

Zeitschrift: Eclogae Geologicae Helvetiae
Herausgeber: Schweizerische Geologische Gesellschaft
Band: 95 (2002)
Heft: 1

Artikel: Cenomanian (early Late Cretaceous) ammonoid faunas of Western Europe. Part I, Biochronology (Unitary Associations) and diachronism of datums
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DOI: <https://doi.org/10.5169/seals-168946>

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Cenomanian (early Late Cretaceous) ammonoid faunas of Western Europe

Part I: Biochronology (Unitary Associations) and diachronism of datums

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Key words: Ammonoids, Late Cretaceous, Western Europe, biochronology, Unitary Associations, diachronism

Mots clés: Ammonites, Crétacé supérieur, Europe de l'Ouest, Biochronologie, Associations Unitaires, Diachronisme

ABSTRACT

Biochronological data of Cenomanian ammonoid faunas of Western Europe are analyzed for three well-documented basins: the Vocontian Basin in south-eastern France, the Münster Basin in Germany, and the Anglo-Paris Basin. A taxonomically standardized data set is constructed for these three basins and includes more than one hundred species and is analyzed with the deterministic Unitary Association Method. Data for each basin are first processed separately, thus yielding three regional biochronological zonations. Then, the three regional sequences are processed together as a three-section data set for the construction of the inter-basin sequence. The latter comprises 24 unitary associations grouped in eight zones for the Cenomanian Stage. These results take into account species that co-occur in time and space (real coexistence), those that only co-occur in time (virtual coexistence), and those that do not co-occur in space nor in time (exclusion of chronological significance). At the paleogeographical scale of Western Europe, this new zonation is in good agreement with the widely used standard zonation, but its resolution is three times higher. This demonstrates the benefits of applying the Unitary Association Method, even to a taxonomic group which is traditionally acknowledged as one of the leading group in dating Mesozoic marine rocks. It also highlights the variable completeness and resolution of the faunal record through space and time, and reveals that a substantial number of the taxa (47%, inclusive of some indexes) have a diachronous distribution across these three Cenomanian basins. However, even with such an enhanced time resolution, no preferred orientation of the diachronous taxa emerges, suggesting that none of these basins seemed to have functioned as a paleobiogeographical source or sink. The absence of any preferred direction of the diachronism of the datums is most likely explained by two, non-mutually exclusive causes: either a random distribution of the incompleteness of the faunal record and/or a common paleobiogeographical history of the faunas in the three basins.

RESUME

Les données biochronologiques des faunes d'ammonites du Cénomanien provenant de trois bassins bien documentés sont analysées. Les bassins sélectionnés pour cette étude comprennent le bassin Vocontien dans le sud-est de la France, le bassin de Münster en Allemagne et le bassin Anglo-parisien. Ces données sont en premier lieu standardisées d'un point de vue taxonomique pour constituer une base de données comprenant plus d'une centaine d'espèces. Cette base est ensuite analysée par la méthode déterministe des Associations Unitaires. Les données propres à chaque bassin sont d'abord traitées séparément, ce qui permet d'obtenir trois zonations régionales. Ces trois séquences régionales sont ensuite traitées comme un problème comprenant trois sections pour la construction de la zonation commune aux trois bassins. Cette dernière comprend 24 Associations Unitaires regroupées en 8 zones pour le Cénomanien. Ces zonations intègrent les espèces qui coexistent dans l'espace (coexistences réelles), celles qui coexistent uniquement dans le temps (coexistences virtuelles) et celles qui ne coexistent ni dans le temps ni dans l'espace (exclusions d'ordre chronologique). La nouvelle zonation intégrant les trois bassins est globalement cohérente avec les zones standard habituellement utilisées pour l'Europe occidentale et de plus, permet de tripler la résolution biochronologique. Ceci montre l'apport bénéfique de l'utilisation des Associations unitaires, même dans le cas d'un groupe taxonomique réputé être parmi les plus performants pour dater les séries marines du Mésozoïque. Elle met aussi en évidence les variations de qualité des enregistrements entre les trois bassins et montre que de nombreux taxons (47%, dont certaines espèces index) possèdent des répartitions diachrones. En dépit de cette résolution accrue, l'analyse du diachronisme ne montre pas d'orientations géographiques préférentielles. Une répartition aléatoire des biais de l'enregistrement faunique ainsi qu'une histoire biogéographique commune sont les deux causes possibles et non mutuellement exclusives pour expliquer l'absence d'orientation préférentielle du diachronisme des datums.

1. Introduction

Considerable efforts have been devoted to the study of marine Cenomanian series because this time interval is recognized as having experienced global changes linked with oceanic circula-

tion, tectono-eustatism, and climate (e.g. Jenkyns et al. 1994; Kauffman & Hart 1995; Fluteau 1999). Around the Cenomanian/Turonian boundary, a whole array of more or less interwoven events has been detected. Among these are a second order

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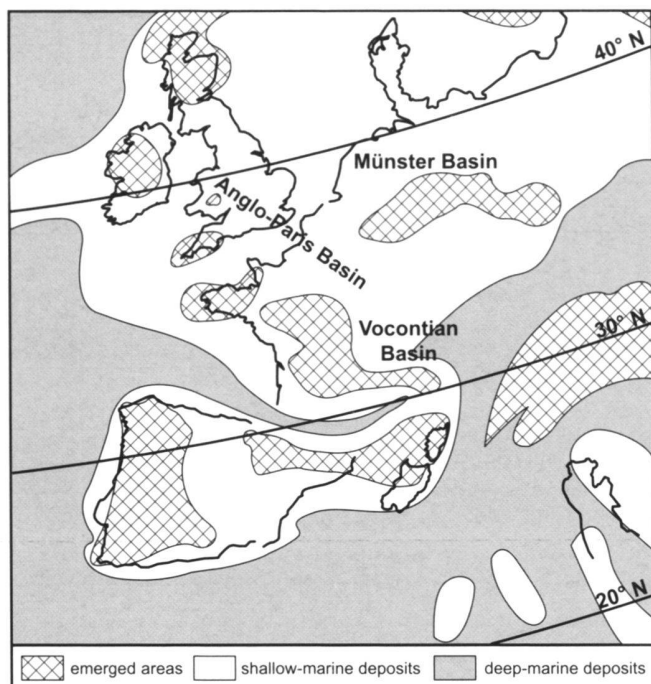


Fig. 1. Cenomanian paleogeography of Western Europe (after Philip et al. 1993, modified and simplified).

transgressive maximum (e.g. Hancock & Kauffman 1979), the deposition of black shales in numerous basins which is commonly interpreted as a response to changing regimes of oceanic circulation (e.g. Schlanger & Jenkyns 1976), changes in the record of carbon stable isotopes such as the $\delta^{13}\text{C}$ positive excursion in the latest Cenomanian (e.g. Scholle & Arthur 1980), and a moderate mass extinction event (e.g. Elder 1985; Jarvis et al. 1988; Harries 1993; Hallam & Wignall 1997) whose timing and magnitude are being currently debated (e.g. Banerjee & Boyajian 1996; Hora & Marshall 1998; Harries & Little 1999; Gale et al. 2000).

Whatever the diverse objectives and approaches of investigations focusing on the Cenomanian/Turonian boundary, they all rely directly or indirectly on available biochronological zonations and correlations. Although alternative methods of correlation have been proposed (event stratigraphy, Ernst et al. 1983; sequence stratigraphy, Haq et al. 1988; chemostratigraphy, Gale et al. 1993; cyclostratigraphy, Gale 1995), biochronology is and remains a major tool in dating and correlating. Incidentally, magnetostratigraphy is also of little help in this endeavor because the critical time interval is included within the Cretaceous Long Normal polarity superchron. Hence, an increased accuracy of the ammonoid zonation may improve the time frame of numerous stratigraphic and paleoenvironmental studies either in a given section, within any particular basin, or throughout Western Europe.

This study comprises ammonoid data from three areas: the Vocontian Basin in southeastern France, the Münster Basin in

northwestern Germany, and the Anglo-Paris Basin in southern England and northern France (Fig. 1). All of the ammonoid faunas of these three epicontinental basins, located on the northern Tethyan margin, were under Boreal influence (Juignet & Kennedy 1976; Thomel 1992). These three basins are selected because of their relatively abundant and well-illustrated ammonoid faunas, substantial and recent taxonomic revisions, as well as adequately documented stratigraphic ranges of taxa. Fundamental and detailed works by Hancock (1960), Juignet & Kennedy (1976), Wright & Kennedy (1981, 1984), Amédéo (1986) and Gale (1995) all contributed to the knowledge of the regional faunal sequence of the Anglo-Paris Basin. The Cenomanian ammonoid zonation proposed by Wright & Kennedy (1984) is currently used as a European standard and comprises seven assemblage zones, some of which may be recognized in other basins. However, numerous minor problems remain unsolved in the correlations between these three basins, mainly because of the use of different biochronological methods and taxonomic conceptions among the various authors (see Wiedmann et al. 1989; Kennedy et al. 1996; Monnet & Bucher 1999).

Recent methodological developments in deterministic biochronology such as the Unitary Associations Method [UAM] (Guex 1991; Savary & Guex 1999) play a key role in the extraction and objective evaluation (i.e. testable and subject to improvement) of the chronological component of the fossil record. A large amount of available data on the ammonoid faunas of Western Europe and the sustained interest in a better understanding of global events during the mid-Cretaceous (e.g. Sellwood et al. 1994; Barron et al. 1995; Norris & Wilson 1998) prompted the present attempt in refining the biochronological framework by means of the UAM.

Ammonoid data from the Vocontian Basin have been analyzed separately with the UAM (Monnet & Bucher 1999). A data set expanded to the Anglo-Paris Basin and the Münster Basin, accompanied by the necessary taxonomic standardization, the processing and critical evaluation of the resulting Unitary Association Zones and their implications are presented in this contribution. Special emphasis is also placed on the methodology of the optimization procedure and the hierarchical biogeographical treatment used for constructing correlations across Western Europe. Achievement of an improved zonation is here conceived as a first part of a broader contribution aiming at a better description and understanding of the ammonoid turnover, diversity dynamics, and evolutionary trends in response to the Cenomanian/Turonian abiotic events. These aspects will be treated in a forthcoming part 2 of this study on the Cenomanian ammonoid faunas of Western Europe for which the best possible time accuracy is desirable.

2. Unitary Associations Method

This deterministic (as opposed to probabilistic) method was developed by Guex (1977, 1991, 1999 in Savary & Guex 1999) to which the reader is referred for a complete explanation. Ed-

wards & Guex (1996) also give a brief summary of the method. Fundamentally, Oppel Zones, Concurrent Range Zones, and Unitary Associations Zones are closely allied because they are all based on the association principle. The absence of any single contradiction between the original data set and the constructed zonation is a prime criterion used for validating biochronological methods. In other terms, all documented real associations (coexistences in space) of taxa must be preserved in the zonation, and this criterion is satisfied by the Unitary Associations Method (UAM). Moreover, UAM differs from other association methods in that it parsimoniously exploits conflicting relationships (=biostratigraphic contradictions) displayed by first occurrences (FOs) and last occurrences (LOs) to infer virtual associations (i.e. coexistences in time but not in space).

Integral preservation of documented real coexistences is generally not satisfied by probabilistic and multivariate treatments of local first and last appearance datums because rare associations are commonly omitted, leading to the artificial superposition of actually coexisting species (e.g. Baumgartner 1984; Boulard 1993). The efficiency of the UAM in solving complicated biochronological problems (i.e. with a large number of conflicting relationships between the datums) has been demonstrated with taxonomic groups having a much less favorable record than ammonoids (e.g. radiolarians; see O'Dogherty 1994; Baumgartner et al. 1995; Carter et al. 1998). The UAM has also been successfully used for archeological seriation (Blackham 1994, 1999). The UAM has been automated in the BioGraph computer program by Savary & Guex (1991, 1999) which can be freely downloaded from <http://www-sst.unil.ch/research/guex/index.htm>.

The central tenet of the UAM is the construction of a discrete and time-ordered sequence of species coexistence intervals of minimal duration. Each interval consists of a maximal set of intersecting ranges (Savary & Guex 1999). The main principles of this deterministic method are illustrated with an imaginary and somewhat simplistic example comprising three sections and seven taxa (Fig. 2A). The sum of the observed biostratigraphic relationships (associations, superpositions, and exclusions) is represented by the biostratigraphic graph (Fig. 2B), whose vertices, edges, and arcs represent species, associations and superpositions, respectively. A unitary association (UA) is defined as a maximal set of actually and virtually coexisting species. The species and/or pairs of species, which are found exclusively within each UA, are said to be the characteristic species or pairs of species. These allow a sample to be attributed to a given UA.

The discontinuous nature of the data (sedimentary gaps, unfavorable facies, insufficient sampling, selective preservation, ecological exclusion, reworking) almost inevitably generates conflicting relationships between taxa (biostratigraphic contradictions). These elementary contradictions can be isolated as subgraphs (Fig. 2C) of the biostratigraphic graph. Each of these elementary structure cannot be polarized against the time arrow because they contain either uncertainties (un-

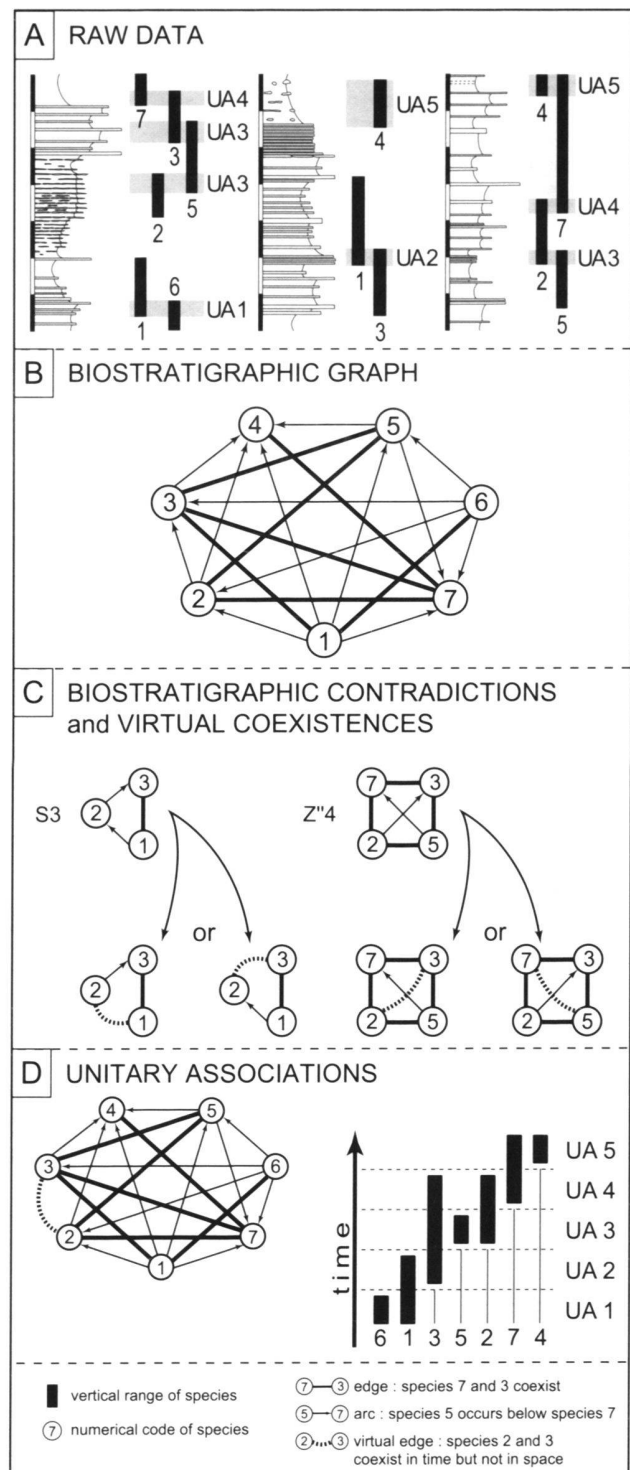


Fig. 2. Simple hypothetical example illustrating the core principle of the Unitary Association Method (see text for explanations).

documented superpositions as illustrated in Fig. 2C) or arcs of opposed directions between two vertices (i.e. trivial virtual coexistences). Virtual coexistences among the species most fre-

quently involved in such contradictions can often be logically inferred. For example, the synthesis of the three sections shows two contradictions (Fig. 2C). One of these involves species 1, 2 and 3: the superpositions of species 1, 2 and 3 (1 below 2 below 3) observed in the left section (Fig. 2A) is conflicting with the association of species 1 and species 3 as observed in the middle section, because in the latter the chronological position of species 2 remains uncertain with regard to species 1 and 3. Such a contradiction implies that either species 1 or species 3 coexisted chronologically with species 2: such coexistences are said to be virtual (Guex 1991). Whatever the real causes of the documentary inadequacies, these will also blur the relative order of first and last appearances (see taxa 3 and 1 or taxa 2 and 5 in Figure 2A). Nevertheless, the three hypothetical sections contain valuable information on the mutual coexistences and exclusions, as well as on the superpositions of the species. In our example, replacing the arc from 2 toward 3 can optimally and logically destroy the two contradictions (termed S3 and Z'4 in graph terminology) by a virtual edge (Fig. 2C). After all biostratigraphic contradictions are detected and destroyed by replacing a minimum number of contradictory arcs by virtual edges, the remaining arcs of the biostratigraphic graph can be uniformly oriented along the time arrow, thus making it possible to extract ordered sequences of unitary associations (Fig. 2D). Our example yields five unitary associations or maximal sets of mutually compatible species. This sequence is called the protoreferential and along with the reproducibility matrix (a sections vs. UAs matrix), they constitute the zonation used to date the fossiliferous content of every bed of every section. Laterally reproducible unitary associations or unions of poorly reproducible unitary associations are separated from each other by intervals of separation.

3. Construction of the data set

Raw data were obtained from a selection of contributions providing adequate information on the ranges of species and illustrations of the taxa. For the Münster Basin, we used the monograph of Kaplan et al. (1998). For the Anglo-Paris Basin, we used the works of Juignet & Kennedy (1976), Juignet et al. (1978), Wright & Kennedy (1981), Amédéo (1986) and Robaszynski et al. (1987). For the Vocontian Basin, we used the monograph of Thomel (1992) for the eastern part of the basin, the contribution of Gale et al. (1996) for the proposed stratotypic section of Mont Risou, and our own new field data for the western part of the basin (section Gipières).

As the data set is constructed from multiple sources where taxonomic definitions may be at variance, a standardization is necessary prior to data processing with UAM (this step is essential in that zonations are highly sensitive to taxonomic definitions). In order to establish reliable correlations and to avoid inconsistencies between the zonations of each basin, it is indeed necessary that the same species must receive the same name in all of the three studied basins. When confusion resulting from the interchangeable use of two species names appears

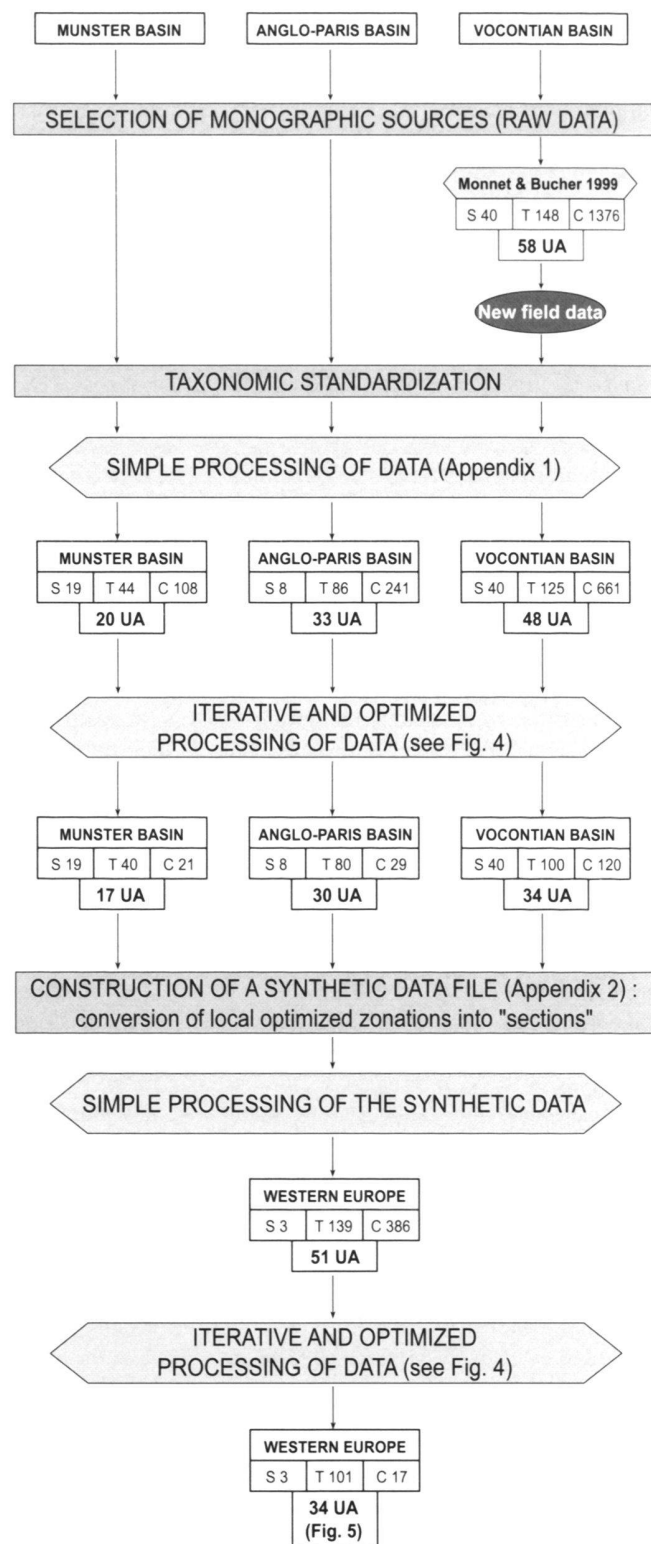


Fig. 3. Flow chart illustrating the successive steps of the process. For each run, scores displayed indicate the number of sections (S), the number of taxa taken into account (T), the number of biostratigraphic contradictions (C), and the number of resulting Unitary Associations.

between several contributions, and if the stratigraphical occurrences are not disjunct, these two names were lumped together. In spite of a potential minor loss of resolution, such groupings of species increases the lateral reproducibility of the zonation and preserves a maximum number of taxa (the opposite and somewhat indiscriminating option would consist in excluding such pairs of ill-defined, closely related, and more or less overlapping species).

Because our purpose is not a taxonomic revision of the Cenomanian ammonoid faunas of Western Europe, the widely used monographic treatments of Wright & Kennedy (1981–96) are taken as a taxonomic basis for this study. However, special attention was devoted to ontogenetic changes and intraspecific variation, with constant reference to the type specimens. It is emphasized that this taxonomic standardization is not meant to replace an in-depth taxonomic revision, but it attempts to lower at best the level of taxonomic noise between the different monographic sources. Inherent limitations to this standardization are obviously imposed by the quality of available taxonomic data. The resulting data set is given in Appendix 1.

4. Processing and optimization

The flow chart of our biochronological revision can be summarized as the successive following analyses: selection of the raw data, taxonomic standardization, simple run of BioGraph, op-

timization procedure, construction of the zonation, correlation of the three basins, analysis of diachronism. It is worth noting that the BioGraph program calculates and then provides the protoreferential from a text file containing the data (presence/absence of taxa in each section). The program will always yield a result even with poor quality data. Therefore, the final interpretation is left to the user. Because biostratigraphic contradictions always occur in the raw data and may lead to arbitrary results in the worst cases, we developed an optimization procedure consisting in an iterative analysis with multiple runs of the program.

The primary results of the biochronological revision are given in Figure 3. Standardized data from each basin are first processed separately with the UAM. For the Vocontian Basin whose data set contains 40 sections and 125 taxa, this first run yields 48 Unitary Associations (UAs) and 661 contradictions. This first result is then optimized according to the procedure of Monnet & Bucher (1999) and illustrated here in Figure 4. After completion of the optimization, 100 taxa, 120 contradictions and 34 UAs are obtained for the local zonation of this basin. Each basin zonation is then converted into a „local section“ for constructing the correlations between the 3 basins (this new data set is given in Appendix 2). A first run yields 386 contradictions and 51 UAs. The same optimization procedure then yields 17 contradictions only for a total of 101 taxa distributed throughout 34 UAs. It is worth noting that the al-

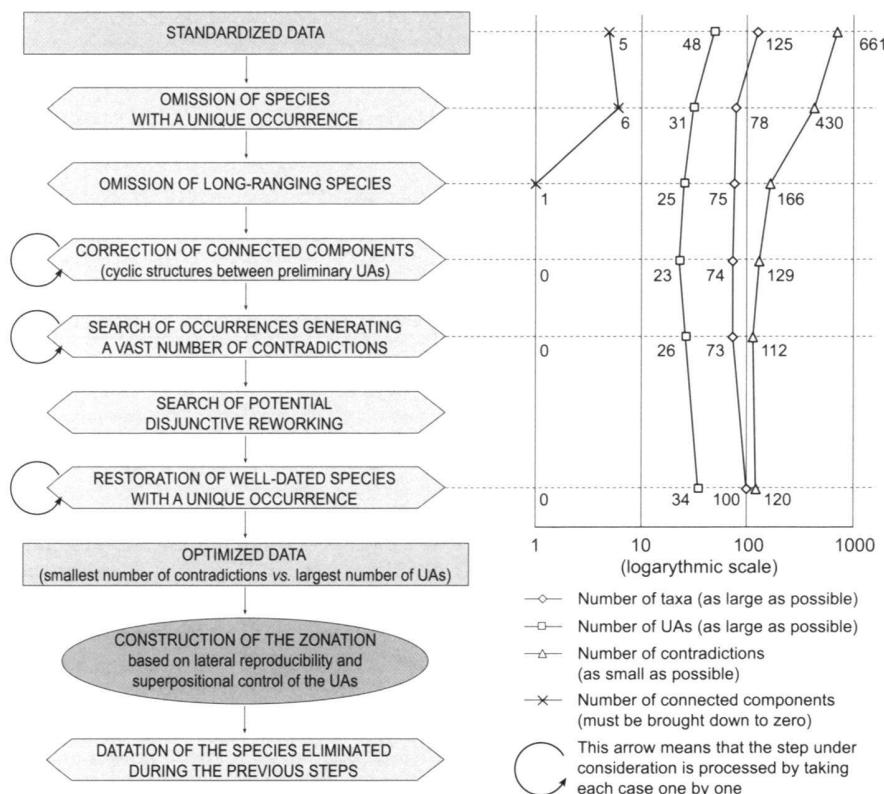


Fig. 4. Flow chart illustrating the iterative processing used for optimizing the data. For each run, scores of number of taxa, number of UAs, number of contradictions and number of connected components (cycles between UAs) are monitored in order to evaluate the optimal data set. The example presented here is that of the Vocontian Basin.

Late (part) ALBIAN	CENOMANIAN																Early (part) TURONIAN	Genus species (numeric code)
	Early								Middle				Late					
1 2 3 4	5 6 7 8 9 0	1 1 1 1 1	1 1 1 1 1	1 1 1 1 1	1 1 1 1 1	1 1 1 1 1	1 1 1 1 1	1 1 1 1 1	1 2 2 2 2 2 2 2 2	1 2 2 2 2 2 2 2 2	1 2 2 2 2 2 2 2 2	1 2 2 2 2 2 2 2 2	2 3 3 3 3 3 3	2 3 3 3 3 3 3	2 3 3 3 3 3 3	2 3 3 3 3 3 3		
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Fig. 5. Chronologically ordered sequence of Unitary Associations of the Cenomanian of Western Europe. This chart represents the synthesis of superposition, exclusion and association relationships observed and deduced from the optimized data set. Taxonomic definitions derived from Wright & Kennedy (1981–96) except for the following taxa : (a) Thomel 1992; (b) Renz 1968; (c) Scholz 1979; (d) Latil 1994; (e) Delanoy & Latil 1988; (f) Kaplan et al. 1998; (g) Gale et al. 1996; (h) Juignet et al. 1978; (i) Amédéo 1986. The symbol # means that this taxa is a grouping of species. Taxa marked by an asterisk * are those with single occurrences and which are not included in the synthetic data set. They are dated and reincorporated into the range chart at the end of the processing. The amount of diachronism of taxa (see text for explanations) is coded with three different symbols (see inset keys).

help for correlations and are well known to generate numerous conflicting stratigraphic relationships (Savary & Guex 1999). Then, we iteratively analyze and destroy all strongly connected components by tracing back and removing the single occurrence at the origin of each cyclic structure.

The next step searches for occurrences that have the highest implication frequencies into the contradictions and each of these are then iteratively removed. In the context of the Cenomanian record of NW Europe, these contradictions are essentially generated by the selective preservation of the ammonoids, as already suggested by Wright & Kennedy (1981) and/or by the scarcity of fossiliferous beds (Lehmann 1998). Our own experience in the Vocontian Basin, where the maximum thickness of Cenomanian strata is approximately 700 m,

is in agreement with these remarks drawn from the two other basins.

The next step deals with the exclusion of known condensed beds and potentially reworked faunas followed by the automated detection of disjunctive reworkings according to the four methods designed by Guex (1991). No such disjunction can be detected in any of the three basins.

The last step of the optimization procedure iteratively reincorporates into the data set species with single occurrence. Some of the species that have been eliminated during the earlier steps can be dated and reintroduced after the zonation has been constructed (these species are not included in the scores of Figure 3 and are marked by an asterisk in Figure 5). Species removed throughout the successive steps are listed in Appendix 3.

5. Results and comparisons

The main result of the processing as described above is a sequence of 34 chronologically ordered UA-Zones (Fig. 5). The Cenomanian of Western Europe is subdivided into 24 UAs, the latest Albian (Vraconian) into 4 UAs and the Early Turonian into 6 UAs. This sequence exactly synthesizes the association, superposition and exclusion relationships of the ammonoid taxa included in this analysis. It fully and clearly defines the characteristic content of each UA and of each zone. The characteristic species and/or pairs of species it includes identify each UA. The three symbols (black and white squares, crosses) indicate the maximal biochronological range of each species for the three basins. The amplitude of diachronism of taxa between the three basins is keyed by these different symbols and is discussed in the next section. This sequence is the revised and improved ammonoid zonation of the Cenomanian of Western Europe. As tested with the Biograph tool T06 (Savary & Guex 1999), it is worth noting that this UA-sequence integrally preserves all of the observed associations documented in the data set and that no reversed sequence of ranges were created. In other words, the integrity of the data is entirely preserved by the processing.

The conventional boundaries of the Cenomanian stage stand out well in this new zonation (Birkelund et al. 1984; Hancock 1991; Tröger & Kennedy 1996; Bengtson 1996). The base of the Cenomanian is characterized by the appearance of *Mantelliceras mantelli*, and more generally by co-occurrence of species belonging respectively to *Mantelliceras* and *Neostlingoceras*. The base of the Turonian is characterized by the appearance of *Watinoceras devonense*.

The UA-zonation proposed here is in relatively good agreement with the empirical zonation developed for the Anglo-Paris Basin (Fig. 6) which is commonly used in the European literature (for discussion, see Juignet & Kennedy 1976; Wright & Kennedy 1981, 1984). However, such an overall similarity is not to be unexpected because the zonation of Wright & Kennedy (1984) is based on the association principle. On the other hand, this traditional zonation subdivides the Cenomanian into only seven zones and a few subzones, the latter being mostly of local significance. The present zonation leads to more than a three-fold increase in resolution, with 24 subdivisions for the Cenomanian. As the standard zonation does not conflict with the UA-zonation, classic names of zones are kept unchanged for subsequent use. Moreover, the standard zones are „assemblage zones, characterized by an association of species that are not necessarily restricted to their zone“ (Kennedy et al. 1996). Therefore, there is no point changing the name of standard zones as long as their faunal content matches that of the UA-zones. The correlation between the UA-zones and the standard zones is shown on Figure 6. The standard zones correlate either exactly with a single UA-zone or with union of UA-zones. For instance, the Dixoni Zone correlates with the union of UA-zone 11 to UA-zone 14, while the Juddii Zone correlates with the single UA-zone 28.

Although the two zonations coincide in their major boundaries, some discrepancies appear at the subzone level as defined by Wright & Kennedy (1984). Indeed, the *Acutus* and *Costatus* subzones of the Rhotomagense Zone, as defined in the Anglo-Paris Basin, have no correlatives in the UA-zones of the two other basins. On the other hand, the UA-zones do not contradict the recognition of the Saxbii and Carcitanense subzones of the Mantelli Zone.

The base of the Dixoni Zone is customarily defined by the first appearance datum (FAD) of the index species but this definition cannot be applied to the Vocontian Basin where the index has an obviously earlier first occurrence (FO). The Dixoni Zone is therefore better defined by the association of the index with *Acompsoceras renevieri*, which gives the lower zone boundary a better lateral reproducibility.

By definition, the boundaries of the Jukesbrownei Zone are defined by the first appearance datum (FAD) and the last appearance datum (LAD) of the index. If this definition is satisfying in terms of association for the upper boundary, it is not for the lower boundary. The basal part of the Jukesbrownei Zone is preferably defined by the co-occurrence of *Acanthoceras jukesbrownei* with *Calycoceras hippocastanum*, *C. bathyomphalum*, and *C. picteti*.

UA19, which is not identified in the Münster and Anglo-Paris basins, has an intermediate faunal content between the Jukesbrownei and Guerangeri zones. Although UA19 does not include *Calycoceras naviculare* or *C. guerangeri*, it is here grouped with the Guerangeri Zone on the grounds that it does not contain *Acanthoceras* and because it corresponds to the best option in terms of lateral reproducibility and superpositional control.

UA27 is a particular association characterized by Tethyan genera (*Vascoceras* spp. and *Nigericeras* spp.). This association corresponds to the „UA30“ of Monnet & Bucher (1999) and to the „unnamed zone“ of Kennedy et al. (1982). Outside Europe, UA27 may correlate with the Clydense Zone from the Western Interior (Kennedy & Cobban 1991).

Other workers also proposed some emendations of the standard zonation of Wright & Kennedy (1984). Gale & Friedrich (1989) proposed a *Schlueteri* subzone intercalated between the Saxbii and Carcitanense subzones (Mantelli Zone) and defined by the occurrence of *Sharpeiceras schlueteri*. This subzone corresponds to the interval composed of UA6, 7 and 8, but it is not based upon a reproducible association and is more or less redundant with the Carcitanense subzone (Fig. 6). Gale (1995) also introduced the *Inerme* Zone at the base of the Middle Cenomanian. This zone is defined by the earlier appearance of *Cunningtoniceras inerme* with respect to *Acanthoceras*. However, this zone is not compatible with the association principle and does not correspond to any characteristic species or pair of species. It must be discarded despite the fact it was recommended at the Brussels symposium (Tröger & Kennedy 1996). However, it is worth noting that the association of *C. inerme* with *Acanthoceras* is in fact the diagnostic association of the first UA-zone of the Middle Cenomanian (Fig. 5).

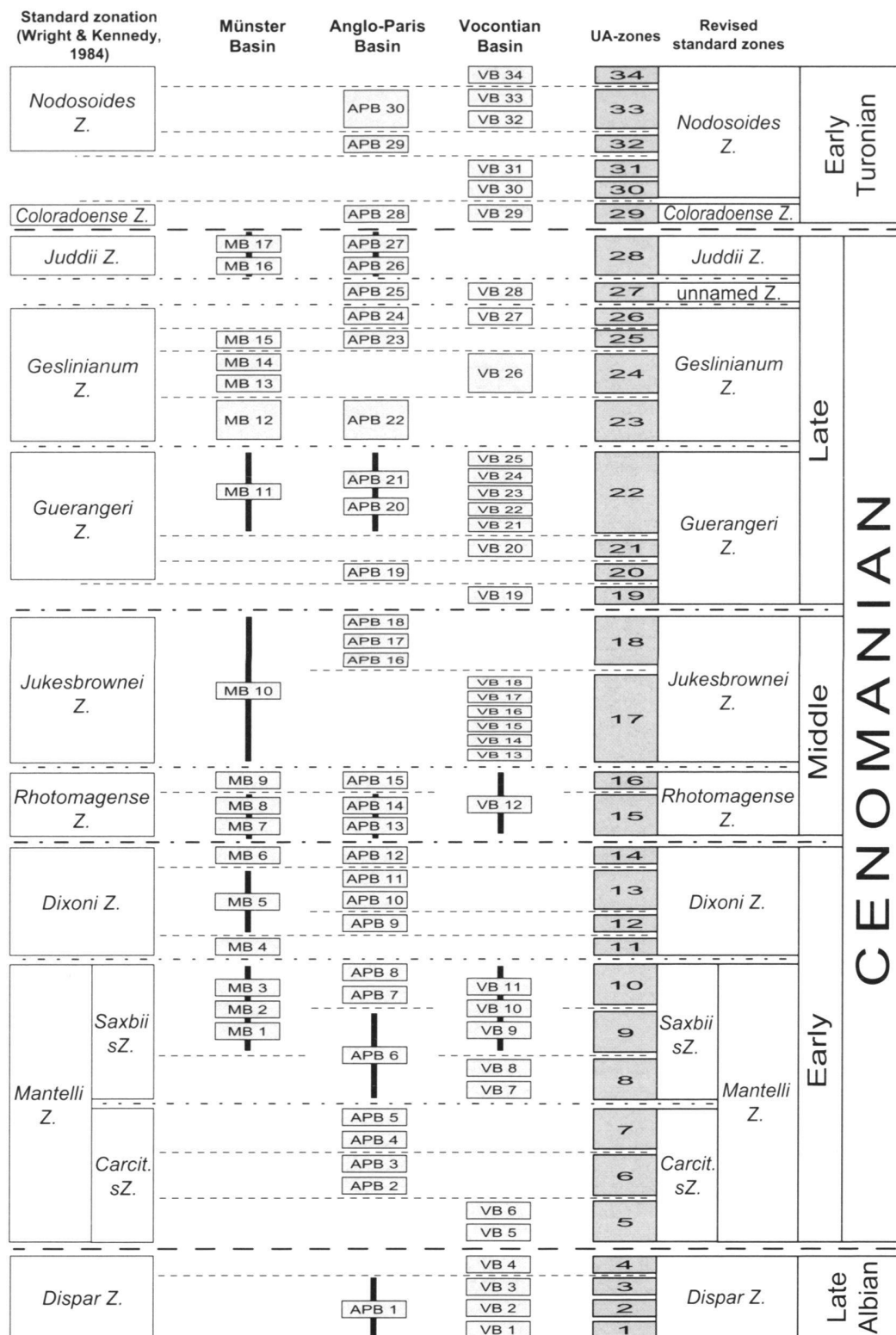


Fig. 6. UA-zonations of each basin and inter-basin UA-zonation. The correlations of the UA-zonation with the standard zonation are given on the left side of the chart. Modifications of the standard zones as suggested by the UA-zones are shown on the right side of the chart (base of the *Guerangeri* Zone and base of the *Nodosoides* Zone). The thick, vertical black lines indicate uncertainties in the correlations. Boxes faithfully reflect the discontinuous nature of the fossil record: all demonstrated correlations and all remaining uncertainties are graphically represented.

Finally, Jolet et al. (1997) made available new biostratigraphic data from the Cassis section, which is paleogeographically located in the Provence Trough of southeastern France. These authors suggested that the Geslinianum and Juddii zones are partly equivalent because of the locally documented overlap of the two indexes. This proposition apparently originates from the misunderstanding that the range of an index may not necessarily coincide with its zone boundaries and that a zone is defined by a characteristic association of taxa instead of a single taxon, be it the index or not. Except for *Neocardioceras* spp., all other taxa do constitute diagnostic associations of the Geslinianum Zone. By no means do the newly documented occurrences from Cassis cast doubt on the validity of the succession of Geslinianum and Juddii zones. The Cassis section simply illustrates that *Neocardioceras* has an earlier local first occurrence (FO). It is worth noting that *Neocardioceras* appears much earlier in the Western Interior, as soon as the base of the Late Cenomanian (Cobban 1988). Moreover, the supposed anomalous range of *Neocardioceras* in the contribution of Jolet et al. (1997) is based on a misidentification of the species as shown by the taxonomic revision of Cecca (2001). Last, this taxonomic reappraisal of the ammonoid faunas from Cassis leads to a biostratigraphic succession in agreement with both our new zonation and the standard zonation.

Beside the correlation between the standard zonation and our UA-zonation, Figure 6 also highlights the detailed correlations between the constructed UA-sequences of the three basins. These new inter-basin correlations confirm that the Dixoni and Juddii zones cannot be identified in the Vocontian Basin, as previously noted by Kennedy et al. (1996) and Monnet & Bucher (1999). The explanation for the absence of the Dixoni Zone is that the poorly fossiliferous rocks bracketed between occurrences of the Mantelli and Rhotomagensis zones do not yield enough diversified ammonoids assemblages that would permit identification of diagnostic associations. Therefore, insufficient sampling or major sedimentary gaps can be probably ruled out, whereas selective ecological exclusions and/or selective preservation biases remain plausible alternatives. As for the Juddii Zone, the relative scarcity of sections straddling the C/T boundary appears as the most likely explanation for its absence in the Vocontian Basin. The correlations also show that a large part of the Guerangeri Zone is not identified in the Münster Basin.

Based on the present state of available data, all demonstrated correlations on one hand, and all remaining uncertainties on the other hand, are graphically represented by boxes in Figure 6, thus faithfully reflecting the discontinuous nature of the fossil record and of Unitary Associations. For instance, UA25 does not occur in the Vocontian Basin but is identified in the Münster (MB15) and in the Anglo-Paris (APB23) basins. The biochronological resolution during a given time interval may also vary across the three basins. This is well illustrated in the upper part of the Guerangeri Zone (UA22). This interval is subdivided into 5 UAs of local value in the Vocontian Basin (VB21 to VB25), the sum of which correlates with

the union of 2 UAs of local significance in the Anglo-Paris Basin (APB 20 and 21), and with a single UA in the Münster Basin (MB11) *without further precision*. Other comparable examples can be noticed for most zones of the Early and Middle Cenomanian. Such changes in resolution at a large paleogeographical scale result from the combined effects of variable primary causes (i.e. ecological controls that shape distributions in space and time) with secondary biases (selective preservation, sampling effort, depositional gaps, etc.). However, this does not alter the validity of local UA-zonations when respectively applied within each basin. Moreover, the absence of a particular UA in a basin is also due to the absence of the age-diagnostic taxa because of a different, possibly random preservation between the three basins. These preservation and documentation controls are critical in explaining anomalous ranges and diachronous datums of taxa. The inter-basin UA-zonation is of crucial importance because it extracts a sequence of associations in which the chronological component largely overrides local ecological controls and preservation contingencies. It also clearly underlines that none of the three basins has a complete faunal record and suggests how these partial records can be objectively reconciled. Such an inter-basin zonation provides invaluable constraints, which must be taken into account when addressing issues like diachronism, phylogeny, evolutionary trends, faunal turnovers, and diversity dynamics.

6. Diachronism

Correlations between the three basins also reveal the diachronous distributions of species and genera. The amplitude of diachronism is graphically keyed for each taxa (Figure 5) according to the following definitions: (a) black squares indicate synchronous species, i.e. species always appearing and disappearing in the same zone(s); (b) white squares indicate moderately diachronous species, i.e. species always having their youngest local appearance earlier than their earliest local disappearance (the occurrences of such species in the zones may vary between the basins, but without disjunction in the distribution across the zonal sequence); (c) crosses indicate regionally diachronous species, i.e. species having at least one youngest local appearance later than their earliest local disappearance. For instance, *Mantelliceras picteti* ranges from UA-zones 7 to 13 in the Anglo-Paris Basin while in the Vocontian Basin it ranges from UA-zones 8 to 9 and is absent from the Münster Basin. Therefore, its range overlaps only from UA-zone 8 to UA-zone 9 across the two basins (as coded by the black squares in Figure 5). Another example is provided by *Acompsoceras renevieri*, which has a disjuncted distribution (coded by crosses in Figure 5): it ranges from UA-zones 12 to 15 in the Anglo-Paris and Münster basins and from UA-zones 17 to 19 in the Vocontian Basin. Diachronism of the main genera is also compiled in Figure 7.

Among the species listed in Figure 5, 53% are synchronous, 37% are moderately diachronous, and 10% are regionally diachronous. Moreover, the amount of diachronism is al-

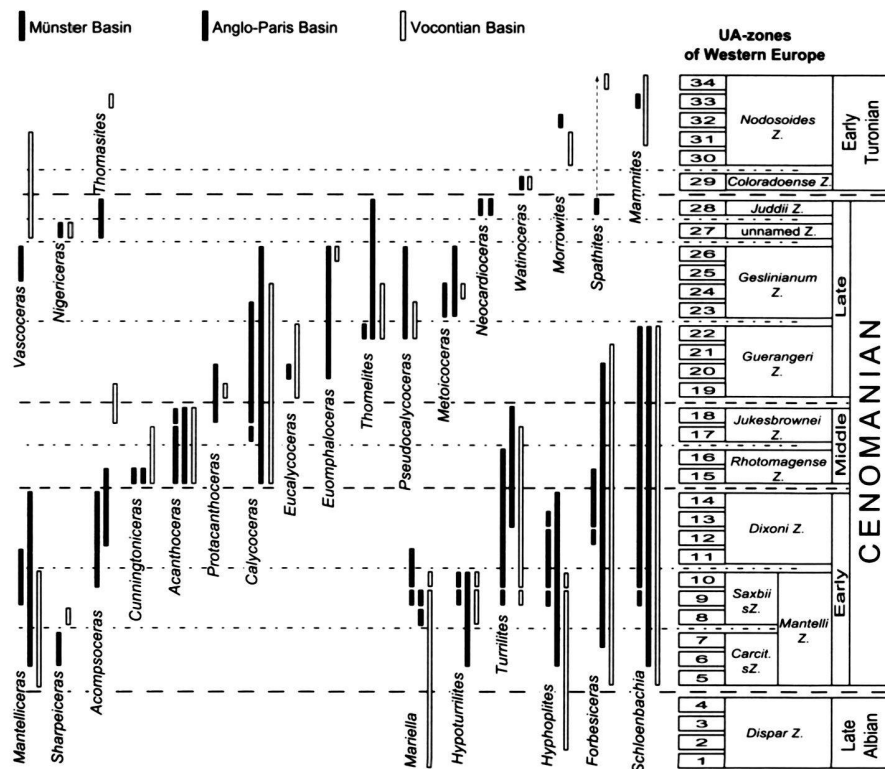


Fig. 7. Diachronism of several ammonoid genera of the Western European Cenomanian. The vertical bars indicate the local ranges of the genera in each basin; the bars are discontinuous where their occurrences are uncertain.

most equally shared between the FOs (18%) and LOs (19%) of moderately and regionally diachronous species. Although values of absolute abundance per samples are usually not reported, some scarce taxa, as exemplified by *Acompsoceras*, do show a comparatively huge amount of diachronism between the three basins (Fig. 7). However, it must be emphasized that there is no clear-cut relationship between abundance and diachronism, because some taxa represented by numerous individuals may also display significant diachronism (e.g. *Turritiles*). On the other hand, an unambiguous positive correlation between longevity and diachronism is here demonstrated (Fig. 8). Incidentally, it appears that even index taxa are no exception with regard to diachronism (e.g. the regionally diachronous *Mantelliceras dixonii*, see Fig. 5). Moreover, taxonomic inconsistencies at the species level will also obviously increase the amount of diachronism, as has been previously underlined for species belonging to *Acompsoceras* and *Turritiles* (Monnet 1999).

Among all potential secondary biases that may alter the local FOs and LOs is dissolution of the aragonitic shell of ammonoids. Evidence for this phenomenon has been substantially documented in the case of the Chalk series of the Anglo-Paris Basin (see discussion in Kennedy & Cobban 1976). Other mechanisms like carbonate solution and migration during diagenesis also probably affected the Vocontian ammonoid record. Such biases are still overlooked by a large number of ammonoid workers who persist in believing that correlations

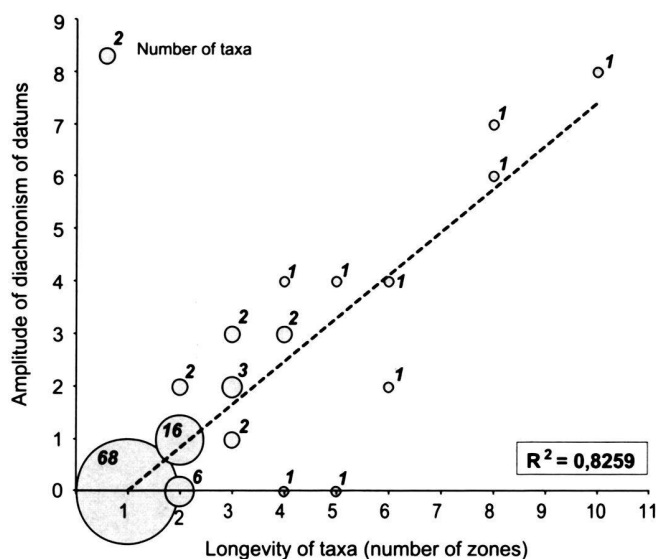
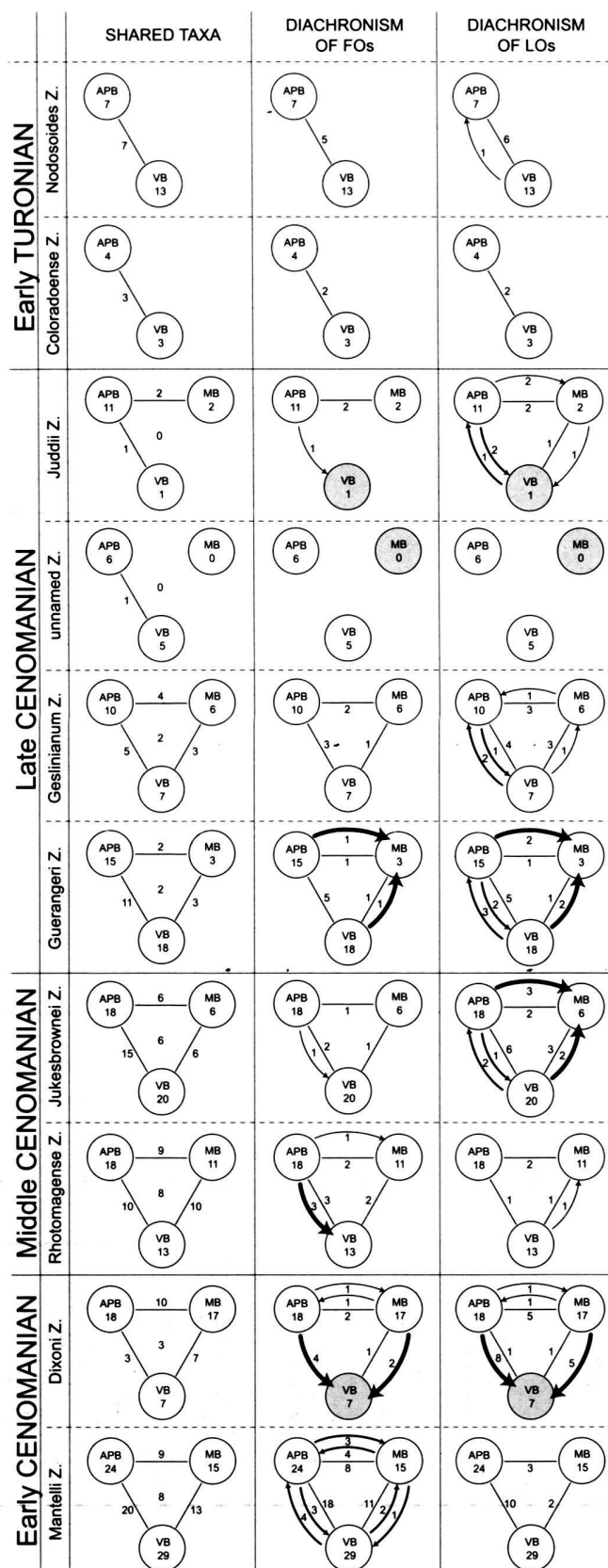


Fig. 8. Plot of longevity against amplitude of diachronism (sum of FO diachronism and LO diachronism) of species listed in Figure 5. It demonstrates a positive correlation between longevity and diachronism for ammonoids of the Western European Cenomanian.

should rest on first appearance of index taxa. The diachronism of the taxa listed in Fig. 5 and of the genera in Fig. 7 obviously shows that few taxa are actually synchronous.



If the vagaries of preservation evidently shortened the true ranges of the Cenomanian ammonoids in Western Europe, it is nevertheless worth searching for any preserved indications of primary controls (e.g. shifts of environmental gradients through time) that may have contributed to the diachronism. For instance, one may legitimately ask if any migratory trends can be detected between these three basins. This can be evaluated by compiling, for each zone in each basin, the diachronous earliest and latest occurrences with respect to the same zone in the two other basins. The results are reported in Figure 9 which displays in three columns: (i) the number of common taxa between two basins (edge) and between the three basins (number in the center of each graph), (ii) the diachronism (arrows) and synchronism (edges) of FOs, (iii) the diachronism and synchronism of LOs. For the three columns, the circles represent the three basins (APB = Anglo-Paris Basin, MB = Münster Basin, VB = Vocontian Basin) and the circled number indicates the number of species in each basin. For instance, in the Mantelli Zone (Early Cenomanian), the three columns of the Figure 9 indicate the occurrence of 24 taxa in the Anglo-Paris Basin, 15 in the Münster Basin, and 29 in the Vocontian Basin. The first column indicates that (for instance) the Münster and Anglo-Paris Basins shared 9 taxa. The second column indicates that 8 taxa have their FO in this zone in the two basins, 4 taxa appeared later in the Anglo-Paris Basin than in the Münster Basin, 3 taxa appeared later in the Münster Basin than in the Anglo-Paris Basin. The third column indicates that 3 taxa disappeared synchronously between the Münster and Anglo-Paris Basins and none has a diachronous LO between the two basins.

It is also worth commenting on the following points. Such a figure will highlight a migratory trend, if in a zone several arrows are oriented towards the same basin, and/or if this preferred orientation pattern is consistent through time. Such preferred orientations apparently occur in the Vocontian Basin during the Dixoni Zone, and in the Münster Basin during the time interval ranging from the Jukesbrownei Zone to the Guerangeri Zone. The Mantelli Zone shows a relatively high diachronism of FOs between the three basins, but it is uniformly distributed. During the Dixoni Zone, the Vocontian Basin apparently acted as a sink with a preferential convergence of the diachronism of FOs and LOs. However, this ap-

Fig. 9. Geographical orientations of diachronism of FOs and LOs of taxa listed in Figure 5 for the three basins. Numbers inside circles indicate the number of taxa in the basin. First column displays the number of common taxa between two basins (edge) and between the three basins (number in the center of each graph). Second column displays the diachronism (arrows) and synchronism (edges) of FOs. Third column displays the diachronism and synchronism of LOs. Shaded circles indicate that the zone is not identified in the basin. No consistent preferred orientation emerges between the three basins, be it for the FOs or for the LOs. The few preferred orientations (bold arrows) are biases resulting either from unidentified zones (Dixoni and Juddii zones in the Vocontian Basin), or from poor faunal records (Jukesbrownei and Guerangeri zones in the Münster Basin) as can be seen in Figure 6.

parent preferential orientation is obviously a bias due to the absence of age-diagnostic, characteristic species or pairs of species of the Dixoni Zone in the Vocontian Basin (see Figure 6). Rocks of potential Dixoni age were deposited in this basin (see Gale 1995), but their faunal content is not rich enough for an *objective* recognition of the Dixoni Zone. The Rhotomagensense Zone (Middle Cenomanian) shows some diachronous FOs in the Vocontian Basin. The Jukesbrownei and Guerangeri zones display a more consistent direction in the diachronism of FOs and LOs converging toward the Münster Basin. Again, these preferential directions are biases generated by gaps in the faunal record of the Münster Basin (see Figure 6).

As shown in Figure 9, no recurrent and consistent oriented pattern emerges between the three basins, be it for the FOs or for the LOs. The few cases showing a preferential orientation are all coincident with poor faunal records as discussed above. In all other cases, diachronism is always weak and more or less uniformly distributed over the three basins. Therefore, the absence of preferential paleobiogeographical orientation in diachronism suggests that none of the three basins may have functioned as a source or as a sink for possible protracted migrations or shifts in environmental gradients influencing the distributions in space and time. A random distribution of gaps in the faunal record, or reciprocal and permanent exchanges suggesting a common paleobiogeographical history are both likely, non-mutually exclusive explanations. However, it is worth noting that UA-zone 27, i.e. the „unnamed zone“ of the Late Cenomanian, has Tethyan affinities as indicated by the occurrence of vascoceratids, which contrasts with the general Boreal composition of the Cenomanian ammonoid faunas of Western Europe dominated by acanthoceratids. Even with the improved time resolution, the northward migration of taxa of Tethyan affinities (*Vascoceras*, *Nigericeras*) seems to have proceeded at a rather high pace over the three studied basins. The fauna of UA27 indicates a significant paleobiogeographical change preceding the C/T boundary. The same pattern of northward migration of low-latitude taxa has also been documented in the Western Interior, although it seems to have occurred somewhat earlier than in Western Europe (Cobban 1993). From the C/T boundary on, recurrent Tethyan influences are known during the Early Turonian (e.g. *Choffaticeras*) in Western Europe (Thomel 1992).

7. Conclusions

From a taxonomically standardized data set including over 100 species, the biochronological analysis of the Cenomanian ammonoid faunas of the Münster, Anglo-Paris, and Vocontian basins of Western Europe yields 24 UA-zones, which leads to a three-fold increase of the resolution in comparison with the 8 zones of the standard scale (Wright & Kennedy 1984). This refined UA scale is summarized in Figure 5, which exactly and fully accounts for all observed and deduced co-occurrences, the species content of each UA-zone being clearly and com-

pletely defined. The validity of these UA-zones is demonstrated by the absence of any contradiction with the raw data set (no omission of any documented association). The separation intervals formerly established between the standard zones are also in good agreement with separation intervals between UA-zones or unions of UA-zones. This study also demonstrates the benefits of applying the UAM even to a taxonomic group which is traditionally acknowledged as one of the leading group in dating Mesozoic marine rocks.

The inter-basin UA-zonation is particularly efficient in uncovering the faunal gaps and varying resolutions between the three basins (Fig. 6). It provides a direct and objective image of the state of the correlations between the basins, based on currently available data. Were these to change, the UA-zonation and correlations would easily be amenable to further updating. It also emphasizes the diachronism of many ammonoid taxa, indexes being no exception. Diachronism is demonstrated to uniformly affect FOs and LOs, to be positively correlated with the longevity of taxa, and to show no preferred geographical orientations between the three basins. The few cases suggesting a preferred orientation of diachronism are biases generated by marked differences in the completeness of the record between the basins. The only robust biogeographical pattern that emerges is the sudden migration of Tethyan taxa at the close of the Cenomanian.

Acknowledgments

An earlier version of this work benefited from comments and suggestions from Neil Landman. Reviews by Jean Guex, Fabrizio Cecca and Jürgen Remane also significantly improved the final version of the manuscript.

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Manuscript received September 3, 2001

Revision accepted February 16, 2002

Appendix 1 – Standardized data sets

Data set used for the construction of the unitary associations.

Data set reads as follow section ALTENBEKEN; 4 fossiliferous levels or beds; taxa 002 ranges from level 4 to level 4; taxa 003 ranges from level 2 to level 3; etc. See Fig. 5 for numerical codes of species.

Münster Basin

SECTION ALTENBEKEN bottom 1 top 4 002 4 4 003 2 3 023 3 3 075 4 4 112 1 1 310 2 3 332 2 2 360 2 3 442 2 3 464 2 3 480 2 3 531 2 3 532 2 3
SECTION AHAUSWULLEN bottom 1 top 1 580 1 1
SECTION BIELEFELD bottom 1 top 2 700 1 1 740 2 2
SECTION BUREN bottom 1 top 2 323 2 2 580 2 2 360 1 1 156 1 1
SECTION DORTMUND bottom 1 top 1 360 1 1 516 1 1
SECTION ESSENBERGEBORBECK bottom 1 top 1 011 1 1 114 1 1 321 1 1 360 1 1
SECTION ESSENDELLWIG bottom 1 top 3 110 1 1 112 3 3 321 2 2 360 2 2 511 2 2 516 2 2 532 3 3
SECTION HALLEASCHELOH bottom 1 top 2 112 2 2 114 1 2 117 2 2 355 2 2 360 1 2 480 2 2 506 2 2 511 2 2 516 2 2 540 2 2 541 1 1 543 1 2
SECTION HALLEHESELTA bottom 1 top 7 002 4 4 003 3 3 023 3 3 072 5 5 112 1 2 175 2 2 220 6 6 310 3 3 323 7 7 360 1 3 440 6 6 442 3 3 464 3 3 480 1 3 531 3 3 532 3 3 580 7 7
SECTION HALLEKUNSEBECK bottom 1 top 5 003 5 5 010 3 3 011 3 3 023 4 4 5 112 3 3 114 1 1 117 1 1 174 5 5 175 3 3 310 5 5 321 1 5 355 1 3 360 1 5 380 3 3 442 1 5 464 4 5 480 1 5 490 5 5 527 2 2 531 5 5 532 1 5 537 3 3 543 2 2
SECTION HORNBADMEINBERG bottom 1 top 1 360 1 1 480 1 1
SECTION HORSTELBIRGTE bottom 1 top 3 010 1 1 011 1 1 110 1 1 112 1 1 114 1 1 321 1 1 355 1 1 360 1 3 380 1 1 442 1 1 464 1 2 480 1 1 532 3 3 537 2 2
SECTION Lengerich bottom 1 top 9 010 1 1 112 1 5 156 7 7 220 8 8 360 1 7 442 4 4 464 2 2 490 1 1 531 6 6 532 5 6 537 3 3 541 1 1 580 8 8 700 9 9
SECTION LICHTENAUATTEL bottom 1 top 2 069 1 1 323 2 2
SECTION RHEINEDUTUM bottom 1 top 4 002 4 4 003 2 3 075 4 4 310 1 2 321 3 3 480 1 4 531 1 1
SECTION RHEINWALDHUGEL bottom 1 top 8 002 7 7 003 5 6 011 4 4 023 5 5 075 7 7 114 1 1 117 1 1 220 8 8 310 4 7 316 2 2 321 1 6 360 1 2 442 1 6 464 6 6 480 6 8 490 1 6 492 1 1 527 6 6 531 5 6 532 4 6 539 6 6 541 1 1
SECTION IBENBUREN bottom 1 top 6 002 4 4 003 1 1 075 4 4 310 3 3 360 1 5 464 2 2 480 3 3 492 2 2 531 1 1 580 6 6
SECTION WETTRINGEN bottom 1 top 3 002 2 3 003 1 1 075 2 2 310 1 3 360 1 1 442 1 2 480 1 3 531 1 1
SECTION WUNNENBERG bottom 1 top 1 114 1 1 360 1 1 480 1 1 516 1 1

Anglo-Paris Basin

SECTION ANGLNORM bottom 1 top 24 002 13 15 003 8 14 005 9 10 050 22 23 063 14 19 066 8 12 067 16 17 069 17 17 072 16 22 075 14 17 110 2 7 112 5 7 114 2 7 117 2 3 131 9 10 146 2 3 156 16 17 170 2 7 171 7 10 180 1 1 190 24 24 220 18 22 351 2 2 354 2 3 355 2 6 360 2 17 440 8 17 442 7 11 480 8 10 481 21 23 530 10 12 531 6 12 543 2 3 660 2 3
SECTION BOULONNAIS bottom 1 top 31 002 17 19 003 12 18 020 13 14 023 13 15 050 25 25 061 15 19 072 21 24 110 1 9 111 4 5 112 10 10 114 1 9 116 7 10 117 3 9 120 1 4 146 1 2 170 9 9 174 6 6 190 28 31 200 30 30 210 29 31 220 23 24 250 28 31 310 5 22 323 24 24 330 28 31 354 1 6 355 3 8 360 1 19 440 7 22 442 7 17 466 3 4 480 14 14 481 24 25 483 27 27 484 2 2 490 14 14 506 3 6 530 15 15 531 12 15 532 10 18 540 1 8 541 1 9 543 1 8 660 1 4
SECTION SARTHENW bottom 1 top 33 011 29 33 110 13 30 111 21 30 112 31 33 114 13 30 116 9 21 117 5 30 120 10 30 146 7 12 170 23 33 171 31 33 180 1 1 344 26 30 351 19 23 352 19 23 354 6 32 355 8 30 360 4 33 442 30 33 470 3 11 511 21 24 532 31 33 537 28 31 543 19 26 660 10 15
SECTION SARTHESE bottom 1 top 21 110 5 16 111 8 16 112 19 21 114 5 21 116 5 12 117 5 18 120 5 16 146 5 12 170 20 21 172 11 15 180 1 1 310 2 21 352 16 17 354 11 20 355 16 17 360 2 21 442 20 21 470 8 12 471 3 12 506 3 13 531 20 21 532 20 21 540 5 7 541 3 5 543 11 15 660 4 6
SECTION SARTHEMS bottom 1 top 21 002 7 11 003 1 7 011 1 1 020 1 2 023 1 2 050 18 19 061 5 11 063 7 9 066 1 9 067 15 17 069 16 16 072 13 19 075 10 11 088 16 16 100 16 16 105 19 19 131 7 11 156 16 17 170 1 8 171 1 13 220 18 19 294 20 20 310 1 7 360 1 8 440 5 9 442 1 8 464 6 8 480 1 7 481 18 19 490 3 7 530 1 7 531 1 8 532 1 2 700 21 21 780 1 19

SECTION AUBE bottom 1 top 10 050 4 5 072 1 1 105 3 4 151 6 6 190 10 10 220 2 4 230 8 8 260 9 9 330 9 10 440 7 7 483 6 7 490 6 7 700 6 7 720 7 7
SECTION DEVONSW bottom 1 top 10 002 1 1 032 6 6 050 4 4 052 2 2 072 2 2 131 2 2 151 7 7 190 10 10 210 10 10 220 3 5 230 8 8 231 8 8 233 8 8 240 7 7 242 6 7 250 9 9 260 9 9 283 7 7 310 9 9 326 6 6 330 10 10 360 2 2 440 2 2 483 7 7 700 7 7 702 7 7 710 6 6 740 7 7
SECTION ENGLANDSE bottom 1 top 12 050 8 9 072 1 4 092 1 1 105 6 6 131 1 1 190 12 12 220 2 8 230 11 11 294 4 4 323 3 4 326 3 4 440 4 4 481 5 9 483 10 10 490 9 9

Vocontian Basin

SECTION FOUX bottom 1 top 27 001 9 9 003 4 7 020 6 6 030 19 19 050 17 17 060 13 13 063 8 12 065 7 7 066 5 8 067 8 11 069 8 15 072 15 16 075 5 5 092 8 11 100 11 14 103 14 14 117 2 2 156 12 16 170 7 9 172 2 2 180 1 1 190 23 27 200 23 24 210 24 24 220 16 16 230 20 20 231 20 20 240 25 25 250 24 24 260 23 23 261 22 22 270 24 24 281 26 26 290 19 19 291 19 19 292 23 23 300 19 19 310 20 21 355 2 2 360 3 13 370 24 24 440 6 6 450 16 16 480 6 16 481 16 18 530 6 7 531 6 7
SECTION VERGONS bottom 1 top 19 001 14 14 003 13 14 040 18 18 061 11 14 080 12 12 111 7 9 112 9 9 116 7 9 117 5 7 310 14 19 321 10 14 330 17 17 355 9 9 360 5 15 380 2 13 390 13 13 400 13 13 401 13 14 420 2 2 430 13 14 431 2 2 432 2 5 440 14 14 442 10 14 470 6 6 471 4 6 480 13 16 490 13 13 512 1 1 521 2 3 531 12 14
SECTION PAILLE bottom 1 top 19 003 5 11 011 10 18 061 6 7 063 8 14 064 19 19 066 7 13 069 19 19 090 19 19 091 19 19 102 19 19 114 4 4 117 3 3 131 15 18 156 19 19 180 1 1 310 10 14 321 2 16 355 4 4 360 4 11 440 11 17 462 5 5 480 6 11 490 4 4 510 1 1 530 12 13 531 5 11 540 4 4
SECTION PALUD bottom 1 top 12 002 6 6 003 4 6 020 6 6 061 6 6 064 9 10 066 6 7 069 6 6 070 6 6 072 10 11 102 9 9 112 3 3 114 2 2 116 2 2 156 10 10 151 12 12 310 8 8 360 2 5 440 6 6 531 4 6
SECTION BOURGUET bottom 1 top 7 002 5 5 003 5 5 011 6 6 020 5 5 066 6 6 114 4 4 116 3 3 290 7 7 360 5 5 460 2 2 461 1 1 531 5 5
SECTION CONSEGUD bottom 1 top 9 003 7 7 020 7 7 066 8 8 072 9 9 080 7 7 110 4 6 111 4 4 114 5 6 116 1 1 351 1 5 352 4 5 354 1 6 355 5 6 360 5 7 442 5 6 462 5 6 480 5 6 511 1 6 530 8 8 531 7 7 541 5 5
SECTION TOURETTE bottom 1 top 9 003 4 4 020 4 4 066 6 6 110 1 2 111 1 1 114 1 2 116 1 1 131 5 5 146 1 2 190 9 9 220 7 7 250 9 9 310 8 8 330 9 9 355 1 2 360 1 4 440 3 3 480 3 4 511 1 2 531 3 4
SECTION PUGET_RO bottom 1 top 4 003 4 4 020 4 4 111 3 3 162 1 1 321 1 1 360 3 4 380 1 1 420 2 2 432 2 2 442 4 4 510 2 2 531 4 4
SECTION MORIEZ bottom 1 top 7 001 6 7 061 5 5 111 1 1 116 2 2 310 7 7 321 3 5 360 1 5 380 5 5 381 5 5 400 5 5 401 5 5 430 4 5 432 3 3 442 4 5 480 5 7 490 5 5 531 5 5
SECTION VILHOSC bottom 1 top 9 003 3 5 072 8 8 111 2 2 114 2 2 116 2 2 180 1 1 310 5 5 340 7 7 355 2 2 360 2 5 511 2 2 540 2 2
SECTION HYGES bottom 1 top 5 061 5 5 114 4 4 321 5 5 360 4 5 380 2 3 382 1 1 390 2 3 401 5 5 420 2 3 430 5 5 431 1 1 442 5 5 480 5 5 531 5 5 535 3 3 536 3 3 560 1 1 570 1 1
SECTION PENNE bottom 1 top 12 003 5 7 020 6 6 050 12 12 066 10 10 092 11 11 111 2 2 114 3 3 116 3 3 310 7 7 321 7 7 360 1 9 440 10 11 442 7 10 462 7 7 480 8 8 531 6 9 532 6 6 540 3 3
SECTION RIGAUD bottom 1 top 5 111 3 5 114 5 5 116 4 4 117 3 3 127 4 4 321 3 3 380 3 3 420 3 3 432 3 3 460 1 1 510 2 2 570 3 3
SECTION BRAUS bottom 1 top 10 003 6 6 020 6 6 063 10 10 064 10 10 114 1 1 116 1 1 131 9 9 321 2 2 360 2 7 440 6 6 442 5 5 490 4 4 530 8 8 531 5 6 532 3 3
SECTION BEYNES bottom 1 top 7 001 6 7 002 5 7 061 7 7 066 7 7 075 5 5 076 7 7 112 1 1 114 2 2 440 4 5 531 3 5 532 2 2
SECTION TRIGANCE bottom 1 top 5 003 3 3 067 4 4 112 1 1 291 5 5 321 2 2 360 2 2
SECTION TARTONNE bottom 1 top 7 061 7 7 117 3 3 146 4 4 321 4 7 360 2 7 380 1 5 401 7 7 420 1 5 431 1 1 480 6 6 531 7 7
SECTION AUTARET bottom 1 top 5 003 4 4 092 5 5 114 3 3 117 2 2 360 1 4 541 2 2
SECTION MUJOUIS bottom 1 top 11 003 9 10 020 10 10 061 10 10 066 10 10 075 10 10 102 11 11 111 3 6 114 6 6 117 6 6 156 11 11 170 9 9 351 3 3 352 6 6 354 3 3 355 6 7 360 2 10 480 3 10 510 1 1 511 6 6 531 9 10

SECTION BARGEME2 bottom 1 top 3 020 1 1 066 1 1 067 2 2 072 3 3
SECTION MURE bottom 1 top 9 001 8 8 003 7 7 061 6 7 116 2 2 117 2 2 310 6
8 321 7 7 360 2 7 380 1 7 401 7 7 420 1 4 430 7 7 442 7 7 462 7 7 480 2 9 490
7 7 531 7 7
SECTION ROUDOULE bottom 1 top 4 020 4 4 111 3 3 420 2 2 432 2 2 460 1 1
510 2 2 531 4 4
SECTION ABADIE bottom 1 top 6 066 1 1 190 4 4 250 2 3 330 5 5 590 6 6
SECTION SAUSSES bottom 1 top 10 002 6 6 003 7 7 020 6 6 114 4 4 117 2 2
156 10 10 310 5 5 355 3 4 360 3 4 460 1 1 530 7 7
SECTION BOURRAS bottom 1 top 3 072 3 3 160 2 2 321 2 2 570 1 1 600 1 1
610 1 1 620 1 1
SECTION PEYROULE bottom 1 top 5 003 3 4 117 2 2 342 5 5 531 4 4 541 1 1
SECTION COURSEGO bottom 1 top 5 003 4 4 066 5 5 116 2 2 117 1 1 360 2 4
531 4 4
SECTION CAUSSOL2 bottom 1 top 10 002 6 7 003 5 6 011 6 6 020 6 6 065 6 7
066 6 7 073 6 6 076 6 6 100 9 9 114 2 4 171 6 6 220 10 10 321 6 6 360 4 4 531
6 6 532 3 3 541 2 3
SECTION MONTFORT bottom 1 top 5 003 2 3 442 3 3 480 4 4 531 1 4
SECTION ANGLES bottom 1 top 8 001 6 7 061 5 6 116 2 2 321 5 5 360 1 7 380
5 5 401 4 5 430 6 6 442 5 5 480 7 7 490 7 7 531 5 7 532 6 6
SECTION SALLAGRI bottom 1 top 4 003 3 3 066 4 4 114 1 1 116 1 1 117 1 1
310 2 2 354 2 2 355 1 1 360 1 4 440 4 4 530 4 4 531 3 3
SECTION DURANUS bottom 1 top 3 111 3 3 117 1 1 360 2 3 480 2 2 541 2 2
SECTION ST_LIONS bottom 1 top 8 001 3 5 003 3 3 020 3 3 061 2 3 080 3 3
310 7 8 321 2 3 360 2 3 380 3 3 390 3 3 400 3 3 401 3 3 430 3 3 431 3 3 442 2
3 462 3 3 464 3 3 480 3 3 490 3 3 531 3 3
SECTION ST_LEGER bottom 1 top 3 360 3 3 380 1 2 460 1 1 510 2 2 570 2 2
SECTION PEILLON bottom 1 top 3 003 3 3 341 2 2 360 1 3 480 1 1 531 2 2
SECTION GARS bottom 1 top 5 003 4 5 020 4 4 117 1 2 310 4 4 360 1 4
SECTION FAYE bottom 1 top 4 003 1 1 066 1 1 067 2 2 156 3 3 481 4 4 531 1 1
SECTION BARGEME1 bottom 1 top 5 003 3 4 220 5 5 355 1 1 360 1 1
SECTION RISOU bottom 1 top 17 111 12 14 114 10 17 160 1 6 165 1 6 180 1 1
181 1 9 321 1 17 351 4 8 354 10 16 359 4 5 360 13 17 368 9 9 380 1 14 420 1
17 431 1 14 441 1 5 460 2 7 461 1 2 467 4 8 471 10 15 484 10 16 491 4 5 510 1
8 570 1 14 660 10 17 960 1 1
SECTION GIPIERES bottom 1 top 52 003 51 51 011 51 51 020 51 51 110 38 46
111 33 38 114 32 46 116 38 50 117 33 49 146 46 46 162 7 20 165 15 26 180 4
24 187 24 24 351 10 38 354 38 38 355 13 40 359 13 13 360 30 52 441 9 29 460
10 25 467 14 22 474 1 28 491 6 18 510 26 27 511 38 47 520 5 27 541 35 38

Appendix 2 – Synthesis of the three basins

Section MUNSTER bottom 1 top 17 002 10 10 003 7 9 010 1 5 011 4 6 023 8 8
072 12 12 075 10 10 110 4 4 112 1 5 114 1 4 117 1 3 156 11 11 174 8 8 175 5 5
220 12 14 310 6 10 321 1 9 323 15 15 332 7 7 355 2 5 360 1 11 380 4 5 440 13
13 442 1 10 464 4 9 480 2 12 490 1 9 506 2 2 511 2 4 516 2 4 531 7 9 532 3 9
537 5 5 539 9 9 540 2 2 541 1 1 543 1 3 580 14 15 700 16 16 492 1 7 527 3 9
740 17 17

Section ANGLOPARIS bottom 1 top 30 002 15 18 003 13 18 005 16 16 011 9
13 020 13 13 023 13 14 032 25 25 050 24 24 052 19 19 061 14 18 063 17 22
066 13 17 067 20 21 069 20 21 072 19 24 075 18 20 088 21 21 092 19 19 100
21 21 105 24 24 110 2 12 111 3 9 112 10 12 114 2 12 116 4 11 117 3 9 120 2 9
131 16 19 146 2 5 151 26 26 156 20 21 170 5 17 171 12 19 172 4 4 180 1 1 190
30 30 200 30 30 210 30 30 220 22 24 230 28 28 231 28 28 233 28 28 240 26 26
242 25 26 250 29 30 260 29 29 283 26 26 294 23 24 323 23 23 330 29 30 344 8
9 351 5 6 352 6 6 354 2 12 355 3 10 360 2 20 442 7 17 464 17 17 466 3 3 470 4
4 471 3 4 480 13 17 481 23 24 483 26 27 484 2 2 506 3 4 511 6 6 530 13 17 531
10 17 532 11 15 537 9 12 540 2 7 541 2 7 543 2 8 660 2 5 700 26 27 702 26 26
710 25 25 720 27 27 740 26 26 310 4 29 440 7 27 490 13 27
Section VOCONTIAN bottom 1 top 34 001 12 15 002 13 18 003 12 18 011 17
19 020 12 18 030 28 28 050 27 27 060 22 22 061 12 16 063 17 23 064 23 25
065 17 18 066 13 20 067 20 21 069 14 25 072 25 26 073 18 18 075 13 16 076
15 18 080 12 12 090 24 24 091 24 24 092 19 21 100 21 24 102 24 24 103 24 24
110 7 11 111 5 9 112 9 9 114 5 11 116 7 9 117 6 7 131 19 19 146 7 8 156 22 26
160 1 2 162 2 2 165 1 3 170 16 20 171 18 18 172 6 6 180 1 3 181 1 2 187 3 3
190 31 34 200 31 32 210 32 32 220 26 26 230 29 29 231 29 29 240 33 33 250
32 32 260 31 31 261 30 30 270 32 32 281 34 34 290 28 28 291 28 28 292 31 31
300 28 28 330 32 32 351 2 11 352 7 11 354 5 11 359 2 2 360 5 22 370 32 32
380 1 12 390 8 12 400 12 12 401 12 13 420 18 430 12 13 431 1 12 432 4 7 440
13 19 441 1 3 442 11 14 450 26 26 460 1 3 461 1 1 462 11 12 464 12 12 467 2
2 471 5 6 474 2 3 481 26 27 484 5 5 490 10 12 491 2 2 510 1 4 511 7 11 520 2
3 530 17 17 531 12 18 532 11 12 540 9 10 541 7 11 570 1 6 660 5 5 310 12 33
321 1 19 355 2 11 368 2 2 470 6 6 480 7 26

Appendix 3 – Numerical codes of taxa eliminated during the process

001 *Acanthoceras confusum* (a); 005 *Acanthoceras basseae*; 040 *Romaniceras kalleis* (a); 064 *Calyccoceras besairiei* (a); 065 *Calyccoceras choffati*; 070 *Calyccoceras meridionale* (a); 073 *Calyccoceras nitidum* (a); 080 *Calyccoceras vergonsense*; 088 *Calyccoceras haugi*; 091 *Eucalyccoceras jeanneti* (a); 102 *Pseudocalyccoceras moustieriense* (a); 103 *Pseudocalyccoceras morpheus* (a); 120 *Mantelliceras lymense*; 127 *Mantelliceras crassecostatum* (a); 174 *Forbesiceras chevillei* (f); 175 *Forbesiceras baylissi* (f); 316 *Epipuzosia europaea* (f); 326 *Puzosia odiensis*; 332 *Lewesiceras wiedmanni* (f); 340 *Neolobites vibrayeanus* (a); 341 *Neolobites fourteau* (a); 342 *Neolobites medininensis* (a); 344 *Neolobites bedoti* (h); 381 *Phylloceras velledae* (a); 382 *Phylloceras subalpinum* (a); 390 *Phyllopachyceras whiteavesi* (a); 400 *Gaudryceras cenomanense* (a); 401 *Gaudryceras leptonema* (a); 430 *Tetragonites subtimotheanus* (a); 431 *Tetragonites rectangularis* (a); 450 *Worthoceras vermiculum* (a); 462 *Anisoceras saussureanum* (a); 466 *Anisoceras auberti* (i); 492 *Hamites duplicatus* (f); 506 *Mariella dorsetense + lewesiense*; 512 *Mariella quadrituberculatus* (a); 516 *Mariella essenensis* (f); 521 *Ostlingoceras puzosiforme* (a); 527 *Ostlingoceras collignoni* (f); 535 *Turrilites gresslyi* (a); 536 *Turrilites oehlerti* (a); 539 *Mesoturrilites serpuliforme* (f); 560 *Kosmatella mühlenbecki* (a); 590 *Glyptoxoceras indicum* (a); 600 *Beudanticeras beudanti* (a); 610 *Lyelliceras lyelli* (a); 620 *Douvilleiceras mamillatum* (a); 720 *Puebloites spiralis*; 780 *Metengonoceras dumbli* (h); 960 *Turrilitoides hugardianus* (g)

