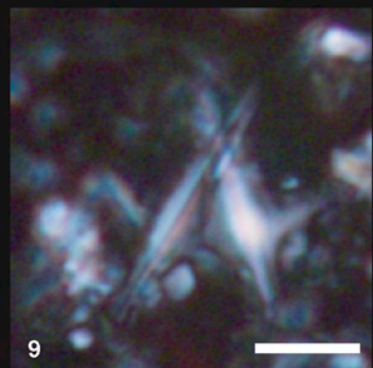
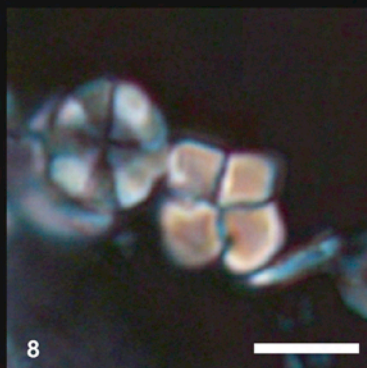
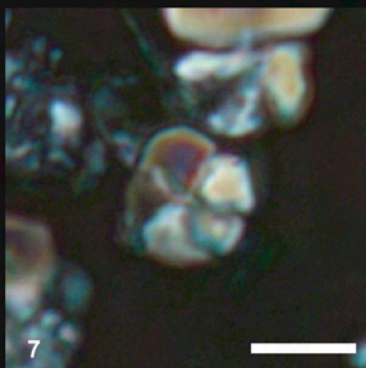
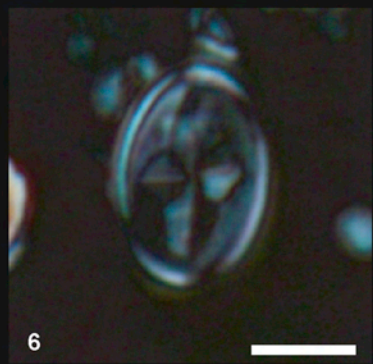
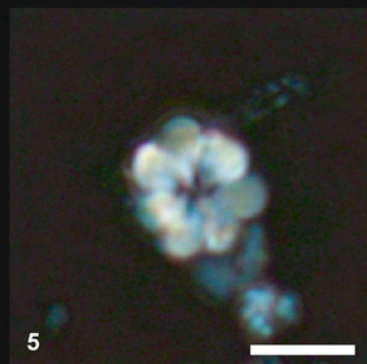
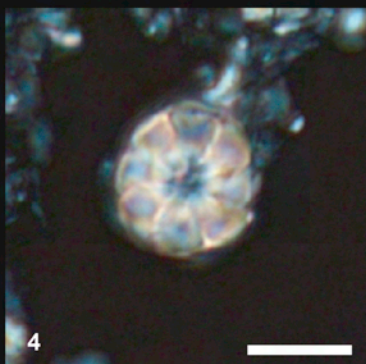
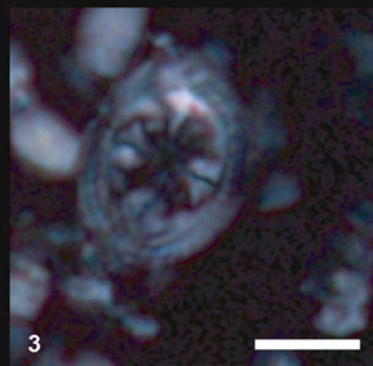
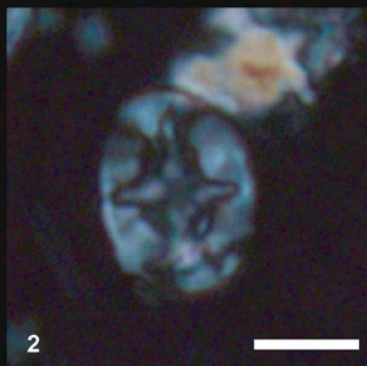
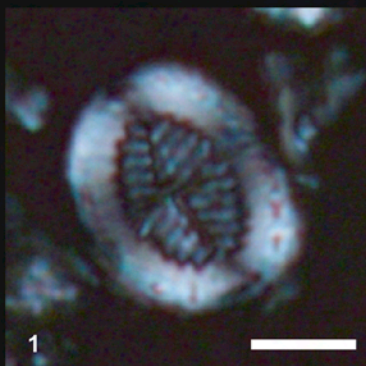


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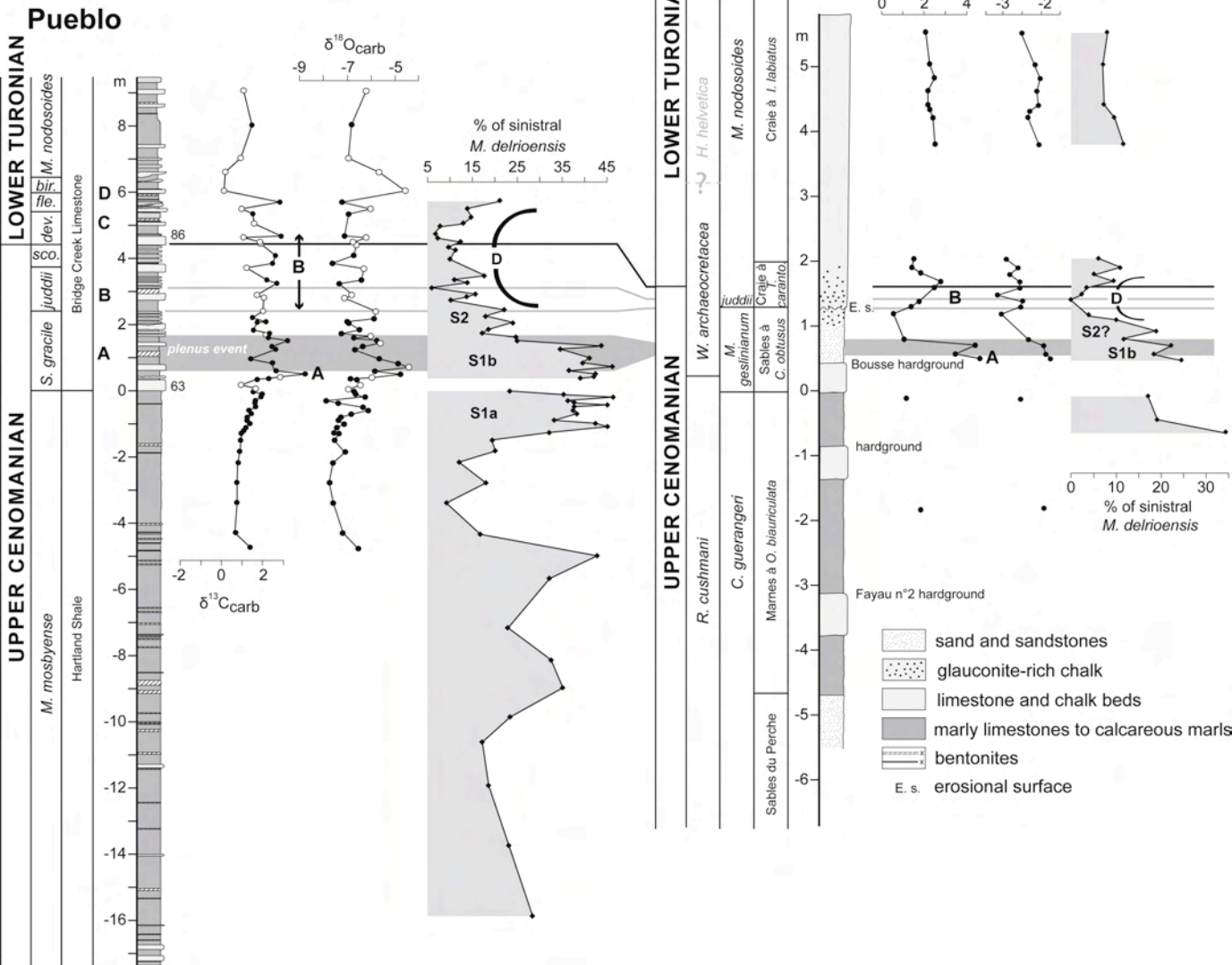
A white horizontal scale bar representing 100 micrometers.



100 μ m

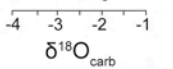
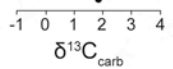
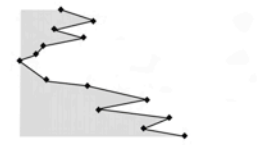
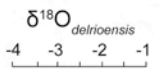
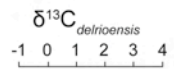
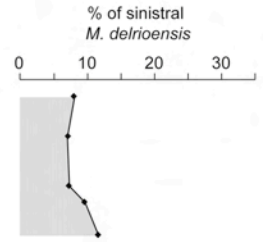
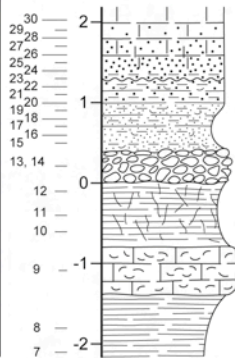
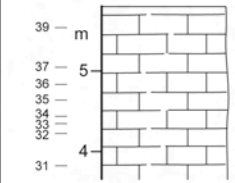


Mézières-sur-Ponthouin



Mézières-sur-Ponthouin

UPPER CENOMANIAN		LOWER TURONIAN	
<i>R. cushmani</i>	<i>W. archaeocretacea</i>	<i>H. helvetica</i>	
<i>C. guerangeri</i>	<i>M. juddii</i>	<i>M. nodosoides</i>	
Marnes à <i>O. biauriculata</i>	Sables à <i>C. obtusus</i>	Craie à <i>I. labiatus</i>	



- dextral morphotype
- sinistral morphotype
- bulk