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

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

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

1. Introduction

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

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

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

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

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

2. Materials and Methods

2.1. Biostratigraphic data

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

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

2.2. Biozonation based on unitary associations (UAs)

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

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

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

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,

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

The second UA analysis on the post-processed, 'optimized' dataset leads to 24 unitary associations after resolving 130 conflicting stratigraphic relationships distributed among 39 maximal cliques and based on 115 multiple-section taxa; as expected, there are no more residual virtual edges. The final results of the biochronological analysis are based on this second analysis and are: 1) a range chart of the 115 multiple-section taxa through the succession of the 24 UAs (discrete maximal sets of mutually coexisting species; Fig. 1) complemented by 2) its reproducibility matrix (Fig. 2), which indicates the UAs identified in the studied sections. The range chart is a sequence synthesizing the association, superposition and exclusion relationships of the ammonite taxa included in the analysis; it defines the characteristic content of each biostratigraphic unit (UA). The single-section taxa automatically removed during the biochronological analysis are dated back with these UAs and their range chart is reported in Appendix C. Among all studied sections, only Clansayes, Salazac and Strépy-Thieu are 'single-bed sections' (Appendix A). We tested the influence of these 'single-bed sections' by doing the very same quantitative biostratigraphic analysis without these localities. The 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 *Hysteroceras* (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), *Eoscaphites circularis* (FO) or *Hysteroceras*
261 *orbignyi* (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

upper Albian; Fig. 3).

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

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

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

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

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

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

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

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

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

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

3.3. Late Albian ammonite palaeobiodiversity

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

4.3. About the Vraconnian substage

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

4.4. Late Albian ammonite palaeobiodiversity

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

4. Conclusions

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

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

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

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

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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.

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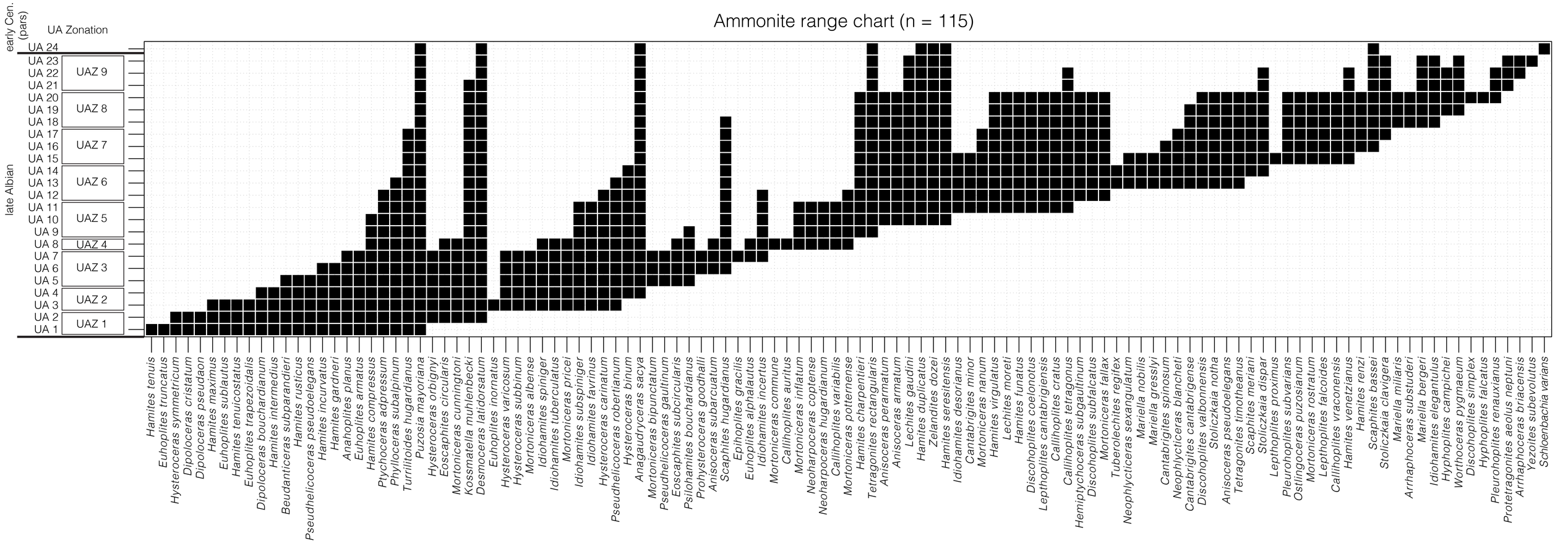
Electronic Supplementary Material

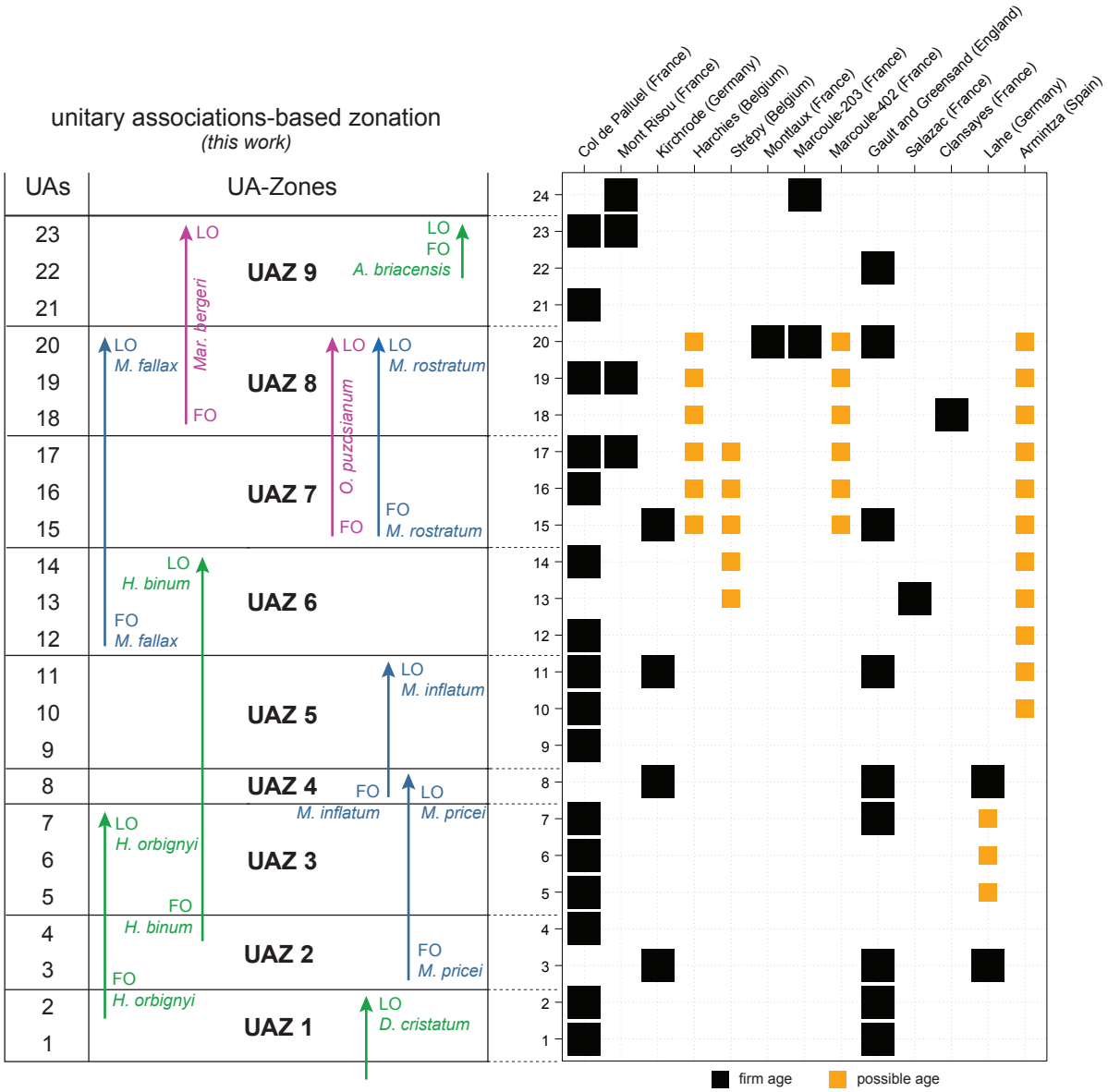
Appendix A. Occurrence ('initial') dataset of late Albian ammonites in western Europe used to perform the quantitative biochronological analysis by means of the unitary associations.

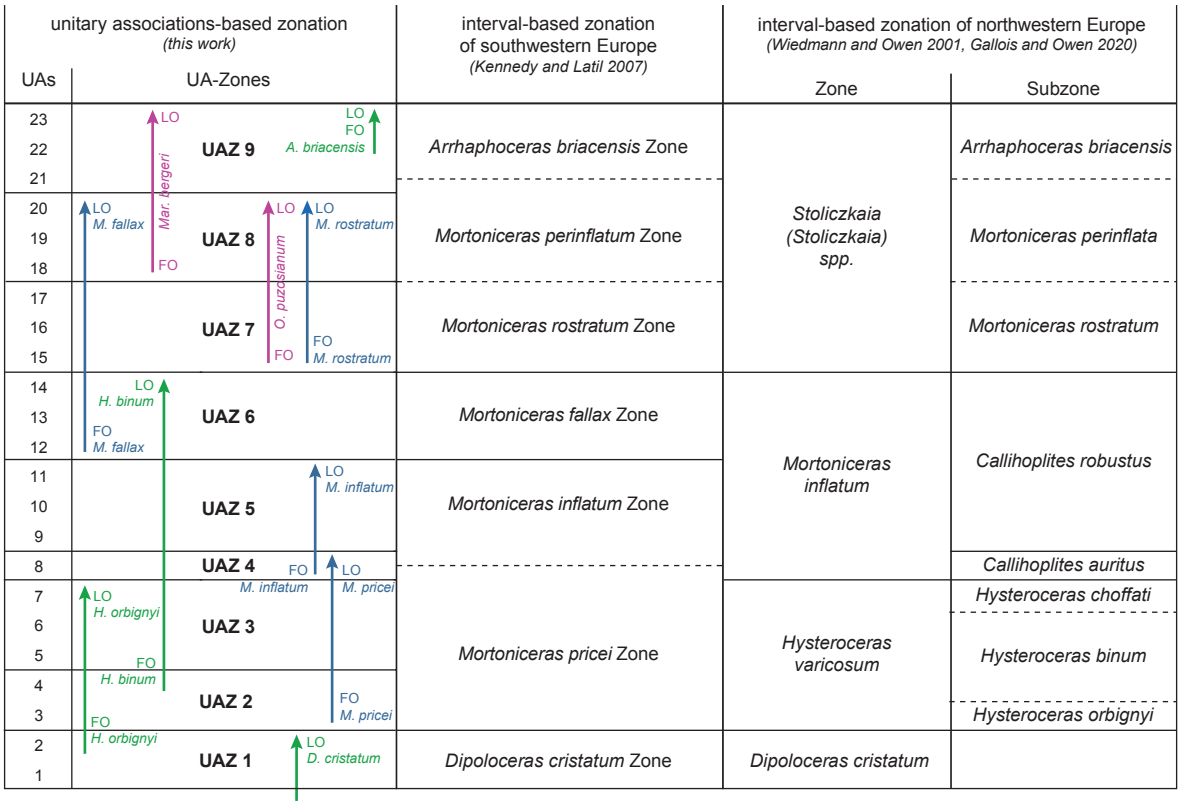
Appendix B. Synthetic range chart of the late Albian ammonites from the Gault and Greensand formations, England.

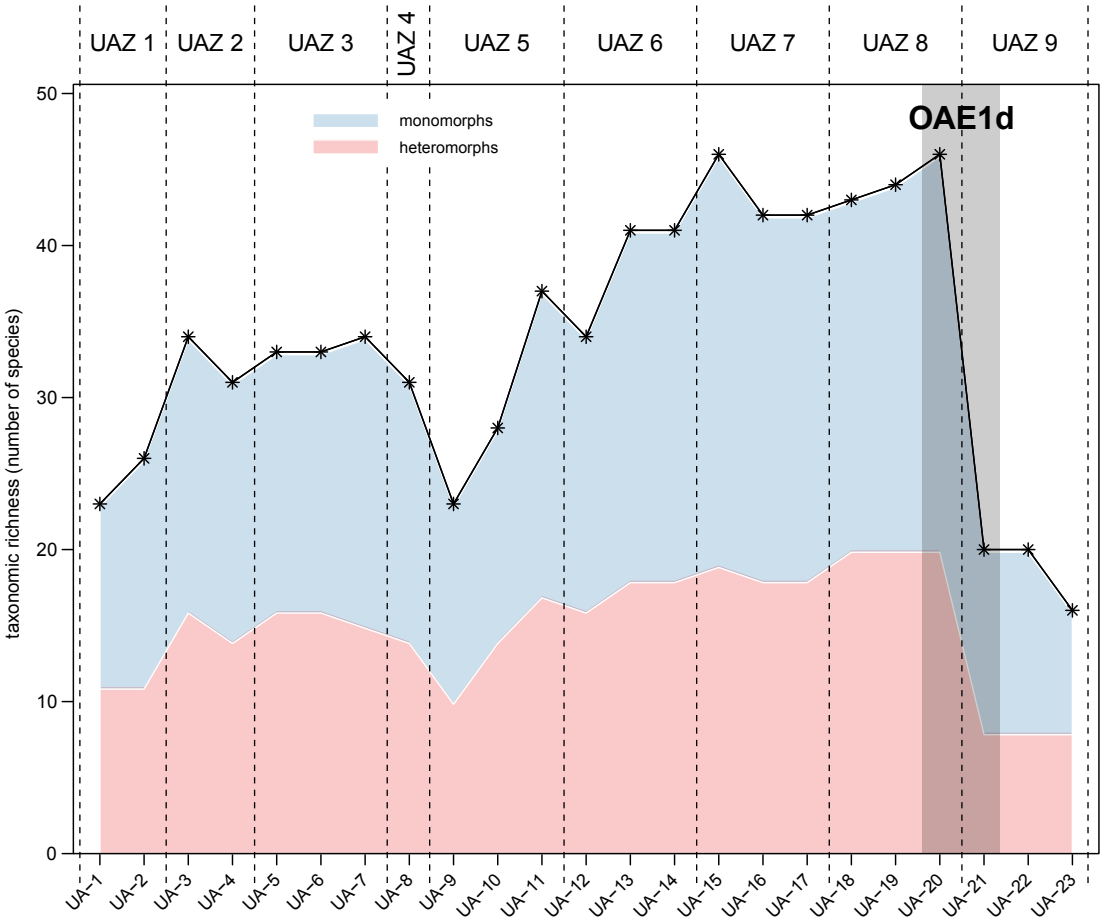
Appendix C. Range chart of the 60 single-section ammonites from the 'initial' dataset dated with the reconstructed unitary associations of the late Albian from Europe (this study).

Ammonite range chart (n = 115)




unitary associations-based zonation
(this work)
UAs
UA-Zones
UAZ 9
UAZ 8
UAZ 7
UAZ 6
UAZ 5
UAZ 4
UAZ 3
UAZ 2
UAZ 1
LO
FO
Mar. bergeri
A. briacensis
M. fallax
O. puzosianum
M. rostratum
H. binum
M. inflatum
M. pricei
H. orbignyi
D. cristatum
Col de Palluel (France)
Mont Risou (France)
Kirchrode (Germany)
Harchies (Belgium)
Strépy (Belgium)
Montlaux (France)
Marcoule-203 (France)
Marcoule-402 (France)
Gault and Greensand (England)
Salazac (France)
Clansayes (France)
Lahe (Germany)
Arminza (Spain)
firm age
possible age


unitary associations-based zonation
(this work)
UAs
UA-Zones
interval-based zonation
of southwestern Europe
(Kennedy and Latil 2007)
interval-based zonation of northwestern Europe
(Wiedmann and Owen 2001, Gallois and Owen 2020)
Zone
Subzone
23
22
21
20
19
18
17
16
15
14
13
12
11
10
9
8
7
6
5
4
3
2
1
UAZ 9
UAZ 8
UAZ 7
UAZ 6
UAZ 5
UAZ 4
UAZ 3
UAZ 2
UAZ 1
LO
FO
A. briacensis
Mar. hergeri
M. fallax
O. puzosianum
M. rostratum
H. binum
M. inflatum
M. pricei
H. orbignyi
D. cristatum
Arrhaphoceras briacensis Zone
Mortoniceras perinflatum Zone
Mortoniceras rostratum Zone
Mortoniceras fallax Zone
Mortoniceras inflatum Zone
Mortoniceras pricei Zone
Dipoloceras cristatum Zone
Stoliczkaia (Stoliczkaia) spp.
Mortoniceras inflatum
Hysteroceras varicosum
Dipoloceras cristatum
Arrhaphoceras briacensis
Mortoniceras perinflata
Mortoniceras rostratum
Callihoplites robustus
Callihoplites auritus
Hysteroceras choffati
Hysteroceras binum
Hysteroceras orbignyi


UAZ 1
UAZ 2
UAZ 3
UAZ 4
UAZ 5
UAZ 6
UAZ 7
UAZ 8
UAZ 9
OAE1d
monomorphs
heteromorphs
taxonomic richness (number of species)
0
10
20
30
40
50
UA−1
UA−2
UA−3
UA−4
UA−5
UA−6
UA−7
UA−8
UA−9
UA−10
UA−11
UA−12
UA−13
UA−14
UA−15
UA−16
UA−17
UA−18
UA−19
UA−20
UA−21
UA−22
UA−23

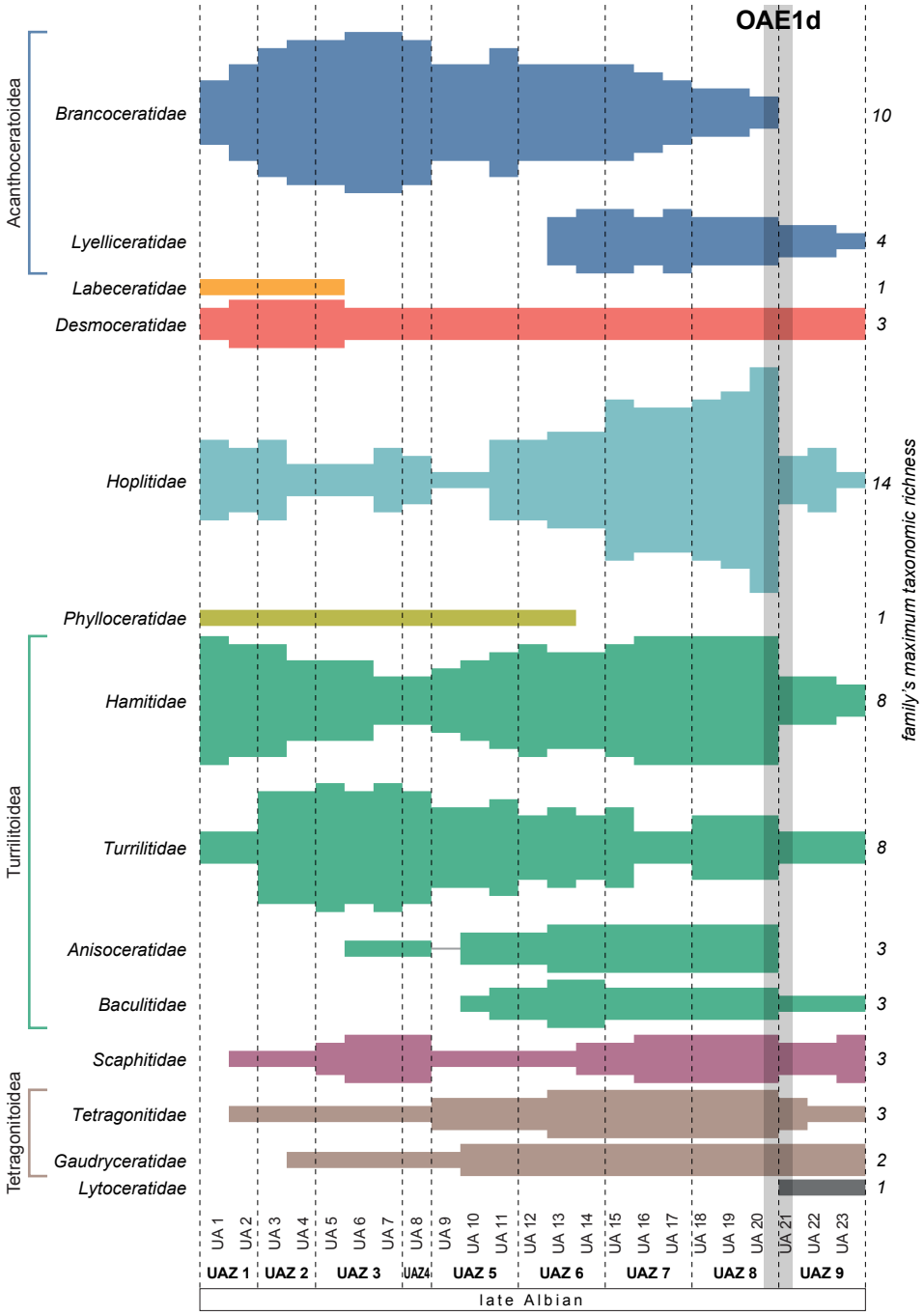

OAE1d
Acanthoceratoidea
Brancoceratidae
Lyelliceratidae
Labeceratidae
Desmoceratidae
Hoplitidae
Phylloceratidae
Turrilitoidea
Hamitidae
Turrilitidae
Anisoceratidae
Baculitidae
Scaphitidae
Tetragonitoidea
Tetragonitidae
Gaudryceratidae
Lytoceratidae
10
4
1
3
14
1
8
8
3
3
3
3
2
1
family's maximum taxonomic richness
UA 1
UA 2
UA 3
UA 4
UA 5
UA 6
UA 7
UA 8
UA 9
UA 10
UA 11
UA 12
UA 13
UA 14
UA 15
UA 16
UA 17
UA 18
UA 19
UA 20
UA 21
UA 22
UA 23
UAZ 1
UAZ 2
UAZ 3
UAZ4
UAZ 5
UAZ 6
UAZ 7
UAZ 8
UAZ 9
late Albian

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 = *Hysteroceras orbignyi*
U4 = *Hysteroceras binum*
U5 = *Hysteroceras choffati*
U6 = early *Procallihoplites auritus*
U7 = late *Procallihoplites auritus*
U8 = *Mortoniceras rostratum*
U9 = *Durnovarites perinflatum*
U10 = early *Praeschloenbachia briacensis*

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

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

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

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

	cristatum		*varicosum*			*inflatum*		*dispar*		
Subzones	U1	U2	U3	U4	U5	U6	U7	U8	U9	U10
Puzosia (*Puzosia*) *spathi* Breistroffer				X						
Puzosia (*Puzosia*) *sharpei* Spath								X	X	
Puzosia (*Puzosia*) *communis* Spath								X		
Gastroplites cantianus Spath	X									
Anahoplites planus (Mantell)	X	X	X	X						
Anahoplites planus discoidea Spath	X									
Anahoplites splendens (J. Sowerby)	X									
Anahoplites picteti Spath			X	X	X	X				
Lepthoplites falcoides Spath								X	X	
Lepthoplites cantabrigiensis Spath							?	X	X	
Lepthoplites proximus Spath								X		
Lepthoplites pseudoplanus Spath								X		
Lepthoplites ornatus Spath							X			
Neanahoplites sp.	X									
Semenoviceras sp.				X						
Hengestites applanatus Casey				X	X	X				
Euhoplitoides inornatus (Spath)			X							
Dimorphoplites glaber Spath	X									
Dimorphoplites chloris Spath	X									
Dimorphoplites tethydis Spath non Bayle	X									
Dimorphoplites tethydis (Bayle)	X									
Dimorphoplites biplicatus (Mantell)	X									
Dimorphoplites parkinson Spath	X									

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

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

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

	cristatum		*varicosum*			*inflatum*		*dispar*		
Subzones	U1	U2	U3	U4	U5	U6	U7	U8	U9	U10
Euhoplites vulgaris Spath			X	X	X					
Euhoplites boloniensis Spath	X	X	X							
Euhoplites alphalautus Spath				X	X	X				
Discohoplites coelonotus (Seeley)							?	?	X	
Discohoplites subfalcatus (Semenov)									X	
Discohoplites simplex Wright & Wright									X	
Savelievella varicosus (Spath)									X	
Savelievella valbonnensis valbonnensis (Hébert & Munier-Chalmas)								X	X	
Savelievella valbonnensis dorsetensis (Wright & Wright)									X	
Spathoplites transitorius (Spath)									X	
Spathoplites anomalus (Spath)								X	X	
Spathoplites arkelli (Wright & Wright)									X	
Wrighthoplites pylorus (Wright & Wright)									X	
Wrighthoplites daedalius (Wright & Wright)									X	
Hyphoplites campichei Spath									X	X
Hyphoplites falcatus aurora Wright & Wright									X	
Hyphoplites falcato-coelonotus (Semenov)									X	
Neophlycticeras brottianum (d'Orbigny)			X							
Neophlycticeras gibbosum Spath			X							
Neophlycticeras sexangulatum (Seeley)								X		
Eotropitoides jayet Breistroffer	X	X								

	cristatum		*varicosum*			*inflatum*		*dispar*		
Subzones	U1	U2	U3	U4	U5	U6	U7	U8	U9	U10
Protissotia itierianum (d'Orbigny)	X	X								
Protissotia orion Casey	X	X								
Stoliczkaia dispar (d'Orbigny)									X	X
Stolicczkaia rhamnonotus (Seeley)								X		
Stoliczkaia notha (Seeley)								X	X	
Stoliczkaia dorsetensis Spath									X	
Stoliczkaia dorsetensis compressa Spath									X	
Engonoceras grimsdalei Spath									X	
Dipoloceroides cornutum multispinosa Spath	X									
Oxytropidoceras cantianum cantianum Spath	X									
Oxytropidoceras cantianum excentricum Spath	X									
Dipoloceras bouchardianum (d'Orbigny)	X									
Dipoloceras bouchardianum rectangularis Spath	X									
Dipoloceras bouchardianum alticarinatum Spath		X	X							
Dipoloceras pseudaon pseudaon Spath	X	X								
Dipoloceras pseudaon moniliforme Spath	X	X								
Dipoloceras cristatum (Brongniart)	X	X								
Dipoloceras cristatum alatum Spath	X									
Dipoloceras britannicum Breistroffer	X	X								
Mortoniceratoides rigidum (Spath)	X									
Hysteroceras (? *Dipoloceras*) *symmetricum* (J. de C. Sowerby)	X									
Hysteroceras (? *Brancoceras*) *capricornu* Spath	X									
Hysteroceras pseudocornutum Spath	X									

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

	cristatum		*varicosum*			*inflatum*		*dispar*		
Subzones	U1	U2	U3	U4	U5	U6	U7	U8	U9	U10
Mortoniceras (*Mortoniceras*) *geometricum* Spath					X					
Mortoniceras (*Mortoniceras*) *inflatum inflatum* (J. Sowerby)						X	X			
Mortoniceras (*Mortoniceras*) *inflatum crassissima* (Kilian)						X				
Mortoniceras (*Mortoniceras*) *inflatum aperta* (Spath)						X				
Mortoniceras (*Mortoniceras*) *inflatum orbignyi* Spath						X				
Mortoniceras (*Mortoniceras*) *inflatum picteti* (Spath)						X	X			
Mortoniceras (*Mortoniceras*) *inflatum gibbosum* Spath						X				
Mortoniceras (*Mortoniceras*) *inflatum rugosum* (Spath)						X				
Mortoniceras (*Mortoniceras*) *arietiforme* (Spath)						X				
Mortoniceras (*Mortoniceras*) *fissicostatum fissicostatum* Spath						X	?			
Mortoniceras (*Mortoniceras*) *fissicostatum ascendens* Spath						X				
Mortoniceras (*Mortoniceras*) *commune commune* Spath						X				
Mortoniceras (*Mortoniceras*) *pachys* (Seeley)							?	X		
Mortoniceras (*Mortoniceras*) *potternense* Spath						X				
Mortoniceras (*Mortoniceras*) *evolutum* Spath						X				
Mortoniceras (*Mortoniceras*) *quadrinodosum* (Spath)						X				
Mortoniceras (*Mortoniceras*) *rostratum* (J. Sowerby)								X		
Mortoniceras (*Mortoniceras*) *fallax* Breistroffer								X		
Mortoniceras (*Mortoniceras*) *alstonense* Breistroffer								X	?	
Mortoniceras (*Mortoniceras*) *nanum nanum* (Spath)							?	X		
Mortoniceras (*Mortoniceras*) *nanum extrema* Spath							?	X		
Mortoniceras (*Durnovarites*) *perinflatum* (Spath)									X	
Mortoniceras (*Durnovarites*) *quadratum* (Spath)									X	

	cristatum		*varicosum*			*inflatum*		*dispar*		
Subzones	U1	U2	U3	U4	U5	U6	U7	U8	U9	U10
Mortoniceras (*Durnovarites*) *postinflatum* Spath									X	
Mortoniceras (*Durnovarites*) *subquadratum* Spath									X	
Mortoniceras (*Durnovarites*) *subquadratum crassicostata* Spath									X	
Mortoniceras (*Durnovarites*) *subquadratum tumida* Spath									X	
Goodhallites goodhalli goodhalli (J. Sowerby)				X						
Goodhallites goodhalli aplanatus Spath				X						
Goodhallites goodhalli shenleyensis Spath				X						
Goodhallites goodhalli tuberculata				X						
Goodhallites tuberculatum Spath				X						
Goodhallites delabechei Spath				X						
Goodhallites delabechei robustus Spath				X						
Goodhallites candollianum Spath non Pictet							X			
Goodhallites falcifer Spath				X						
Neoharpoceras coptense Spath						X	X			
Neoharpoceras hugardianum (d'Orbigny)						X	X			
Neoharpoceras irregulare Spath						X	X			
Elobiceras pseudelobiensis (Spath)						X				
Cantabrigites cantabrigensus (Spath)								X		
Cantabrigites cantabrigensus gracile Spath								X		
Cantabrigites subsimplex Spath								X		
Cantabrigites minor Spath							X	X		
Cantabrigites minor serpentinus 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, Inflaticeras* (*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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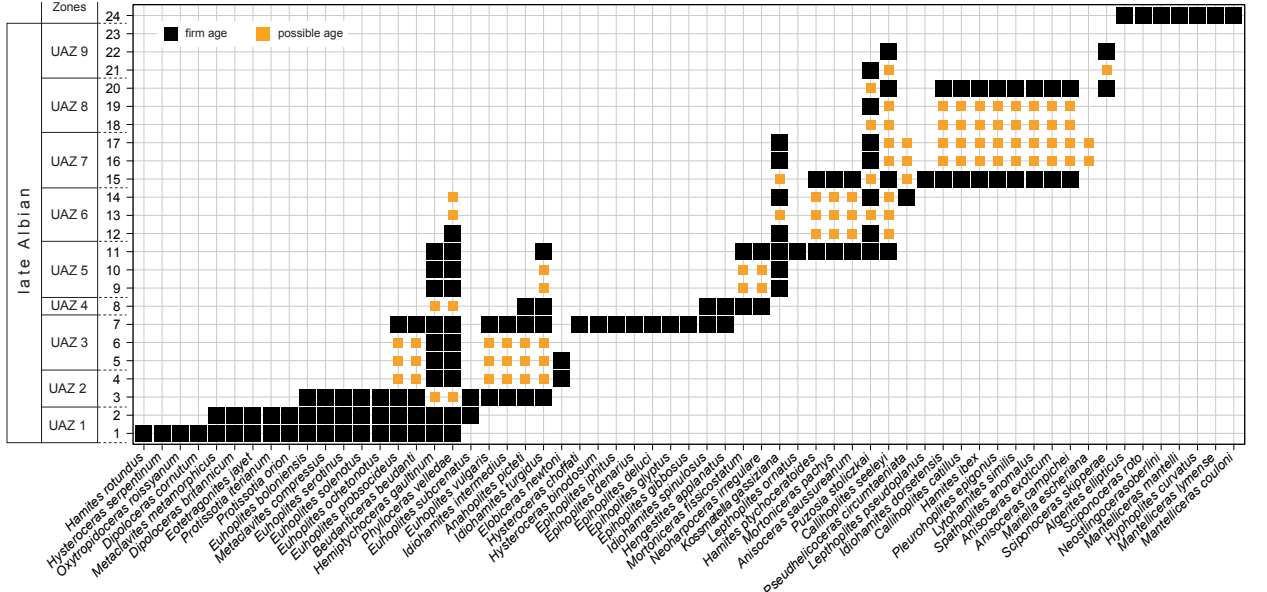
UA-Zones
UAs
late Albian
UAZ 1
UAZ 2
UAZ 3
UAZ 4
UAZ 5
UAZ 6
UAZ 7
UAZ 8
UAZ 9
firm age
possible age
Hamites rotundus
Hysteroceras serpentinum
Oxytropidoceras roissyanum
Diplomoceras cornutum
Metaclavites metamorphicus
Dipoloceras brinnicum
Eotetragonites jayeti
Protissotia terfanum
Protissotia orion
Euhoplites bolbinensis
Metaclavites compressus
Euhoplites solenotus
Euhoplites serotinus
Euhoplites ochetonotus
Euhoplites proboscideus
Beudanticeras beudanti
Hemiptychoceras gaultinum
Phylloceras velledae
Euhoplites subcrenatus
Euhoplites vulgaris
Idiohamites intermedius
Idiohamites picteti
Idiohamites turgidus
Arrhaphoceras newtoni
Elobiceras newtoni
Hysteroceras binodosum
Hysteroceras choffati
Epihoplites ignitus
Epihoplites dehanus
Epihoplites deluci
Epihoplites gryphus
Epihoplites gibbosus
Idiohamites spinulosus
Hengestites applanatus
Hengestites fissicostatum
Mortoniceras irregulare
Neoharpoceras irregulare
Kossmatella gessiziana
Leptohoplites ornatus
Hamites ptychoceratoides
Anisoceras saussureanum
Mortoniceras pachys
Puzosia stoliczkai
Callihoplites seeleyi
Pseudhelicoceras circumtaeniata
Leptohoplites pseudoplanus
Idiohamites dorsetensis
Callihoplites catillus
Hamites ibex
Pleurohoplites epigonus
Lytohamites similis
Spathohamites anomalus
Anisoceras exoticum
Mariella escheriana
Scipionoceras campichei
Scipionoceras skipperae
Algeriites elliptocus
Neosaynoceras soberlini
Mantelliceras roto
Mantelliceras mantelli
Hypohoplites curvatus
Mantelliceras lymense
Mantelliceras couloni