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1 **Quantitative biochronology by unitary associations of late Albian ammonites**  
2 **from Europe and their biodiversity**

3

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5

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15

16 **Abstract.** The chronostratigraphic subdivision into an Early and Late Cretaceous is preceded by a global  
17 turnover in marine faunas, called the middle–late Albian Boundary Bio-Event. Thus, the late Albian is  
18 a critical time interval, especially with respect to the evolution and radiation of ammonites, which are  
19 by far the most abundant nektic organisms at that time. In this context, achieving the best possible  
20 biochronological resolution has direct implications on the various geological, geochemical,  
21 palaeoclimatic and biotic hypotheses related to this period. Over the past decades, several quantitative  
22 biochronological methods have been developed to achieve more accurate biozonations and correlations.  
23 Using strict and well-defined algorithms allow for the processing of large datasets and ensure a rigorous,  
24 exhaustive, and consistent treatment of the biostratigraphic data. Here, by means of the Unitary  
25 Association Method (UAM), we perform a quantitative biochronological analysis on a substantial  
26 dataset of late Albian ammonite occurrences from western Europe (comprising 175 species among 13

27 sections). This led to the construction of a sequence of 23 UAs for the whole late Albian, which  
28 represents a higher resolution than the standard empirical interval-based zonations for northwestern and  
29 southwestern Europe (7 zones and 9 subzones, respectively). These UAs can also be merged into 9 more  
30 geographically reproducible association zones, which correlate very well with the two standard  
31 zonations. Based on our results, the UAM enables accounting for and highlighting the range of actually  
32 all taxa, and not just a few selected index taxa whose ranges very often extend before and/or after their  
33 eponymous interval zone. Finally, the UA quantitative biochronology enables us to measure western  
34 European ammonite diversity throughout the whole Albian in detail. Consequently, we identified a  
35 major and sharp diversity decrease during the uppermost Albian (UAZ 8/9 boundary; = *M.*  
36 *perinflatum*/*A. briacensis* zones boundary), concomitant with the well-known Oceanic Anoxic Event  
37 OAE1d.

38

39 **Keywords.** Albian, Ammonoidea, Europe, quantitative biochronology, correlation, palaeobiodiversity.

40

## 41 1. Introduction

42

43 The Early Cretaceous is a highly-disturbed time interval witnessing global fluctuations in climate, sea-  
44 level and carbon cycle (e.g., Schlanger and Jenkyns 1976, Haq et al. 1987, Weissert et al. 1998, Leckie  
45 et al. 2002, Puc at et al. 2003, Reboulet et al. 2005, Bornemann et al. 2005, Watkins et al. 2005, Bjerrum  
46 et al. 2006, Am dro 2008, Gale et al. 2011, 2020, Littler et al. 2011, F llmi 2012, Bodin et al. 2015, Xu  
47 et al. 2020). More specifically, the late Albian records the widening of the North Atlantic (Fenner 2001)  
48 and two Oceanic Anoxic Events: the OAE1c and the OAE1d (Reboulet et al. 2005, Watkins et al. 2005,  
49 Gale et al. 2011). The late Albian also includes a major double eustatic event with a third-order cycle as  
50 well as a transgression peak within a second-order cycle (Am dro 2008). Simultaneously to these  
51 palaeoenvironmental changes, this period is also marked by major palaeoecological changes (e.g.,  
52 Leckie et al. 2002). Regarding ammonites, this time interval is characterized by a remarkable increase  
53 in ammonite taxonomic diversity, a sudden rise of heteromorphic ammonites, as well as a protracted

54 trend toward more cosmopolitan faunas (Amédro 1992, Owen 1996, Reboulet et al. 2005, Amédro 2008,  
55 Lehmann 2015). In this context, resolution of correlations necessarily impacts the understanding and  
56 interpretation of the various geological, geochemical, palaeoclimatic and biotic evolutionary hypotheses  
57 related to this period. Therefore, achieving robust and high-resolution biochronological correlations  
58 remains critical. Regarding the Early Cretaceous, calpionellids, calcareous nannofossils, planktic  
59 foraminifers and ammonoids are the major groups providing exceptionally high-resolution marine  
60 biostratigraphic scales, as illustrated by the selected GSSP boundary markers (see Gale et al. 2020).

61       Albian ammonite faunas from the European province and associated biostratigraphy has been the  
62 focus of considerable work, beginning in the late 19<sup>th</sup> century (e.g., Hébert and Munier-Chalmas 1875,  
63 Jacob 1905, 1907, Spath 1923–1943, Breistroffer 1936, 1940a, b, 1946, 1947, Renz and Luterbacher  
64 1965, Renz 1968, Kennedy 1970, Scholz 1973, 1979, Owen 1975, 1984a, 1984b, 1996, 1999, Cooper  
65 and Kennedy 1977, 1987, Wright and Kennedy 1979, 1994, Delanoy and Latil 1988, Latil 1989, 1994,  
66 Amédro 1992, 2002, 2008, Kennedy and Delamette 1994a, b, Gale et al. 1996, 2011, Amédro and  
67 Robaszynski 2000, Kennedy et al. 2000, 2008, 2014, 2017, Szives 2007, Kennedy and Latil 2007, Joly  
68 and Delamette 2008, Lehmann et al. 2007, 2008, Lehmann 2011, Robaszynski et al. 2008, Bujtor 2010,  
69 Cooper and Owen 2011a, b, Petrizzo et al. 2012, Amédro and Matrimon 2014, Kennedy and Machalski  
70 2015, Tajika et al. 2017, 2018a, b, Reboulet et al. 2018, Jattiot et al. 2021, 2022). However, despite this  
71 considerable effort, correlation and subdivision of the Albian by ammonites remain debated, especially  
72 regarding the late Albian in Europe (e.g., Amédro 2002, 2008, Robaszynski et al. 2007, Amédro and  
73 Robaszynski 2008, Scott 2009). The late Albian is particularly highly debated since Renevier (1868),  
74 who proposed the establishment of a Vraconnian stage within this time interval. Noteworthy, based on  
75 a number of criteria and very detailed and reliable stratigraphic data, Amédro (2002, 2008) argued for  
76 the revival of the Vraconnian stage between the Albian *sensu stricto* and the Cenomanian. Conversely,  
77 Scott (2009), based on his biostratigraphic work, came to the conclusion that the reinstatement of a  
78 Vraconnian stage was not recommended. These contrasted opinions demonstrate that the current  
79 biostratigraphic schemes and their correlation for the late Albian in Europe are questionable.

80 Consequently, the timing of all palaeoenvironmental and palaeoecological events occurring during the  
81 late Albian in the European province is yet not well constrained.

82 Most previous ammonite zonations for the Albian were established by classical, empirical and  
83 non-quantitative approaches. However, an increasing number of available biostratigraphic data and  
84 increasing need of higher resolved correlation prompt to use modern quantitative biochronological  
85 analyses based on robust algorithms in order to overcome the correlative increasing amount of  
86 biostratigraphic contradictions. This is especially the case for the late Albian in Europe with ammonites  
87 highly endemic and most species found in very few sections only (Amédéo 2008), therefore hampering  
88 straightforward correlation. Scott (2009) already underlined the need of quantitative biostratigraphic  
89 approaches to achieve better biozonation and correlation for the late Albian in Europe. Although he  
90 applied Graphic Correlation (GC) to tackle this problem, his study focuses on a few key sections only,  
91 and GC remains a semi-quantitative technique requiring the empirical, subjective fit of a non-global  
92 correlation line for pairs of sections. Hence, the goal of this study is to revise the ammonite zonation of  
93 the entire late Albian in Europe (encompassing the Vraconnian) by means of an appropriate quantitative  
94 biochronological approach, namely the Unitary Association Method (UAM; Guex 1991, Guex et al.  
95 2016). This approach has been already successfully applied to ammonites (e.g., Dommergues and  
96 Meister 1987, Pálffy et al. 1997, 2003, Pálffy and Vörös 1998, Monnet and Bucher 1999, 2002, 2007,  
97 Monnet et al. 2011, Galfetti et al. 2007a, b, Brühwiler et al. 2010, Guex et al. 2012, Jattiot et al. 2017)  
98 and other organisms (e.g., Abdelhady et al. 2018, 2021, Xiao et al. 2018, Chen et al. 2019, Wu et al.  
99 2020, Leu et al. 2022, 2023), and it has proven appropriate to cope with conflicting data such as the  
100 necessarily incomplete fossil record (Baumgartner 1984, Boulard 1993, Galster et al. 2010, Monnet et  
101 al. 2011). Furthermore, the here reconstructed quantitative UA-zonation will be compared with the  
102 standard western European empirical ammonite zonations and will help gaining insights into the  
103 palaeobiodiversity changes recorded during the entire late Albian and their potential link with the  
104 Vraconnian substage.

105

106 **2. Materials and Methods**

107

## 108 2.1. Biostratigraphic data

109

110 This study focuses on Albian sedimentary successions, and more precisely the late Albian of western  
111 Europe. Biostratigraphic data are compiled from the literature by including all contributions providing  
112 adequate information on the (possibly bed-by-bed) occurrences of species, as well as possibly  
113 illustrations of these ammonites. This compilation leads to a dataset including 13 sections: from France,  
114 Col de Palluel (Gale et al. 2011), Mont Risou (Gale et al. 1996), Montlaux (Kennedy and Latil 2007),  
115 Salazac (Jattiot et al. 2021), Clansayes (Jattiot et al. 2022), as well as two cores near Marcoule (Amédéo  
116 and Robaszynski 2000); from Germany, Kirchrode (Wiedmann and Owen 2001) and Lahe (Lehmann  
117 2011); from Belgium, Harchies (Amédéo 2008) and Strépy-Thieu (Kennedy et al. 2008); from England,  
118 the Upper Gault and Upper Greensand formations (unpublished data by one of us, HGO); and from  
119 northern Spain (Lopez-Horgue et al. 2009). The dataset is composed of 175 species belonging to 55  
120 genera and 14 families.

121 Because the dataset is constructed from multiple sources with taxonomic definitions slightly  
122 different, the taxonomy has been revised if necessary before performing the biochronological analysis.  
123 Additionally, since the occurrences with some taxonomic uncertainties tend to create additional  
124 biostratigraphic contradictions and disjunctive taxon ranges (Guex 1991, Monnet et al. 2011), they have  
125 been discarded in our dataset. Importantly, the following changes were made at that stage: 1) the species  
126 *Mortoniceras (Subschloenbachia) perinflatum* was merged with *Mortoniceras (Subschloenbachia)*  
127 *rostratum*, following the suggestion of Jattiot et al. (2022) that firm evidence for the separation of *M.*  
128 *(S.) rostratum* and *M. (S.) perinflatum* as two distinct species is still lacking in the literature; 2) the taxon  
129 *Hysterocheras serpentinum* was removed from the Col de Palluel section since, in our opinion, it does  
130 not match the holotype; and 3) the occurrence of *Mariella bergeri* and *M. miliaris* from the level U8 in  
131 England are discarded because they were already questionable in the original dataset (unpublished data).  
132 The ‘initial’ dataset including these previous changes compared to the original publications is provided  
133 as supplementary material (Appendices A, B).

134

135 *2.2. Biozonation based on unitary associations (UAs)*

136

137 Over the past decades, several quantitative biochronological methods have been developed to achieve  
138 more accurate biozonations and correlations by using strict and well-defined algorithms that allow for  
139 the processing of large datasets and ensure a rigorous, exhaustive, and consistent treatment of the  
140 biostratigraphic data (see Hay and Southam 1978, Guex 1991, Agterberg and Gradstein 1999, Sadler  
141 2004, Cody et al. 2008, Sheets et al. 2012, Monnet et al. 2015, Fan et al. 2020). Here, the biostratigraphic  
142 data of Albian ammonites are processed by means of the deterministic unitary associations (UAs; Guex  
143 1977, 1991). For an in-depth description and review of the method, the reader is referred to Savary and  
144 Guex (1991, 1999), Monnet al. (2011, 2015) and Guex et al. (2016). The fundamentals of the method  
145 are that 1) it focuses on the observed co-existences among taxa (and not their  
146 appearance/disappearance), 2) it infers virtual associations (i.e., coexistences in time but not in space)  
147 of taxa to resolve the biostratigraphic contradictions (i.e., conflicting stratigraphic relationships among  
148 taxa), and 3) it outputs discrete biozonations composed of unique maximal sets of coexisting (actually  
149 or virtually) taxa (= UAs). The data are analysed with the widely distributed palaeontological analysis  
150 freeware PAST (Hammer et al. 2001) version 4.07b. With the software, a pre-processing procedure is  
151 applied to the data before the actual biochronological analysis: taxa found only in one section  
152 ('singletons') are removed as they are known to significantly increase the amount of biostratigraphic  
153 contradictions while being of no help for correlation purposes (Boulard 1993, Monnet and Bucher 1999,  
154 2002, Savary and Guex 1999, Monnet et al. 2011).

155 Here, the biochronological analysis follows the stepwise protocol of Monnet et al. (2011): 1) first,  
156 the 'initial' biostratigraphic dataset (Appendix A) is directly analyzed by means of the unitary  
157 associations; 2) then, the preliminary results are post-processed to identify and remove the occurrences  
158 at the origin of the most critical biostratigraphic contradictions; 3) next, a second UA analysis is  
159 performed on this second 'optimized' biostratigraphic dataset; and 4) last, the reconstructed UAs are  
160 possibly merged to construct the biozonation. Because there is an unavoidable trade-off between the

161 intrinsic quality (completeness) of the data and the resolution of the constructed biozones, the ammonite  
162 biozonation is here reconstructed in two steps with an ‘optimization’ of the data in between. Importantly,  
163 the goal of this optimization is not to reduce the number of biostratigraphic contradictions to minimum  
164 (there will always be a large amount of them and UAs are designed to cope with them). Instead, the  
165 optimization consists in 1) identifying the most problematic occurrences, which could result from  
166 multiple sources (e.g. sparse data, taxonomic misidentification, reworking, diachronism, preservation,  
167 ecological exclusion, or endemism), and 2) removing inappropriate results such as cycles of cliques and  
168 residual virtual edges (the former can lead to partly uncertain results, while the latter can lead to UAs  
169 identified in a single section because based only on inferred coexistences). Noteworthy, this  
170 optimization step enables to get feedback on the data and to produce a more robust biozonation (Monnet  
171 et al. 2011). Importantly, the implementation of UAs in the PAST software contains several tools (lists  
172 of maximal cliques, their content and their graph of relationships, as well as lists of contradictions and  
173 their content; for details, see Monnet et al. 2011 and Guex et al. 2016) for tracing back the possible  
174 origin (in terms of occurrences) of the conflicting stratigraphic relationships among taxa. The  
175 optimization process iteratively and parsimoniously removes the few occurrences at the origin of the  
176 cliques’ cycles and of the residual virtual edges. The removal of such conflicting occurrences is  
177 recommended by the fact that UAs are sensitive to false coexistences and resolve the contradictions by  
178 extending some taxon ranges (i.e., the virtual coexistences). Finally, as suggested and discussed by Guex  
179 (1991; see herein for more details), some UAs may be merged into UA-Zones (UAZs) to increase their  
180 lateral reproducibility (for higher correlation power) and on the basis of the similarity of their faunal  
181 content (for other examples with such methodology, see Chen et al. 2019 and Leu et al. 2023, among  
182 others). Note that these UAZs are just secondary practical groupings of some UAs to ease correlation;  
183 the primary basic biostratigraphic units remain the UAs, which synthetize at best (after resolving the  
184 inter-taxon stratigraphic contradictions) the co-existences in time (not necessarily in space) and the  
185 relative bioevents (apparition/ extinction) of all taxa considered.

186



### 187 2.3. Ammonite palaeobiodiversity

188

189 As demonstrated by Escarguel and Bucher (2004), biochronozones based on the principle of maximal  
190 association (such as the unitary associations) provide a very robust and reliable basis for counts of  
191 taxonomic richness. Therefore, using the resulting species ranges of the 23 UAs covering the entire late  
192 Albian in western Europe (this study), we counted the values of species richness (total diversity) for all  
193 multiple-section taxa, as well as for Ancyloceratina (= heteromorphs) and other ammonites (=  
194 monomorphs), separately. Furthermore, the species richness of each family was quantified and reported  
195 in a spindle diagram. These biodiversity curves will enable to document the regional (western Europe)  
196 diversity patterns of ammonites at a high temporal resolution.

197

## 198 3. Results

199

### 200 3.1. European late Albian ammonite biozonation

201

202 The UA analysis of the ‘initial’ dataset of European late Albian ammonite occurrences (Appendix A)  
203 leads to 27 UAs after resolving 145 conflicting inter-taxa stratigraphic relationships (= biostratigraphic  
204 contradictions) distributed among 40 maximal cliques and based on 118 multiple-section taxa. Note that  
205 without removing the 57 single-section taxa, the dataset leads to 199 biostratigraphic contradictions.  
206 Importantly, this dataset leads to no cycle among maximal cliques and to 13 residual virtual edges.

207 The post-processing/optimization of these preliminary results highlights that the origin of the  
208 residual virtual edges results from four occurrences only, each of them creating virtual UAs. First, the  
209 occurrence of *Idiohamites tuberculatus* at the depth of 61.60 m in Kirchrode borehole (see Wiedmann  
210 and Owen 2001, pl. 1, fig. J) is at the origin of five residual virtual edges. In our opinion, the illustrated  
211 specimen is part of a very unusually large spiral, larger than any other *Idiohamites* species described  
212 from the Boreal realm, and therefore should better be considered as an indeterminate species. Second,

213 the occurrence of *Leptoplites pseudoplanus* at the depth of 136.82 m in Kirchrode borehole (see  
214 Wiedmann and Owen 2001, pl. 2, fig. C) is also at the origin of five residual virtual edges. In our opinion,  
215 the illustrated specimen does not belong to this species, and should instead be considered as an  
216 indeterminate species given its fragmentary state. Third, the occurrence of *Euhoplites vulgaris* at the  
217 depth of 204.08 m in Kirchrode borehole (see Wiedmann and Owen 2001, pl. 4, fig. C) is at the origin  
218 of one residual virtual edge; similarly, the illustrated specimen is, in our opinion, too fragmentary to  
219 reach a firm identification at the species level. And fourth, the occurrence of *Leptoplites ornatus* at the  
220 depth of 1168.53 m in MAR 402 borehole (Amédro and Robaszynski 2000) is at the origin of two  
221 residual virtual edges; unfortunately, this occurrence is not supported by any figuration. Because these  
222 four occurrences are unusual, questionable, and contribute to the majority of identified biostratigraphic  
223 contradictions, they are removed from the dataset. Finally, the level at about 459 m in a section in  
224 northern Spain described by Lopez-Horgue et al. (2009) was also removed as it produces around 10%  
225 of all biostratigraphic contradictions; the lack of figuration prevents re-evaluating its taxonomy.

226 The second UA analysis on the post-processed, ‘optimized’ dataset leads to 24 unitary  
227 associations after resolving 130 conflicting stratigraphic relationships distributed among 39 maximal  
228 cliques and based on 115 multiple-section taxa; as expected, there are no more residual virtual edges.  
229 The final results of the biochronological analysis are based on this second analysis and are: 1) a range  
230 chart of the 115 multiple-section taxa through the succession of the 24 UAs (discrete maximal sets of  
231 mutually coexisting species; Fig. 1) complemented by 2) its reproducibility matrix (Fig. 2), which  
232 indicates the UAs identified in the studied sections. The range chart is a sequence synthesizing the  
233 association, superposition and exclusion relationships of the ammonite taxa included in the analysis; it  
234 defines the characteristic content of each biostratigraphic unit (UA). The single-section taxa  
235 automatically removed during the biochronological analysis are dated back with these UAs and their  
236 range chart is reported in Appendix C. Among all studied sections, only Clansayes, Salazac and  
237 Strépy-Thieu are ‘single-bed sections’ (Appendix A). We tested the influence of these ‘single-bed  
238 sections’ by doing the very same quantitative biostratigraphic analysis without these localities. The  
239 results remain overall the same, thus demonstrating the absence of faunal mixing in these beds.

240

## 241 3.2. Description of the biozones

242

243 The reconstructed UAs enable to revise and construct a quantitative ammonite biozonation for  
244 the entire late Albian of Europe. Because the UA24 marks the earliest Cenomanian, which is not fully  
245 covered by the studied dataset, this UA is not considered in this study. Noteworthy, since unitary  
246 associations focus on the coexistence of species, this method constructs discrete assemblage biozones  
247 and not interval-based (first/last appearances) zones; a UA is therefore characterized by the restricted  
248 occurrence of taxa and/or by the coexistence of specific pairs of taxa having their last occurrence (LO)  
249 and their first occurrence (FO), respectively, within this UA. The 23 unitary associations of the late  
250 Albian are merged into 9 UA-zones (UAZ; Fig. 2), which are briefly described below. Among all studied  
251 sections, the distribution of the UAs reveals Col de Palluel as by far the most complete section (16 out  
252 of the 23 late Albian UAs are documented there; Fig. 2). This supports Gale et al. (2011) who claims  
253 that this section provides the most detailed record known of the upper Albian substage with a thickness  
254 of nearly 330 m and with an excellent ammonite, inoceramid, planktic foraminiferal, nannofossil,  
255 geochemical, and cyclostratigraphic record (Kennedy et al. 2004).

256

257 UAZ 1: This zone composed by the UAs 1–2 contains 16 genera and 28 species, distributed  
258 mostly among the genera *Euhoplites*, *Dipoloceras*, *Hamites*, and *Hysterocheras* (Fig. 1). It is mainly  
259 characterized by *Euhoplites truncatus* in its lower part, and in its upper part by the pairs of *Dipoloceras*  
260 *cristatum* (LO) with *Mortoniceras cunningtoni* (FO), *Eoscaphtes circularis* (FO) or *Hysterocheras*  
261 *orbigny* (FO). *Euhoplites truncatus* is already known to occur both in the uppermost middle Albian and  
262 lowermost upper Albian (Gale et al. 2011); it is here the *Euhoplites truncatus* late form that characterizes  
263 this UAZ. The species *Dipoloceras cristatum* occurs throughout this zone, whereas the appearance of  
264 the genus *Mortoniceras* marks the upper part of this zone. The zone is documented (Fig. 2) in France  
265 (Col de Palluel) and in England. It correlates with the standard *Dipoloceras cristatum* Zone (lowermost

266 upper Albian; Fig. 3).

267

268 UAZ 2: This zone composed by the UAs 3–4 contains 18 genera and 36 species, distributed  
269 mostly among the genera *Mortoniceras*, *Dipoloceras*, *Euhoplites*, *Idiohamites*, *Hamites*, and  
270 *Hysterocheras* (Fig. 1). Noteworthy, this zone marks the first occurrence of *Mortoniceras pricei* and of  
271 *Hysterocheras varicosum*, as well as the last occurrence of the genus *Dipoloceras*. It is also characterized  
272 by the last occurrence of many *Euhoplites* species and by the first occurrence of *Idiohamites* spp. The  
273 zone is documented (Fig. 2) in France (Col de Palluel), Germany (Kirchrode and Lahe) and England. It  
274 correlates with the lower part of the *Mortoniceras pricei* and the *Hysterocheras varicosum* zones (lower  
275 upper Albian; Fig. 3).

276 UAZ 3: This zone composed by the UAs 5–7 contains 22 genera and 39 species, distributed  
277 mostly among the genera *Mortoniceras*, *Euhoplites*, *Epihoplites*, *Idiohamites*, *Hamites*, and  
278 *Hysterocheras* (Fig. 1). The species *Mortoniceras bipunctatum* is restricted and ranges throughout the  
279 entire zone, and is among the most widespread and diagnostic species of this zone by being present in  
280 France, England and Germany (Fig. 2). The middle part of the zone is characterized by the first  
281 representatives of the renowned genera *Anisoceras* and *Scaphites* with *A. subarcuatum* and *S.*  
282 *hugardianus*. The upper part of the zone is characterized by several species of *Epihoplites* and also  
283 marks the last occurrence of *Hysterocheras orbigny* and *H. varicosum*. The zone correlates with the  
284 upper part of the *Mortoniceras pricei* and *Hysterocheras varicosum* zones (lower upper Albian; Fig. 3).

285 UAZ 4: This zone composed only by the UA8 contains 19 genera and 31 species, distributed  
286 mostly among the genera *Callihoplites*, *Euhoplites*, *Mortoniceras* and *Idiohamites* (Fig. 1). It is mainly  
287 characterized by *Callihoplites auritus* and *Mortoniceras commune*, which are restricted to this zone, and  
288 by the coexistence of *Mortoniceras pricei* (LO) and/or *Anisoceras subarcuatum* (LO) with *Mortoniceras*  
289 *inflatum* (FO), as well as by the coexistence of the genus *Callihoplites* (FO) with the last occurrence of  
290 *Anahoplites* and *Euhoplites*. This zone is peculiar because it shows the coexistence of two *Mortoniceras*  
291 species (last occurrence of *M. pricei* and first occurrence of *M. inflatum*) usually considered as index of

292 their eponym zone. The zone is documented in Germany and England, but not in France (Fig. 2). It  
293 correlates with the lowermost part of the *Mortoniceras inflatum* Zone and to the *C. auritus* Subzone  
294 (lower upper Albian; Fig. 3).

295 UAZ 5: This zone composed by the UAs 9–11 contains 23 genera and 39 species, distributed  
296 mostly among the genera *Mortoniceras*, *Callihoplites*, *Anisoceras* and *Idiohamites* (Fig. 1). It is mainly  
297 characterized by the coexistence of *Mortoniceras inflatum* (LO) or *Callihoplites variabilis* (LO) with  
298 *Anisoceras armatum/perarmatum* (FO), *Cantabrigites minor* (FO) or *Callihoplites tetragonus* (FO).  
299 Noteworthy, the classical index *M. inflatum* occurs throughout this zone, which also marks its last  
300 occurrence. The zone is documented in France, Germany and England (Fig. 2). It correlates with the  
301 *Mortoniceras inflatum* Zone and the lower part of the *Callihoplites robustus* Subzone (middle upper  
302 Albian; Fig. 3).

303 UAZ 6: This zone composed by the UAs 12–14 contains 26 genera and 46 species, distributed  
304 mostly among the genera *Mortoniceras*, *Stoliczkaia*, *Callihoplites*, *Cantabrigites*, *Mariella*, and  
305 *Hamites* (Fig. 1). It is mainly characterized by the coexistence of *Hysterocheras binum* (LO) or *H.*  
306 *carinatum* (LO) with *Mortoniceras fallax* (FO), *Neophlycticeras blancheti* (FO), *Stoliczkaia dispar* (FO)  
307 or *Mariella nobilis* (FO). Therefore, this zone records the first occurrence of many classical index  
308 species. It also contains the first occurrence of *Anisoceras pseudoelegans* and of the major  
309 heteromorphic genus *Mariella* (*M. nobilis*, *M. gresslyi*). The zone is firmly documented (Fig. 2) only in  
310 France (Col de Palluel and Salazac). It correlates with the *Mortoniceras fallax* Zone and the upper part  
311 of the *C. robustus* Subzone (middle upper Albian; Fig. 3).

312 UAZ 7: This zone composed by the UAs 15–17 contains 23 genera and 49 species, distributed  
313 mostly among the genera *Mortoniceras*, *Stoliczkaia*, *Pleurohoplites*, *Lepthoplites*, *Callihoplites*,  
314 *Cantabrigites*, *Hamites*, *Anisoceras*, and *Scaphites* (Fig. 1). It is mainly characterized by the coexistence  
315 of *Neophlycticeras blancheti* (LO) or *Anisoceras campichei* (LO) with *Mortoniceras rostratum* (FO),  
316 *Callihoplites campichei* (FO) or *Ostlingoceras puzosianum* (FO). Noteworthy, *Mortoniceras fallax* still  
317 occurs throughout this zone, which also records the first representatives of *Pleurohoplites* and  
318 *Ostlingoceras*, as well as the first occurrence of *Stoliczkaia clavigera* in the upper part of the zone. The

319 zone is documented (Fig. 2) in France (Col de Palluel, Mont Risou), Germany (Kirchrode), England,  
320 and possibly Belgium (Harchies, Strépy). It roughly correlates with the *Mortoniceras rostratum* Zone  
321 (upper upper Albian; Fig. 3).

322 UAZ 8: This zone composed by the UAs 18–20 contains 24 genera and 48 species, distributed  
323 mostly among the genera *Mortoniceras*, *Stoliczkaia*, *Callihoplites*, *Pleurohoplites*, *Hyphoplites*,  
324 *Anisoceras*, *Mariella*, *Ostlingoceras*, and *Scaphites* (Fig. 1). It is mainly characterized by the  
325 coexistence of *Mortoniceras rostratum* (LO), *Anisoceras perarmatum* (LO), *Callihoplites vracensis*  
326 (LO) or *Ostlingoceras puzosianum* (LO) with *Mariella bergeri* (FO), *Hyphoplites campichei* (FO) or  
327 *Idiohamites elegantulus* (FO). Noteworthy, the zone records the occurrence of the first representatives  
328 of *Hyphoplites* and *Arrhaphoceras*, as well as the last occurrence of *M. fallax* and *M. rostratum*.  
329 Additionally, *Hyphoplites falcatus* and *Pleurohoplites renauxianus* have their first occurrence in the  
330 upper part of this zone. The zone is documented (Fig. 2) in France (Col de Palluel, Mont Risou,  
331 Montlaur, Marcoule, Clansayes), England, possibly Belgium (Harchies), but not in Germany;  
332 nevertheless, this zone is the most widely documented. It roughly correlates with the *Mortoniceras*  
333 *perinflatum* Zone (upper upper Albian; Fig. 3).

334 UAZ 9: This zone composed by the UAs 21–23 contains 19 genera and 22 species, distributed  
335 mostly among the genera *Stoliczkaia*, *Hyphoplites*, *Arrhaphoceras*, *Scaphites*, *Mariella*, and  
336 *Idiohamites* (Fig. 1). It is mainly characterized by the coexistence of *Stoliczkaia dispar* (LO), *S.*  
337 *clavigera* (LO), *Callihoplites tetragonus* (LO) or *Scaphites meriani* (LO) with *Arrhaphoceras*  
338 *briacensis* (FO). Noteworthy, the genus *Mortoniceras* is not documented in this zone, as well as many  
339 species from the previous zone, therefore reflecting an important diversity dropdown during this zone.  
340 The zone is documented (Fig. 2) in France (Col de Palluel, Mont Risou) and England. It correlates with  
341 the *Arrhaphoceras briacensis* Zone (uppermost Albian; Fig. 3).

342

343 3.3. Late Albian ammonite palaeobiodiversity

344

345 The ammonite palaeobiodiversity in terms of total richness and based on the reconstructed quantitative  
346 UAs is reported on Figure 4 for all ammonites and on Figure 5 at the family level. Late Albian  
347 ammonites show a slight protracted increase of total diversity throughout the entire late Albian that is  
348 sharply interrupted in the latest Albian (Fig. 4) by a major diversity dropdown at the boundary between  
349 the UAZ 8 (i.e., the *M. perinflatum* Zone) and the UAZ 9 (i.e., the *A. briacensis* Zone; see Fig. 3).  
350 Additionally, a short decrease of diversity is recorded in the UA 9 (= lower part of the *M. inflatum* Zone).  
351 Interestingly, these two diversity decreases impact almost equally all families (Fig. 5) and the relative  
352 proportion of heteromorphs/monomorphs remains rather stable (Fig. 4). There are yet slight differences:  
353 Brancoceratidae and Turrilitidae are more diverse before the diversity decrease at the UA 9, whereas  
354 Hoplitidae are more diverse and Lyelliceratidae appear and diversify thereafter (Fig. 5). Furthermore,  
355 this turnover is well marked at the species level with clearly two different sets of species before and  
356 after the UA 9 (Fig. 1). Therefore, the late Albian in Europe is marked by two different events: 1) an  
357 ammonite turnover not really associated with a diversity drop in the middle upper Albian (UA 9; = *M.*  
358 *inflatum* Zone), and 2) a major and sharp diversity decrease during the uppermost Albian (UAZ 8/9  
359 boundary; = *M. perinflatum*/*A. briacensis* zones boundary).

360

#### 361 4. Discussion

362

363 The correlation of the UA-based biozonation built here with traditionally developed late Albian  
364 ammonite zonations of western Europe is reported on Figure 3. The two most classical ammonite  
365 zonations are those of southwestern Europe (Kennedy and Latil 2007 for SE France) and of northwestern  
366 Europe (Gallois and Owen 2020 for England). Noteworthy, the resolution between the quantitative  
367 association-based zonation (this work) and these two empirical interval-based zonations is almost  
368 similar at the zone/subzone level (9 UAZs versus 7 and 9 subdivisions, respectively; Fig. 3).  
369 Nevertheless, despite a roughly equal number of zones, the quantitative UA method produces a more  
370 than two-fold higher resolution with up to 23 UAs. Given its completeness (see Fig. 2), the Col de

371 Palluel section in SE France can be considered as the reference section for recognition of this empirical  
372 late Albian ammonite zonation in southwestern Europe. Besides, the zonation of this work underlines  
373 that many index taxa have their range extending outside their eponymous zone and often coexist. For  
374 instance, the ranges of *M. pricei* and *M. inflatum* overlap, as well as those of *M. fallax* and *M. rostratum*  
375 (Figs 1, 2; coexistences actually documented in England). Because the empirical zonations of western  
376 Europe rely on fewer data and on the bioevents (mostly first occurrence) of specific index taxa, there  
377 are inevitable discrepancies with the association-based zonation of this work and their correlation is thus  
378 discussed below.

379

#### 380 4.1. Correlation with the interval-based zonation for southwestern Europe

381

382 The ‘standard’ biostratigraphic scheme for late Albian ammonites in southwestern Europe has  
383 been established by Kennedy and Latil (2007). Historically, the late Albian is broadly subdivided by the  
384 *Mortoniceras inflatum* Zone and the overlying *Stoliczkaia dispar* Zone (Latil 1994, Owen 1999); the  
385 latter zone roughly correlates with the Vraconnian substage, and both taxa are known to be more  
386 restricted than their historical eponymous zone. Subsequently, the *S. dispar* Zone has been further  
387 subdivided into three zones (Owen 1999, Amédéo 2002), which are, in stratigraphic order: *Mortoniceras*  
388 *fallax* Zone, *Mortoniceras perinflatum* Zone, and *Arrhaphoceras briacensis* Zone. Finally, Kennedy and  
389 Latil (2007) further introduced a fourth zone before the *M. perinflatum* Zone, namely the *Mortoniceras*  
390 *rostratum* Zone. Then, this four-fold subdivision of the latest Albian (*ca.* the ‘old’ *S. dispar* Zone), has  
391 been widely used as the reference in western Europe (e.g., Kennedy et al. 2008, Amédéo and Matrimon  
392 2014, Reboulet et al. 2018) and also worldwide (e.g., Kennedy et al. 1998, Kennedy, 2004).

393 Overall, the two zonations correlate relatively well with a slightly higher resolution for the UA-  
394 zones (*M. pricei* and *M. inflatum* zones are both subdivided into two UAZs; Fig. 3), notwithstanding the  
395 fact that the 23 UAs still reach a two-fold resolution. Since these two ammonite zonations are  
396 constructed on different principles (association among all data vs. first appearance of a few ‘index’ taxa)



397 their correlation is not straightforward. When comparing both zonations by focusing on the index taxa  
398 defining the interval zones, four major discrepancies between the two zonations can be highlighted.

399 First, the *C. auritus* Zone (i.e., UAZ 4), which is documented in Germany and England, but not  
400 in France (Fig. 2), already contains *M. inflatum*, which supposedly defines the overlying eponymous  
401 zone (Fig. 3). This *C. auritus* Zone is defined (here) mainly either by the restricted occurrence of its  
402 eponymous taxon or by the coexistence of *M. pricei* and *M. inflatum*. However, these two evidences are  
403 absent in SE France (Col de Palluel), therefore preventing the recognition of this intermediate zone  
404 between the *M. pricei* and *M. inflatum* zones. Referring to the Col de Palluel section (Gale et al. 2011),  
405 this interval possibly corresponds to the strata at about the level of the “Petite Vérole”, which is known  
406 to reflect a hiatus in the Col de Palluel section (that may represent as much as 2 Ma) as highlighted by  
407 cyclostratigraphic analysis (see Gale et al. 2011, p. 124) and previously identified as marking a  
408 significant firmground discontinuity (Bréhéret 1997). Therefore, in contrast to Gale et al. (2011), who  
409 claimed that there is no biostratigraphic gap at this level, we believe that there is indeed one preventing  
410 the recognition of this *C. auritus* Zone. Last but not least, considering only the FO of *M. inflatum* for  
411 correlation will *de facto* prevent the recognition of this *C. auritus* zone.

412 Another discrepancy is related to the ranges of the index species *M. fallax* and *M. rostratum*. On  
413 the basis of various sections from SE France, Kennedy and Latil (2007) proposed that *M. rostratum*  
414 succeeds *M. fallax*, with no temporal overlap. However, Owen (2012) stressed that in England *M. fallax*  
415 is fully associated with *M. rostratum* (Rockshaw section; see Owen 1976). According to this author, *M.*  
416 *fallax* is merely a slightly more coarsely tuberculate *M. rostratum*. Although we do not concur with  
417 synonymizing the two species, our study corroborates that *M. fallax* and *M. rostratum* coexist for a  
418 significant amount of time (Figs 1, 3). Consequently, on the one hand the FO of *M. fallax* is not sufficient  
419 by itself to identify its eponymous zone and differentiate it from the overlying *M. rostratum* Zone. On  
420 the other hand, our study supports the distinction of these two zones based on the associated taxa (Fig.  
421 1): 1) the *M. fallax* Zone is clearly defined by the co-occurrence of *M. fallax* with *Hysterocheras binum*;  
422 and 2) the *M. rostratum* Zone is clearly characterized by the co-occurrence of *M. rostratum* with either  
423 *O. puzosianum* or *Callihoplites vracensis*.

424 Third, a discrepancy is related to the *M. perinflatum* Zone. Kennedy et al. (1998) argued for the  
425 discrimination of *M. perinflatum* from *M. rostratum*. Then, Kennedy and Latil (2007) firmly established  
426 it as a zone by assuming that *M. perinflatum* succeeds *M. rostratum* without stratigraphic overlap.  
427 However, as recently discussed by Jattiot et al. (2022), evidence for the separation of *M. rostratum* and  
428 *M. perinflatum* as two distinct species is still lacking. Briefly, *M. rostratum* could supposedly be  
429 separated from *M. perinflatum* on the basis of its less depressed whorl section (Kennedy et al. 1998,  
430 Kennedy and Latil 2007). However, as underlined by Jattiot et al. (2022), there are published specimens  
431 not complying with this criterion (e.g., Latil et al. 2021), notwithstanding the fact that discriminating an  
432 ammonite species only on a ‘less depressed whorl section’ is somehow complicated when most  
433 described specimens are distorted (see, e.g., Kennedy and Latil 2007) and when this criterion is largely  
434 recognized as being typical of intraspecific variation (see, e.g., Monnet et al. 2015). Therefore, the  
435 identification of *M. perinflatum* is still puzzling and controversial and, thus, a *M. perinflatum* Zone  
436 following the *M. rostratum* Zone remains highly speculative and precarious. Consequently, in our study  
437 *M. perinflatum* was merged with *M. rostratum*, thus preventing the recognition of the so-called *M.*  
438 *perinflatum* Zone based solely on this species. However, despite the absence of it in our dataset, our  
439 association-based biochronological analysis still support the existence of a zone corresponding to the  
440 time interval usually attributed to the *M. perinflatum* Zone (i.e., the UAZ 8, see Fig. 3). As described in  
441 the results (Fig. 1), the UAZ 8 is clearly distinguishable, even in the absence of *M. perinflatum*, by the  
442 restricted occurrence of *Arrhaphoceras substuderi*, as well as by the co-occurrence of *M. rostratum*  
443 (LO), *M. fallax* (LO) or *Ostlingoceras puzosianum* (LO) with *Mariella bergeri* (FO) or *Hyphoplites*  
444 *campichei* (FO).

445 Fourth, regarding the latest Albian *A. briacensis* Zone, the correlation of its base is equivocal  
446 (Fig. 3). The *A. briacensis* Zone was introduced by Scholz (1973) for an uppermost Albian interval in  
447 which *Mortoniceras* and *Ostlingoceras puzosianum* are absent, and *Hyphoplites* have already appeared.  
448 The studies on the Mont Risou (Gale et al. 1996) and Col de Palluel (Gale et al. 2011) corroborated this  
449 pattern, but led their authors to the statement that the *A. briacensis* Zone remains an ambiguous unit,  
450 mostly characterized by what taxa are absent rather than by what taxa are present. This is especially

451 evident in the current analysis, which highlights a sharp diversity dropdown at the UAZ 8/9 boundary  
452 leading to a depauperate terminal Albian zone (see results). In this context, the index species *A.*  
453 *briacensis* is absent at the base of the UAZ 9 (i.e., the UA 21), while *Mortoniceras* and *O. puzosianum*  
454 have already disappeared. Therefore, this zone cannot be recognized by the FO of its eponymous species.  
455

#### 456 4.2. Correlation of the UA zonation with the standard interval-based zonation for west northern Europe 457

458 Another major interval-based zonation has been proposed for northwestern Europe (i.e., England;  
459 Wiedmann and Owen 2001, Owen and Mutterlose 2006, Cooper and Owen 2011a, b, Gallois and Owen  
460 2020), which is well-known to contain ammonite faunas with Boreal affinities during the Cretaceous  
461 ('Hoplitid Arctic–European province'; Fenner 2001, Amédéo and Robaszynski 2005, Lehmann et al.  
462 2015). Overall, the two zonations correlate relatively well with both 9 zones/subzones, while the  
463 association-based zonation reach a two-fold resolution with 23 UAs (Fig. 3). However, there is a partial  
464 mismatch among some zones (e.g., UAZs 2–3 vs. the *H. orbigny*, *H. binum*, and *H. choffati* subzones,  
465 and UAZs 5–6 vs. the *C. robustus* Subzone). Furthermore, similarly to southwestern Europe (see  
466 discussion above), our association-based analysis highlights that many index taxa have their range  
467 extending outside their eponym zone and often coexist such as *Hysterocheras orbigny* and *H. binum*  
468 (Fig. 3). When comparing both zonations by focusing on the index taxa defining the interval zones, two  
469 major discrepancies between the two zonations can be highlighted.

470 First, although the *Hysterocheras varicosum* Zone fully correlates with the UAZs 2–3 (its index  
471 species ranging throughout these two UAZs), the three subzones of the *H. varicosum* Zone (*H. orbigny*,  
472 *H. binum* and *H. choffati* subzones) cannot be directly correlated with UAZ 2 and UAZ 3. Indeed, *H.*  
473 *choffati* is a 'single-section' taxon, only occurring in the Upper Gault and Upper Greensand formations  
474 (England), and was not taken into account in our UA analysis. Nevertheless, the level containing *H.*  
475 *choffati* can be dated back to UA 7 (England level U4; see Appendix C); therefore, despite absence of  
476 its eponymous species in our analyzed data, the *H. choffati* subzone can be tentatively correlated with  
477 the upper part of the UAZ 3. Noteworthy, the UA 7 is characterized by a peculiar assemblage with the

478 restricted occurrence of several *Epihoplites* species (Fig. 1, Appendix C). Regarding the *H. binum*  
479 Subzone, the species has its FO in the UA 4, therefore within the UAZ 2. Thus, the base of this subzone  
480 does not correlate with the base of a UAZ. Then, regarding the *H. orbignyi* Subzone, the species has its  
481 FO in the UA 2, thus within the UAZ 1 (i.e., within the preceding *Dipoloceras cristatum* Zone).  
482 Altogether, although the index species of the three subzones have their FO in the expected order  
483 (*orbignyi* → *binum* → *choffati*), they do not match with the bases of the reconstructed UA-zones.  
484 Additionally, the fact that the biostratigraphic ranges of *H. binum* and *H. orbignyi* largely extend outside  
485 their eponymous interval zone (Fig. 3) could actually impede their use as interval index taxa.

486         Second, the *Mortoniceras inflatum* Zone correlates with three UA-zones (UAZs 4–6). However,  
487 the name of this zone in northwestern Europe is inopportune because the index species is largely  
488 restricted to the lower part of the zone and this zone only partially matches the southwestern zone based  
489 on the same index species (Fig. 3). Noteworthy, the *Callihoplites auritus* Subzone correlates particularly  
490 well with the UAZ 4, whereas this zone is poorly recognized in southwestern Europe (see above). The  
491 overlying *Callihoplites robustus* Subzone fully correlates with both UAZs 5–6. Again, *C. robustus* is  
492 only documented in England and therefore cannot be used as a reliable taxon for correlation.  
493 Nevertheless, this species is documented in association with *M. inflatum*, *C. tetragonus*, and  
494 *Cantabrigites minor* indicative of the upper part of the UAZ 5. It must be stressed that the interval of  
495 UAZs 5–6 is poorly documented in England. At that time, this area contains just a few assemblages  
496 predominated by endemic species of *Callihoplites*. For example, there is currently no evidence for the  
497 UAZ 6 (= *M. fallax* Zone; Fig. 2); *M. fallax* is actually documented in England but already with *M.*  
498 *rostratum*, thus indicating the overlying UAZ 7 and highlighting a late FO for *M. fallax* compared to  
499 southwestern Europe. This case clearly illustrates that association-based zones are more reliable for  
500 correlation than interval zones based on a single FO.

501         Finally, above the *C. robustus* Subzone, the interval-based zonation for northwestern Europe does  
502 not differ from that of southwestern Europe with the succession of *M. rostratum*, *M. perinflatum*, and  
503 *A. briacensis*, corresponding to the three UAZs 7–9 (Fig. 3). However, fewer UAs are recognized in  
504 England compared to SE France. This difference in resolution is probably induced by the state of data

505 available: in England only synthetic ranges among already defined biostratigraphic units are available,  
506 whereas in SE France bed-by-bed occurrence data are available. Only the latter case is able to produce  
507 high resolution biozonations and, therefore, are nowadays the recommended data type, not only for  
508 quantitative biostratigraphy and correlation, but also for palaeobiodiversity analyses (see Fan et al.  
509 2020).

510

#### 511 4.3. About the *Vraconnian* substage

512

513 The position of the *Vraconnian* chronostratigraphic unit (uppermost Early Cretaceous) as an  
514 independent stage or a late Albian substage is still debated (see, e.g., Amédro 2002, 2008 *contra* Scott  
515 2009) with arguments mostly related to faunal changes and shortening of the very long Albian stage.  
516 Although the present work does not aim to close the debate, the application of the quantitative UA  
517 method allows to bring a few more elements to this discussion. According to Amédro (2008), the base  
518 of the *Vraconnian* (*ca.* the historical *S. dispar* Zone) is marked by the FO of *Mortoniceras fallax*, which  
519 in this work correlates with the base of the UAZ 6 (i.e., the UA 12; Fig. 3). Noteworthy, the reconstructed  
520 late Albian ammonite diversity in western Europe based on the UA-zonation (Fig. 4) does not show any  
521 diversity drop and/or high turnover rates at UAZ 6; instead, the ammonite turnover and slight diversity  
522 decrease documented here occurred one UA-zone earlier (UA 9; Figs 1, 4, 5). Importantly, it is  
523 commonly recognized that a change of stage should be linked with a marked change of faunas. Yet, this  
524 is not the case for the proposed *Vraconnian* and, therefore, this constitutes an argument against its  
525 reinstatement as a stage. Furthermore, this UAZ6/*M. fallax* Zone is poorly documented through space  
526 and, thus, is not an excellent correlation marker (based on ammonite evidence).

527

#### 528 4.4. Late Albian ammonite palaeobiodiversity

529

530 The newly reconstructed quantitative biochronology of late Albian ammonites in western Europe  
531 enables investigating their palaeobiodiversity changes at a high-resolution. It highlights two different  
532 biotic events among ammonites: 1) a turnover not really associated with a diversity drop in the middle  
533 late Albian (UA 9; = *M. inflatum* Zone; Figs 1, 4, 5), and 2) a major and sharp diversity decrease during  
534 the latest Albian (UAZ 8/9 boundary; = *M. perinflatum/A. briacensis* zones boundary; Fig. 4). Although  
535 these two diversity events correspond to time intervals with a lower sampling in terms of available  
536 outcrops and collected ammonites, at least the second one is probably not an artefact. Interestingly, the  
537 depauperate state of the *A. briacensis* zone is already known (see Owen 1989, Gale et al. 1996,  
538 Wiedmann and Owen 2001), and this uppermost Albian ammonite diversity dropdown is concomitant  
539 with a well-known Oceanic Anoxic Event, namely the OAE1d. In Western Tethys, the latest Albian  
540 OAE1d is mainly characterized by the deposition of organic-rich sediments and carbon isotope  
541 fluctuations (Gale et al. 1996, Wilson and Norris 2001, Bornemann et al. 2005, Jenkyns 2010, Richey  
542 et al. 2018). Although the mechanisms responsible for OAEs have been strongly debated and are not yet  
543 definitely understood, there is no doubt that they significantly contributed to changes and evolution of  
544 the biological marine community, especially particularly in the planktic assemblages (Erbacher and  
545 Thurow 1997, Erbacher et al. 1998, Leckie et al. 2002, Giraud et al. 2003, Reboulet et al. 2005, Watkins  
546 et al. 2005). Therefore, this OAE1d also impacted nektonic communities as illustrated here with  
547 ammonites.

548

#### 549 4. Conclusions

550

551 The use of the unitary association method on a large dataset led to the construction of a quantitative  
552 biochronology constituted of 23 UAs (merged into 9 UA-zones to increase their geographical  
553 reproducibility) for the whole late Albian. We showed that the UA method enables accounting for and  
554 highlighting the range of actually all taxa, and not just a few selected index taxa whose ranges very often  
555 extend before and/or after their eponymous interval zone. The UA approach also enables tracing back

556 the possible origin of the conflicting stratigraphic occurrences. Besides, although the resolution between  
557 the quantitative association-based zonation and these two empirical interval-based zonations is almost  
558 similar at the zone/subzone, the quantitative UA method produces a more than two-fold higher  
559 resolution. Therefore, in our opinion, this work demonstrates that the UA method proved itself very  
560 appropriate and efficient for improving the ammonite biostratigraphy and biozonation of the late Albian  
561 in western Europe.

562         Furthermore, we correlated the UA-based biozonation with the two most classical ammonite  
563 zonations of southwestern and northwestern Europe. Overall, these correlate relatively well with the  
564 UA-based biozonation, although we could highlight major discrepancies often due to ranges of index  
565 species that extend outside their eponymous zones. All these discrepancies underline that it is better, if  
566 not mandatory, to establish a biozonation by accounting for as much data as possible (as done in this  
567 work) and not focusing on a single section to avoid missing zones due to local sedimentary/preservation  
568 hiatuses. Additionally, it may be risky to correlate using only the first occurrence (or the LO) of a single  
569 taxon for the very same reasons. Last but not least, in our opinion, trying to make the various species of  
570 *Mortoniceras* follow an anagenetic pattern (chronospecies) as done in previous analyses (e.g., Kennedy  
571 and Latil 2007, p. 457) to obtain a perfect succession of FOs is completely elusive, as underlined by the  
572 fact that many *Mortoniceras* species coexisted in time (if not in space; see Figs. 1, 3 and discussion  
573 above).

574         Finally, since biochronozones based on the principle of maximal association (such as the unitary  
575 associations) provide a very robust and reliable basis for counts of taxonomic richness, we were able to  
576 measure ammonite species richness through the late Albian in western Europe based on the  
577 reconstructed UA-biozonation (Fig. 4). We showed that the late Albian in Europe is marked by a major  
578 and sharp ammonite diversity decrease during the latest Albian (UAZ 8/9 boundary; = *M. perinflatum*/*A.*  
579 *briacensis* zones boundary), which is concomitant with the well-known Oceanic Anoxic Event OAE1d.

580

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585

586 **Figure captions.**

587 **Fig. 1.** Range chart of the 115 studied ammonites among the reconstructed 24 unitary associations for  
588 the entire late Albian of Europe (see text for explanations).

589 **Fig. 2.** UA-based ammonite zonation of the late Albian and identification of the UAs in the studied  
590 European sections. Abbreviations: FO, first occurrence; LO, last occurrence.

591 **Fig. 3.** Correlation of the UA-based ammonite zonation (this study) of the European late Albian with  
592 the standard zonation of west southern Europe (Kennedy and Latil 2007) and of west northern Europe  
593 (Gallois and Owen 2020).

594 **Fig. 4.** Species richness of heteromorphic and monomorphic ammonites through the late Albian in  
595 western Europe based on the reconstructed UA-biozonation. Notably, the sharp diversity dropdown at  
596 the UAZ 8/9 boundary correlates with the spreading of the Oceanic Anoxic Event OAE1d (Breistroffer  
597 level).

598 **Fig. 5.** Species richness of each ammonite family through the late Albian in western Europe based on  
599 the reconstructed UA-biozonation. The sharp diversity dropdown in the UAZ 9 correlates with the  
600 Oceanic Anoxic Event OAE1d.

601

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1021

## 1022 **Electronic Supplementary Material**

1023

1024 **Appendix A.** Occurrence (‘initial’) dataset of late Albian ammonites in western Europe used to  
1025 perform the quantitative biochronological analysis by means of the unitary associations.

1026

1027 **Appendix B.** Synthetic range chart of the late Albian ammonites from the Gault and Greensand  
1028 formations, England.

1029

1030 **Appendix C.** Range chart of the 60 single-section ammonites from the ‘initial’ dataset dated with the  
1031 reconstructed unitary associations of the late Albian from Europe (this study).

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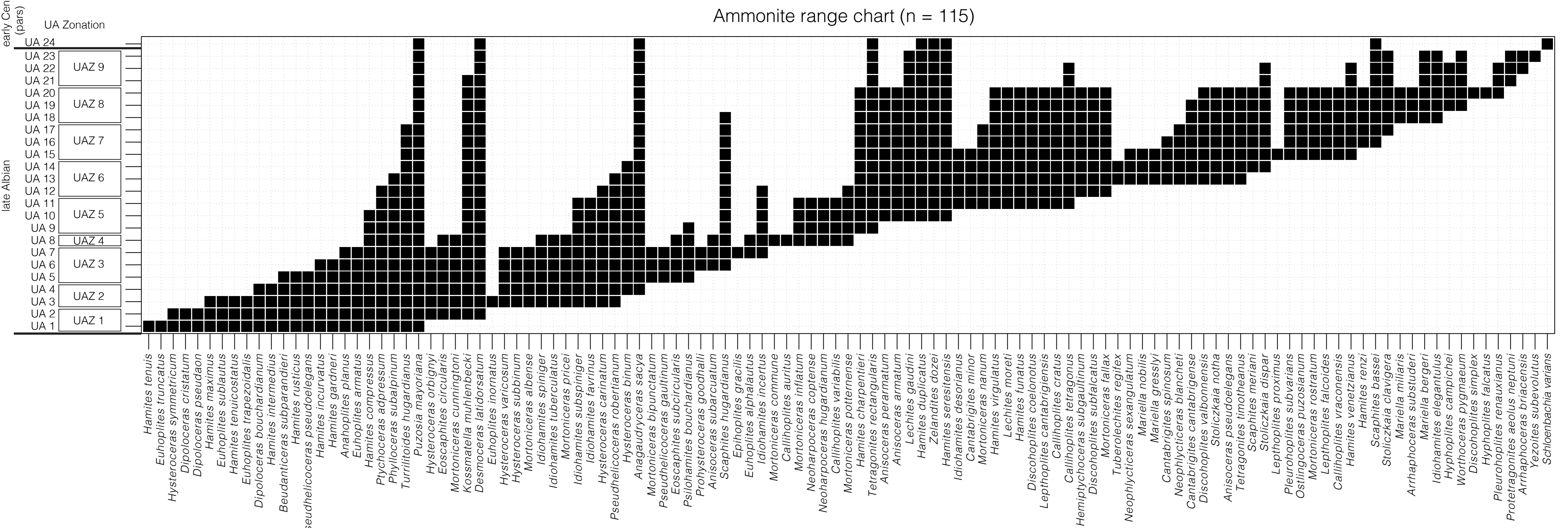
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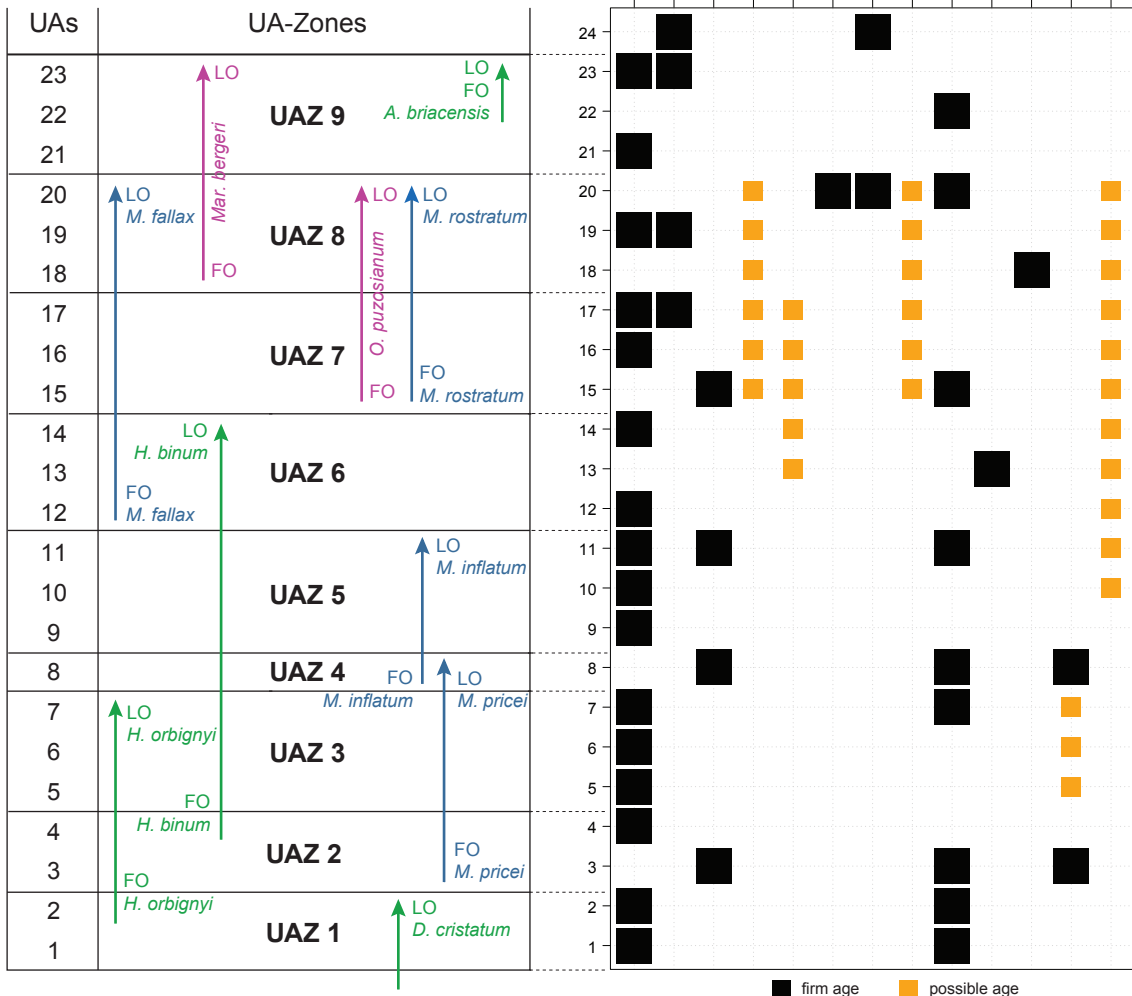
1039



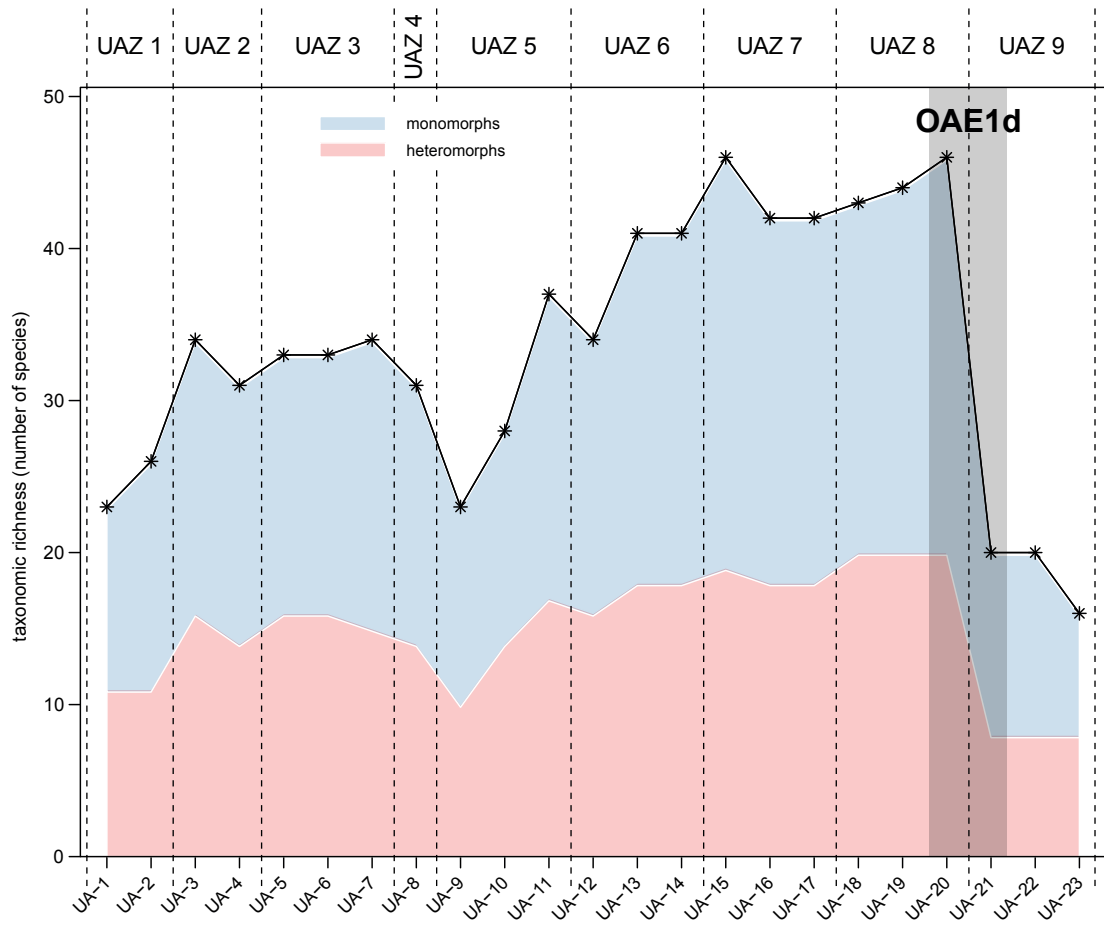
Ammonite range chart (n = 115)

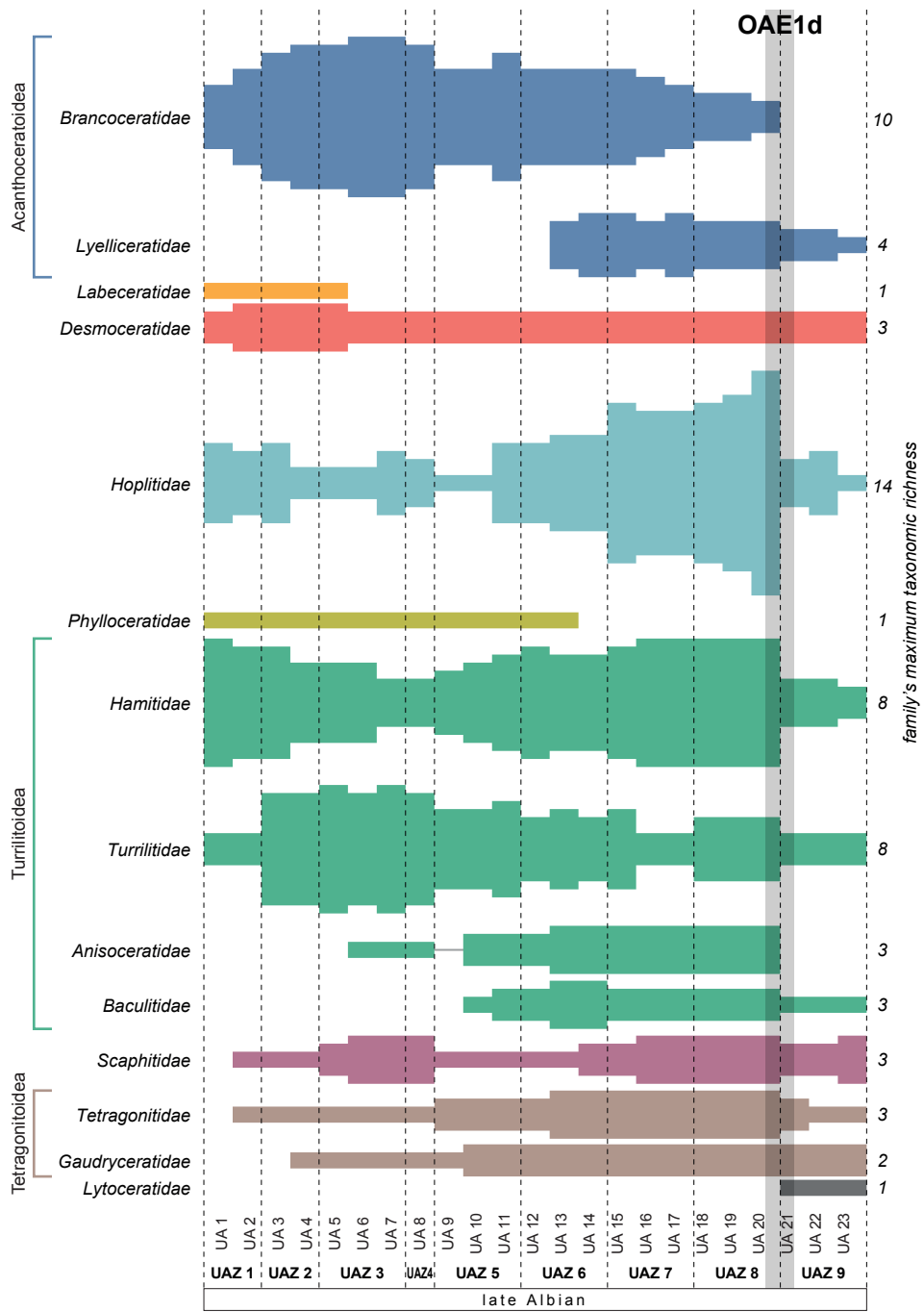


unitary associations-based zonation  
(this work)



unitary associations-based zonation (this work)		interval-based zonation of southwestern Europe (Kennedy and Latil 2007)	interval-based zonation of northwestern Europe (Wiedmann and Owen 2001, Gallois and Owen 2020)	
UAs	UA-Zones		Zone	Subzone
23 22 21	<p>UAZ 9</p>	<i>Arrhaphoceras briacensis</i> Zone	<i>Stoliczkaia</i> ( <i>Stoliczkaia</i> ) spp.	<i>Arrhaphoceras briacensis</i>
20 19 18	<p>UAZ 8</p>	<i>Mortoniceras perinflatum</i> Zone		<i>Mortoniceras perinflata</i>
17 16 15	<p>UAZ 7</p>	<i>Mortoniceras rostratum</i> Zone		<i>Mortoniceras rostratum</i>
14 13 12	<p>UAZ 6</p>	<i>Mortoniceras fallax</i> Zone	<i>Mortoniceras inflatum</i>	<i>Callihoplites robustus</i>
11 10 9	<p>UAZ 5</p>	<i>Mortoniceras inflatum</i> Zone		<i>Callihoplites auritus</i>
8	<p>UAZ 4</p>	<i>Mortoniceras pricei</i> Zone	<i>Hysterocheras varicosum</i>	<i>Hysterocheras choffati</i>
7 6 5	<p>UAZ 3</p>			<i>Hysterocheras binum</i>
4 3	<p>UAZ 2</p>			<i>Hysterocheras orbigny</i>
2 1	<p>UAZ 1</p>	<i>Dipoloceras cristatum</i> Zone	<i>Dipoloceras cristatum</i>	





**Table of ammonite ranges in the English Upper Gault and Upper Greensand Formations  
(Gault Group), Late Albian**

**Key to Subzones**

U1 = early *Dipoloceras cristatum*  
 U2 = late *Dipoloceras cristatum*  
 U3 = *Hysterocheras orbigny*  
 U4 = *Hysterocheras binum*  
 U5 = *Hysterocheras choffati*  
 U6 = early *Procallihoplites auritus*  
 U7 = late *Procallihoplites auritus*  
 U8 = *Mortoniceras rostratum*  
 U9 = *Durnovarites perinflatum*  
 U10 = early *Praeschloenbachia briacensis*

Subzones	<i>cristatum</i>		<i>varicosum</i>			<i>inflatum</i>		<i>dispar</i>		
	U1	U2	U3	U4	U5	U6	U7	U8	U9	U10
<i>Hamites maximus maximus</i> J. Sowerby	X	X	X							
<i>Hamites maximus rectus</i> Brown	X									
<i>Hamites tenuicostatus</i> Spath	X	X	X							
<i>Hamites gardneri</i> Spath	X	X	X							
<i>Hamites gibbosus</i> J. Sowerby	?									
<i>Hamites tenuis</i> J. Sowerby	?									
<i>Hamites intermedius intermedius</i> J. Sowerby	X	X	X	X						
<i>Hamites intermedius opalinus</i> Spath	X	X	X	X						
<i>Hamites intermedius distinctus</i> Spath	X	X	X	X						
<i>Hamitella annulatum</i> (d'Orbigny)	X									
<i>Planohamites compressus</i> J. Sowerby	X									
<i>Planohamites incurvatus</i> Brown	X	X	X							
<i>Stomohamites virgulatus</i> (Brongniart ?) P & C.								X	X	
<i>Stomohamites venetianus</i> Pictet								X	X	X
<i>Stomohamites duplicatus</i> Pictet & Campiche							X	X	X	
<i>Stomohamites charpentieri</i> Pictet							X	X	X	
<i>Stomohamites subvirgulatus</i> Spath							X	X	X	

Subzones	cristatum		varicosum			inflatum		dispar		
	U1	U2	U3	U4	U5	U6	U7	U8	U9	U10
<i>Stomohamites ibex</i> Spath								X	X	
<i>Stomohamites funatus</i> Brongniart							X	X	X	
<i>Stomohamites ptychoceratoides</i> Spath							?	X		
<i>Stomohamites parkinsoni</i> (Fleming)							X	X	X	
<i>Lytohamites similis</i> Casey								X	X	
<i>Psilohamites bouchardianus</i> d'Orbigny				X	X					
<i>Lechites gaudini</i> Pictet & Campiche								X	X	
<i>Lechites moreti</i> Breistroffer							X	X	X	
<i>Lechites communis</i> Spath								X	X	
<i>Sciponoceras skipperae</i> Monks									X	X
<i>Ptychoceras (Mastigoceras) adpressum</i> (J. Sowerby)				X						
<i>Hamitoides? rusticus</i> Spath	X									
<i>Hamitoides</i> sp.						X				
<i>Idiohamites tuberculatus</i> (J. Sowerby)			X	X	X	X				
<i>Idiohamites spiniger</i> (J. Sowerby)			X	X	X	X				
<i>Idiohamites subspiniger</i> Spath			X	X			X			
<i>Idiohamites intermedius opalinus</i> Spath			X	X						
<i>Idiohamites intermedius distinctus</i> Spath			X	X						
<i>Idiohamites turgidus turgidus</i> (J. Sowerby)			X	X	?					
<i>Idiohamites turgidus robustus</i> Spath				X	X					
<i>Idiohamites turgidus subannulatus</i> Spath				X	X	X	X			
<i>Idiohamites spinulosus</i> (J. Sowerby)				X	X	X				
<i>Idiohamites favrinus</i> (Pictet)			?	X	X	X	X			
<i>Idiohamites ellipticoides</i> Spath				X						

Subzones	crisatum		varicosum			inflatum		dispar		
	U1	U2	U3	U4	U5	U6	U7	U8	U9	U10
<i>Idiohamites? incertus incertus</i> Spath				X	X	X				
<i>Idiohamites? incertus costatus</i> Spath				X	X	X				
<i>Idiohamites desorianus</i> (Pictet)							X	X		
<i>Idiohamites dorsetensis</i> Spath								?	X	
<i>Idiohamites elegantulus</i> Spath									X	
<i>Anisoceras subarcuatum</i> Spath				X	X	X				
<i>Anisoceras saussureanum</i> (Pictet)							X	X		
<i>Anisoceras armatum</i> (J. Sowerby)							?	X	X	
<i>Anisoceras perarmatum</i> (Pictet & Campiche)							?	X	X	
<i>Anisoceras picteti</i> Spath									X	
<i>Anisoceras exoticum</i> Spath								X	X	
<i>Anisoceras pseudoelegans</i> Pictet & Campiche								?	X	
<i>Anisoceras campichei</i> Spath								X	X	
<i>Pseudhelicoceras pseudoelegans</i> Spath	X									
<i>Pseudhelicoceras robertianum</i> (d'Orbigny)			X	X	X	X				
<i>Pseudhelicoceras robertianum ornatum</i> Spath			X	X	X	X				
<i>Pseudhelicoceras gaultinum</i> Spath				X						
<i>Eoscaphtes circularis</i> (J. de C. Sowerby)			?	X	?	?				
<i>Eoscaphtes circularis depressus</i> Spath				X	?					
<i>Eoscaphtes circularis rugosus</i> Spath				X	?					
<i>Eoscaphtes subcircularis</i> Spath				X	X	X				
<i>Scaphites simplex</i> Jukes-Browne				X	X	X	?			
<i>Scaphites hugardianus hugardianus</i> d'Orbigny							?	X		
<i>Scaphites hugardianus nodata</i> Spath							?	X		



Subzones	<i>cristatum</i>		<i>varicosum</i>			<i>inflatum</i>		<i>dispar</i>		
	U1	U2	U3	U4	U5	U6	U7	U8	U9	U10
<i>Scaphites hugardianus sublaevis</i> Spath							?	X		
<i>Mariella bergeri</i> (Brongniart)								?	X	
<i>Mariella miliaris</i> (Pictet & Campiche)								?	X	
<i>Mariella gresslyi</i> (Pictet & Campiche)								X		
<i>Mariella cantabrigiensis</i> (Jukes Browne)								X		
<i>Mariella nobilis</i> (Jukes Browne)								X		
<i>Mariella cf. escheriana</i> (Pictet)								X		
<i>Ostlingoceras puzosianum</i> (d'Orbigny)								X	X	
<i>Turrilitoides hugardianus hugardianus</i> (d'Orbigny)								X		
<i>Turrilitoides hugardianus crassicosata</i> Spath								X		
<i>Turrilitoides toucasi</i> (Hébert & Munier-Chalmas)								X		
<i>Hypophylloceras subalpinum</i> (d'Orbigny)	X									
<i>Hypophylloceras seresitense</i> Pervinquière								?	X	
<i>Gaudryceras aff. madraspatanum</i> (Blandford Stoliczka)								?	X	
<i>Tetragonites timotheanus</i> (Pictet)									X	
<i>Desmoceras latidorsatum</i> (Michelin)								?	X	
<i>Uhligella derancei</i> Casey	X									
<i>Beudanticeras beudanti beudanti</i> (Brongniart)	X	X	X							
<i>Beudanticeras beudanti ibeciforme</i> Spath				X						
<i>Beudanticeras subparandieri</i> Spath	X	X	X							
<i>Beudanticeras sphaerotum</i> (Seeley)			X							



Subzones	cristatum		varicosum			inflatum		dispar		
	U1	U2	U3	U4	U5	U6	U7	U8	U9	U10
<i>Dimorphoplites? silenus</i> Spath	X									
<i>Metaclavites metamorphicus</i> (Spath)	X	X								
<i>Metaclavites compressus</i> (Parona & Bonarelli)	X	X	X							
<i>Metaclavites trifidus</i> (Spath)			X							
<i>Metaclavites trifidus plana</i> Spath			X							
<i>Epihoplites iphitus</i> Spath				X	X					
<i>Epihoplites gracilis</i> Spath				X	X					
<i>Epihoplites denarius</i> (J. de C. Sowerby)				X	X					
<i>Epihoplites deluci</i> (Brongniart)				X	X					
<i>Epihoplites costosus</i> Spath						X				
<i>Epihoplites glyptus</i> Spath				X	X					
<i>Epihoplites gibbosus</i> Spath				X	X					
<i>Epihoplites-Procallihoplites</i> transitions					X					
<i>Procallihoplites auritus</i> (J. Sowerby) (syn. <i>Procallihoplites srigosus cristata</i> Spath)						X				
<i>Procallihoplites formosus</i> Spath						X				
<i>Procallihoplites strigosus</i> Spath						X				
<i>Procallihoplites patella</i> Spath						X				
<i>Procallihoplites horridus</i> Spath						X				
<i>Callihoplites variabilis</i> Spath						X	X			
<i>Callihoplites potternensis</i> Spath						X				
<i>Callihoplites catillus</i> (J. de C. Sowerby) (syn. <i>Callihoplites fuscus</i> Spath)								?	X	
<i>Callihoplites advena</i> Spath								X		
<i>Callihoplites glossonotus</i> (Seeley)								X	X	
<i>Callihoplites leptus</i> Spath								X	X	

Subzones	cristatum		varicosum			inflatum		dispar		
	U1	U2	U3	U4	U5	U6	U7	U8	U9	U10
<i>Callihoplites seeleyi</i> Spath							?	X	X	X
<i>Callihoplites tetragonus</i> (Seeley)								X	X	X
<i>Callihoplites tetragonus vulgaris</i> Spath								X	X	
<i>Callihoplites tetragonus compressa</i> Spath								X	X	
<i>Callihoplites tetragonus dorsetensis</i> Spath							?	X	X	
<i>Callihoplites tetragonoides</i> Spath									X	
<i>Callihoplites pulcher</i> Spath									X	
<i>Callihoplites vraconensis</i> (Pictet & Campiche)								X	X	
<i>Callihoplites vraconensis inflata</i> Spath								X	X	
<i>Callihoplites gymnus</i> Spath								X		
<i>Callihoplites anglicus</i> Breistroffer								X		
<i>Callihoplites atavus</i> Spath								X		
<i>Callihoplites paradoxus</i> Spath								X		
<i>Callihoplites multifidus</i> (Breistroffer)								X		
<i>Callihoplites robustus</i> Spath							X	X	X	
<i>Callihoplites cratus</i> (Seeley)								X		
<i>Callihoplites glossonotus</i> (Seeley) C. F. Breist								X		
<i>Callihoplites leptus</i> (Seeley)								X		
<i>Callihoplites leptus laevis</i> Spath								X		
<i>Callihoplites pulcher</i> Spath								X		
<i>Callihoplites senilis</i> Spath								X		
<i>Callihoplites senilis laevigata</i> Spath								X		
<i>Callihoplites senilis serrigera</i> Spath								X		
<i>Callihoplites pseudoglaber</i> Spath								X		
<i>Callihoplites acanthonotus</i> (Seeley)								X		

Subzones	cristatum		varicosum			inflatum		dispar		
	U1	U2	U3	U4	U5	U6	U7	U8	U9	U10
<i>Arrhaphoceras studeri</i> (Pictet & Campiche)									X	
<i>Arrhaphoceras substuderi</i> Spath									X	
<i>Arrhaphoceras precoupei</i> Spath									X	
<i>Arrhaphoceras transitorium</i> Spath									X	
<i>Arrhaphoceras woodwardi</i> (Seeley)									X	
<i>Pleurohoplites subvarians</i> Spath								?	X	
<i>Pleurohoplites renauxianus</i> (d'Orbigny)									X	?
<i>Pleurohoplites renauxianus gracilis</i> Spath									X	?
<i>Pleurohoplites epigonus</i> Spath								?	X	
<i>Pleurohoplites serpentinus</i> Spath									X	
<i>Pleurohoplites serpentinus subglabra</i> Spath									X	
<i>Euhoplites truncatus</i> Spath late form	X									
<i>Euhoplites opalinus</i> Spath late form	X									
<i>Euhoplites proboscideus proboscideus</i> Spath	X	X	X	X	X					
<i>Euhoplites proboscideus intermedius</i> Spath	X	X								
<i>Euhoplites proboscideus ultimus</i> Spath				X						
<i>Euhoplites armatus</i> Spath	X	X	X	X	X					
<i>Euhoplites trapezoidalis trapezoidalis</i> Spath	X	X	X							
<i>Euhoplites trapezoidalis formosus</i> Spath	X	X								
<i>Euhoplites serotinus</i> Spath	X	X	X							
<i>Euhoplites solenotus</i> (Seeley)	X	X	X							
<i>Euhoplites ochetonotus</i> (Seeley)	X	X	X							
<i>Euhoplites ochetonotus nodosa</i> Spath		X								
<i>Euhoplites sublautus sublautus</i> Spath	X	X	X							
<i>Euhoplites sublautus monocantha</i> Spath		X	X							
<i>Euhoplites subcrenatus</i> Spath		X	X							





Subzones	cristatum		varicosum			inflatum		dispar		
	U1	U2	U3	U4	U5	U6	U7	U8	U9	U10
<i>Hysterocheras simplicicostata</i> Spath	X									
<i>Hysterocheras serpentinum</i> Spath	X									
<i>Hysterocheras varicosum</i> (J. de C. Sowerby)			X	X	X					
<i>Hysterocheras binodosum</i> (Stieler)				X	X					
<i>Hysterocheras orbigny</i> (Spath)		X	X	X						
<i>Hysterocheras binum</i> (J. Sowerby)				X						
<i>Hysterocheras subbinum</i> Spath			X	X	X					
<i>Hysterocheras carinatum</i> Spath			X	X	X	X				
<i>Hysterocheras carinatum ascendens</i> Spath					?	X				
<i>Hysterocheras choffati</i> Spath					X					
<i>Hysterocheras bucklandi</i> (Spath)						X				
<i>Rhytodoceras</i> cf. <i>undatum</i> van Hoepen						X				
<i>Aidoceras</i> sp					X					
<i>Cechenoceras</i> sp.					X					
<i>Mortoniceras</i> ( <i>Deiradoceras</i> ) <i>cunningtoni</i> <i>cunningtoni</i> Spath				X	X	X				
<i>Mortoniceras</i> ( <i>Deiradoceras</i> ) <i>cunningtoni</i> <i>flexuosum</i> Spath				?	?					
<i>Mortoniceras</i> ( <i>Deiradoceras</i> ) <i>bipunctatum</i> Spath				X						
<i>Mortoniceras</i> ( <i>Deiradoceras</i> ) <i>devonense devonense</i> Spath				X						
<i>Mortoniceras</i> ( <i>Deiradoceras</i> ) <i>devonense</i> <i>compressa</i> Spath				X						
<i>Mortoniceras</i> ( <i>Deiradoceras</i> ) <i>albense albense</i> Spath				X						
<i>Mortoniceras</i> ( <i>Deiradoceras</i> ) <i>albense transitoria</i> Spath			X	X						
<i>Mortoniceras</i> ( <i>Mortoniceras</i> ) <i>pricei</i> Spath			X	X	X	X				
<i>Mortoniceras</i> ( <i>Mortoniceras</i> ) <i>pricei intermedius</i> Spath						X				





Subzones	cristatum		varicosum			inflatum		dispar		
	U1	U2	U3	U4	U5	U6	U7	U8	U9	U10
<i>Mortoniceras (Durnovarites) postinflatum</i> Spath									X	
<i>Mortoniceras (Durnovarites) subquadratum</i> Spath									X	
<i>Mortoniceras (Durnovarites) subquadratum crassicosata</i> Spath									X	
<i>Mortoniceras (Durnovarites) subquadratum tumida</i> Spath									X	
<i>Goodhallites goodhalli goodhalli</i> (J. Sowerby)				X						
<i>Goodhallites goodhalli aplanatus</i> Spath				X						
<i>Goodhallites goodhalli shenleyensis</i> Spath				X						
<i>Goodhallites goodhalli tuberculata</i>				X						
<i>Goodhallites tuberculatum</i> Spath				X						
<i>Goodhallites delabechei</i> Spath				X						
<i>Goodhallites delabechei robustus</i> Spath				X						
<i>Goodhallites candollianum</i> Spath non Pictet							X			
<i>Goodhallites falcifer</i> Spath				X						
<i>Neoharpoceras coptense</i> Spath						X	X			
<i>Neoharpoceras hugardianum</i> (d'Orbigny)						X	X			
<i>Neoharpoceras irregulare</i> Spath						X	X			
<i>Elobiceras pseudelobiensis</i> (Spath)						X				
<i>Cantabrigites cantabrigensis</i> (Spath)								X		
<i>Cantabrigites cantabrigensis gracile</i> Spath								X		
<i>Cantabrigites subsimplex</i> Spath								X		
<i>Cantabrigites minor</i> Spath							X	X		
<i>Cantabrigites minor serpentinus</i> Spath								X		

## Notes

1. The above list is compiled from my own collecting or other material examined by me or sent to me for identification from known stratigraphical horizons. In some cases, specimens in Museum collections (including BGS) without specific stratigraphical horizons, have had these determined by lithological matching where possible.
2. The list does not include undescribed taxa or transitions between genera (for example between *Euhoplites alphalautus* and *Discohoplites* occurring in the *Procallihoplites auritus* Subzone).
3. *Mortoniceras* (*Mortoniceras*) is capable of further taxonomic revision and in my view some of van Hoepen's genera are applicable to the English species. However, *Pervinquieria*, *Inflatoceras* (*inflatum* group) and *Subschloenbachia* (*rostratum* group) are synonyms of *Mortoniceras* as understood currently. However, if the type of *Mortoniceras* (*M. vespertinum* (Morton)) is proved to be generically separate from the English forms, *Pervinquieria* Bohm 1910 becomes valid for the *inflatum-rostratum* lineage,

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