

Chapter 11

Ammonoids and Quantitative Biochronology—A Unitary Association Perspective

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11.1 Introduction

Biochronology is the branch of paleontology and stratigraphy, which assigns relative ages to rock strata by exploiting the time component embedded in the fossil record (biostratigraphy is a more commonly used term, but it applies to the study of the fossil content of the sedimentary rocks in general and not necessarily to its time component; Guex 1979, 1991; Gradstein 2012). Biochronology has profound implications not only for reconstructing past geological events but also for constraining phylogenetic hypotheses. It is one of the fundamental cornerstones of Geology and the Evolution of Life. Indeed, no matter what aspect of Geology one is working on, the most common question asked by geologists is “*what age is it?*”? Biochronology and geochronology provide the framework for answering this question.

William Smith (1769–1839) and Alexandre Brongniart (1770–1847) were the first to formulate the principle of faunal successions based on the observation that sedimentary strata contain fossilized organisms, and that these fossils succeed each other vertically in a particular, reliable order that can be recognized over wide geographic distances. Leopold von Buch (1774–1853) coined the term “*index fossils*”, and, in 1856, Albert Oppel first introduced the concept of biozone based on time intervals defined by the overlapping ranges of fossil species independently of the rock

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C. Klug et al. (eds.), *Ammonoid Paleobiology: From macroevolution to paleogeography*, Topics in Geobiology 44, DOI 10.1007/978-94-017-9633-0_11

or facies, in which they are found. Opper zones were a fundamental breakthrough in that they first made the distinction between lithological units (which can be diachronous) and biozones (which each represent a unique time interval). Biochronology is thus one of the founding fields within Geology and Biology and as illustrated by Opper's own work, ammonoids played a leading role in this field since its inception. The crucial role of the tandem ammonoid/biochronology is exemplified by the cornerstone contribution of Alcide d'Orbigny (1802–1857), who defined most Mesozoic stages based mainly on ammonoids. He also was the first to precisely identify species characteristics with the purpose of using them to define stratigraphic stages. Because of their high evolutionary rates, broad paleogeographic distributions, and frequent preservation in marine deposits, ammonoids are one of the prime fossil groups for dating Paleozoic and Mesozoic marine strata (e.g., House 1985).

Most biostratigraphers have resisted, stubbornly the use of numerical methods and the construction of biochronological time scales has sometimes been perceived as an “*art*” by some scientists who were distant from the field (Brower 1982). Part of such a simplistic image may arise from various sources of noise. This is probably caused by the fact that many quantitative methods are rather complex and utilize methodologies that are basically foreign to biostratigraphers. The identification of species is obviously another major source of errors. As far as ammonoids are concerned, the initial typological approach has now been largely replaced by a dynamical approach, which integrates ontogenetic and inter-individual variation (see the precursory work of Silberling 1956 for such a “*biological*” approach). This purely taxonomic and systematic aspect is not the focus of this chapter and is addressed in other chapters of this volume (De Baets et al. 2015; Monnet et al. 2015). Another source of errors focuses directly on the intrinsic properties of the utilized biochronological approaches. These cover the whole spectrum from probabilistic to deterministic treatments depending on the various perceptions of the nature of the fossil record. A critical overview of these methods is the central topic of this chapter.

Some ammonoid biostratigraphers still use interval zones, whose bases are defined by the first appearance datum (FAD) of index species. However, the fossil record cannot be read at its face value. First, only a small fraction of organisms become fossilized. Second, sedimentary successions do not necessarily faithfully reflect the true relative order of evolutionary events (origination = First Appearance Datum/FAD; extinction = Last Appearance Datum/LAD) through time because of a whole array of primary and secondary causes that may blur their actual succession (e.g., ecological exclusions, selective preservation, sedimentary gap or reworking, taxonomic vagaries, sampling effort, amount of available exposures, etc.). For example, see studies on range offset and simulation of fossil occurrences among sections within a basin (Holland 2000, 2003; Holland and Patzkowsky 2002). Therefore, both first and last local occurrences of a taxon (FOs, LOs) in the rock record may result from a wealth of causes other than true evolutionary speciation or extinction (i.e. FADs, LADs). Finally, in most cases, the confusion or amalgamation between a local first occurrence (FO) and a FAD, or a local last appearance (LO) and a LAD, derives from the deeply entrenched practice of arbitrary segmentation of supposed anagenetic lineages assumed to have evolved gradually. Last but not

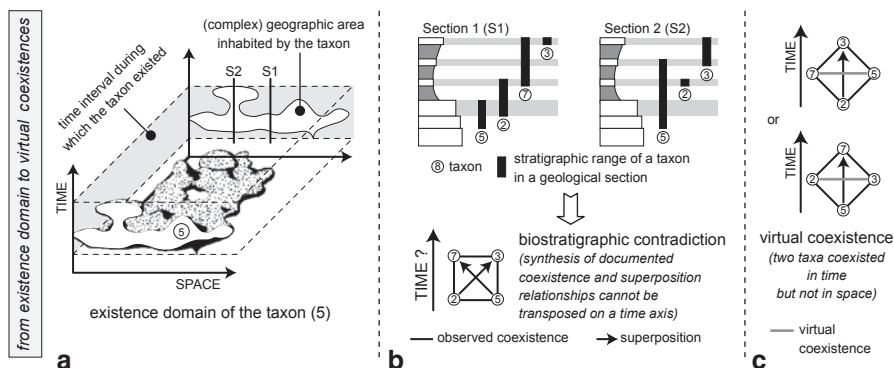


Fig. 11.1 Notions of existence domain (a), biostratigraphic contradiction (b), and virtual coexistence (c). See text for details

least, in the very exceptional situation where a FO or a LO may be demonstrated to match exactly a FAD or a LAD, respectively, speciation and extinction remain intrinsically restricted biological processes in space, thus complicating the use of evolutionary datum for constructing synchronous time lines across long distances. The theoretical applicability of any evolutionary datum is strictly restricted to the area where speciation or extinction took place. The practical applicability of evolutionary datum has thus limitations depending on the properties of the studied group (e.g., evolutionary rates, preservation states) and of the record (information degraded by the vagaries of the record and sampling efforts). Some will argue that the dispersion of a peculiar new species (e.g., planktonic foraminifers, conodonts, ammonoids) is geologically instantaneous, but unless this can be tested by means of an independent and truly isochronous time marker, such a statement will remain an *ad hoc* and circular statement. Interval zones, grade-datation and Global Boundary Stratotype Section and Point (GSSPs) are all based on the use of such FADs. The effects of all these parameters that generate conflicting stratigraphic positions between taxa across several sections are the so-called biostratigraphic contradictions (Fig. 11.1). Indeed, each taxon is characterized by a very irregular and complex paleogeographic distribution in space, which is in turn altered through time (Fig. 11.1a). Since biostratigraphic data are obtained from a necessarily finite number of sections, they represent only a small fraction of the true distribution in time and space of the studied taxa. Because of all these factors that degrade the true time and space distribution of species, real data usually contain contradictions, i.e. inconsistent superposition relationships between FOs and LOs, which make it impossible to obtain a unique order of species ranges along the time axis (Fig. 11.1b). Some of those biostratigraphic contradictions may result from virtual coexistences, i.e. species that actually coexisted in time but not in space (Fig. 11.1c).

With increasing size of biostratigraphic datasets including larger numbers of taxa and sections, the number of contradictions usually grows exponentially. In such cases, computerization has facilitated the development in biochronology of

different quantitative methods welcomed by industrial requirements (Simmons and Lowe 1996). Over the last decades, quantitative biochronology has seen a consolidation of methods and a better understanding of their advantages and limitations has emerged. These methods are robust and allow resolving the numerous problems encountered in dating and correlating fossiliferous strata, be it at a global scale, across different basins, within a single basin, or within an oil field. This chapter aims to give an overview of some of these methods and their applications to ammonoids.

11.2 Quantitative Biochronological Methods

The construction of robust and highly resolved biozonations is a necessary prerequisite both in academic and in oil and mining studies using fossils for dating and correlating sections. In addition to these direct applications, such biozonations are also of primary importance for reconstructing changes of taxonomic diversity in time and space, especially in relation with mass extinctions and recoveries (e.g., Brayard et al. 2009b; Brühwiler et al. 2010). To achieve these goals of accuracy and precision, a number of quantitative biochronological methods have been developed during the last decades (Hay and Southam 1978; Guex 1979; Cubitt and Reyment 1982; Gradstein et al. 1985; Boulard 1993; Sadler 2004; Gradstein 2012). All these methods utilize strict and well-defined algorithms that allow not only the processing of large datasets but also to test the reliability of the underlying methods with sets of either real or simulated data of different quality. Some methods will always produce results whatever the quality of the data, some others will not as soon as a certain threshold in the decreasing quality (i.e. number of contradictions) of the dataset is reached. Computerized methods ensure a rigorous, exhaustive, and consistent treatment of the biostratigraphic data. They often produce better-resolved biozonations than empirical studies (Boulard 1993; Monnet and Bucher 2002; Sadler 2004). However, these quantitative methods often lead to partly different results (Baumgartner 1984; Agterberg 1985; Boulard 1993; Galster et al. 2010; Monnet et al. 2011). Such divergences are expected since these methods are based on different types of available biostratigraphic data (e.g., coexistence vs. apparition/extinction of taxa), on different theoretical assumptions and practical algorithms (e.g., probabilistic vs. deterministic approaches) in how to resolve the biostratigraphic contradictions, and on the expected types of results (e.g., continuous vs. discrete biozonations).

Among the existing quantitative biochronological methods the three most popular are Ranking and Scaling (RASC), Constrained Optimization (CONOP), and Unitary Associations (UAs). All these methods have computer softwares either separately or altogether (but often with less options) in the widely used free software of paleontological data analysis PAST (Hammer et al. 2001; <http://folk.uio.no/ohammer/past/>). These methods use different approaches and data (see below) and consequently their results often diverge (Galster et al. 2010; Monnet et al. 2011). Therefore, the biostratigrapher doing a quantitative biochronological analysis must make a choice based on his/her data and expectations in agreement with

the advantages and constraints of each method (compare Gradstein 2012). The main properties of these three methods are briefly outlined below.

RASC (Agterberg and Nel 1982a, b; Agterberg and Gradstein 1999) is a probabilistic approach based on the distances among bioevents of taxa (i.e. their First Occurrence and Last Occurrence) along wells or sections to correlate. Basically, the method first (“*ranking*”) produces a single, comprehensive ordering of bioevents, even if the data contains contradictions or longer cycles. This sequence of bioevents is constructed by following a “*majority rule*” (frequency), counting the number of times each event occurs above, below or together with all others. Then (“*scaling*”), it estimates the most probable stratigraphic distances between the consecutive bioevents by counting the number of observed superpositional relationships between each pair of consecutive events. This method resulted from a pragmatic approach to biostratigraphy in oil industry, which developed biozonation schemes that, rather than using classical bioevents, use local acme events and slight changes in assemblage characteristics to develop high resolution biozonations. These are essentially of local (i.e. field-wide) significance and are efficient in this context. This method has thus been commonly used in oil industry. It enables correlation of geographically closely related sections, and assigns the most probable age of studied stratigraphic levels. RASC has excellent graphic outputs, is optimal for large datasets with many fossil events, and handles noise (e.g., outliers and missing data) relatively well. One downside of the method may be that it may shorten the range of taxa and lead to dissociate actually coexisting taxa (Baumgartner 1984; Boulard 1993). Example applications can be found in Gradstein et al. (1999), among others.

CONOP (Kemple et al. 1989, 1995; Sadler and Cooper 2003; Sheets et al. 2012) is partly derived from the empirical Graphic Correlation method (Shaw 1964; Edwards 1989; Carney and Pierce 1995; Zhang and Plotnick 2006). It can be viewed as a multidimensional piecewise linear correlation of the position of bioevents along sections to correlate. Using the so-called Simulated Annealing method, CONOP searches for a global (composite) ordered sequence of events that implies a minimal total amount of range extension (penalty) in the individual sections. This method is efficient, robust, and good in handling and evaluating ranges of studied taxa. It can be used to directly correlate studied sections and evaluate changes in sedimentation rates. Its major constraints are long computation time with some parameters not easily tuned and it may also artificially lengthen the range of taxa, thus generating false coexistences as graphic correlations already did (Galster et al. 2010; Monnet et al. 2011). Example applications can be found in Cuartas et al. (2006) and Cody et al. (2008), among others.

UA (Guex 1977, 1991) is a deterministic approach based on the observed coexistences of studied taxa (and not their bioevents). It takes advantage of the fact that the intrinsic nature of biostratigraphic data (associations, superpositions, unknown relations) is identical with the kind of data processed by the mathematical graph theory founded by Euler (1741). This approach resolves the biostratigraphic contradictions by inferring virtual associations. A virtual association is defined as the coexistence of taxa in time, but not in space (Fig. 11.1). The biozonations constructed by means of the UAs are consequently composed by an ordered sequence of discrete units (the UAs), which are unique maximal sets of coexisting (really or

virtually) taxa. This method has several advantages, which are discussed below. The major challenging requirement of the UAs is that it forces the biostratigrapher to think in four dimensions (space and time) instead of the usual one dimension of a section or a time axis. It is less intuitive for biostratigraphers used to work with continuous scales such as interval zones (as stimulated by stage boundaries defined on the FAD of index taxa).

A complete review of all available quantitative methods in biostratigraphy is beyond the scope of this study, and the reader is referred to previously cited references for further details and applications. Finally, note that the UAs method stands in sharp contrast to RASC and CONOP (for a recent review, see Gradstein 2012). UAs are based on the co-occurrences of taxa in successive levels, resolve biostratigraphic contradictions by focusing on coexistences and inferring virtual coexistences, and yield discrete biozonations. RASC and CONOP are based on the bioevents of studied taxa spotted on profiles, resolve biostratigraphic contradictions by focusing on the relative range of taxa and by modifying these ranges, and produce continuous biozonations made of interval zones based on the FOs and/or LOs of index taxa.

11.3 The Unitary Associations

Comparing the previously described quantitative methods in biostratigraphy, our preferred choice goes to the UAs. This selection is mainly driven by the theoretical and practical properties of the UAs (e.g., production of discrete bio-zones and preservation of all observed co-occurrences; for more details, see below), by its efficiency as shown by comparative studies (Baumgartner 1984; Boulard 1993; Galster et al. 2010; Monnet et al. 2011), and last but not least, by its panel of supplementary tools enabling critical assessment of the studied dataset (Monnet et al. 2011). Despite an ever increasing number of datasets and the need of higher resolved correlations, there are still a few studies applying these quantitative and robust biochronological methods to ammonoids. This is unfortunate since quantitative stratigraphic approaches produce results with a much higher resolution potential than empirical zonations (Boulard 1993; Monnet and Bucher 1999, 2002, 2007; Sadler 2004; Cody et al. 2008). Even if ammonoids have a long-standing reputation as excellent age biomarkers, ammonoid biozonations can be significantly improved by using these quantitative methods. Among these, it appears that UAs are most commonly used with ammonoids (e.g., Pálffy et al. 1997, 2003; Pálffy and Vörös 1998; Monnet and Bucher 1999, 2002, 2005a, b, 2007; Monnet et al. 2003, 2011; Galfetti et al. 2007a, b; Pálffy 2007; Brühwiler et al. 2010; Guex et al. 2012; Brayard et al. 2013).

11.3.1 History and Properties

The Unitary Associations method was developed by Guex (1977, 1991). It was initially based on the empirical rearrangement of matrices compiling the coexistences

of taxa. It has been then largely expanded with the use of mathematical graph theory (Euler 1741), thus enabling a formal and logical treatment of the biochronological “problem”. The development of personal computers led to the creation of a first software (Guex and Davaud 1984, 1986). Subsequently, the method was improved and associated with new computer software (Savary and Guex 1991, 1999). Finally, it is now replaced by a more robust implementation, which includes new options and improvements, available as a stand-alone software called UA-graph (<http://folk.uio.no/ohammer/uagraph/>) or within the paleontological software package PAST (Hammer et al. 2001). For typical applications with BioGraph, see Guex (1991), Angiolini and Bucher (1999) or Monnet and Bucher (1999), and with UA-graph, see Carter et al. (2010), Galster et al. (2010), Monnet et al. (2011), or Guex et al. (2012).

UAs have several attractive properties, some of which are listed below. It is a quantitative and deterministic method based on the co-occurrences of species in successive stratigraphic levels, which corresponds to the primary state of the fundamentally incomplete fossil record. Accordingly, it produces discrete (discontinuous) biozones in agreement with the nature of the fossil record. It preserves the integrity of the original dataset by preserving in the outputs all raw documented associations of taxa (coexistence in space). It is efficient to resolve complicated biochronological problems produced by taxonomic groups with very different completeness of their fossil record (from marine unicellular organisms like nannoplankton and radiolarians, over marine invertebrates like ammonoids and brachiopods to terrestrial mammals: Boulard 1993; Baumgartner et al. 1995; Angiolini and Bucher 1999; Guex and Martinez 1996; Monnet and Bucher 2002, 2007; Brühwiler et al. 2010; Carter et al. 2010). It usually leads to a significant improvement of biochronological resolution, even in the case of ammonites (Monnet and Bucher 2002, 2007). It allows also an *a posteriori* objective assessment of the diachronism of the studied taxa and the choice of actual characteristic taxa of each zone (compare Pálfy and Vörös 1998; Pálfy 2007). Finally, Escarguel and Bucher (2004) demonstrated that the unknown duration of the discrete UA-based biozones does not introduce a significant bias when using UA-zones as time bins for counts of species richness. Therefore, the UAs are a very powerful method to resolve biochronological problems, to rapidly produce robust zonations, and to assess critically the quality of the dataset. The quality of a dataset relates to the amount of discrepancy in the ranges of species. The longer the ranges of species, the more likely they will be discontinuous, thus generating larger amounts of contradictions. Unlike other methods, UAs will not yield “good looking”—but unreliable—solutions if the dataset is pervaded with contradictions. In such cases, UAs will yield low resolution—but robust—biozones. For instance, Mesozoic radiolarians have an intrinsically low quality record, because they are composed of mostly long ranging species with extremely discontinuous vertical occurrences (Baumgartner et al. 1995). Ammonoids, with their vast majority of short ranging species, provide an opposite example characterized by intrinsically good quality data. There is an unavoidable trade-off between the intrinsic quality of the data and the resolution of the constructed biozones. This obvious trade-off does not exist with other quantitative methods, which will always yield apparently highly resolved solution—but will either fail to recover all real

documented associations or will generate false associations (i.e. neither real, nor virtual). Monnet et al. (2011) recently proposed directions of research for additional tools dedicated to evaluate in more details the results of the method (but see Guex 2011).

11.3.2 Major Principles and Steps of UAs

The method of UAs is logical and comprises a number of steps (Guex 1991; Savary and Guex 1991, 1999). The major principles and steps of the UAs are here illustrated with an imaginary and simple example, based on the occurrences of eight taxa within four sections (Fig. 11.2a). The first step is the construction of the biostratigraphic graph (Fig. 11.2b), which compiles and represents all observed biostratigraphic relationships. Its vertices represent the taxa, its edges represent their association (the range of corresponding taxa overlap), and its arcs represent the superposition between taxa.

The next step is the extraction of all unique maximal sets (a set is maximal if not contained in a larger set; see Guex 1988) of mutually coexisting species, called “*maximal cliques*” (Fig. 11.2c). The example proposed here contains 6 maximal cliques, among which one (“*mc4*”, Fig. 11.2c) includes taxa 3, 5, and 7 that coexist altogether in time (but not necessarily in the same section). Then, the method resolves the superpositional relationships between these maximal cliques by the comparison of documented stratigraphic relationships of taxa in the biostratigraphic graph between each pair of cliques. Usually, conflicting stratigraphic relationships occur between some of the taxa (“*biostratigraphic contradictions*”). For instance, Fig. 11.2d reports one case (top), in which the superpositional relationships between the taxa are congruent (arcs in the same direction) and another one (bottom), in which the relationships are contradictory (arcs of opposed directions). The method solves such conflicting stratigraphic relationships by assuming that one of these contradictory arcs is wrong and is in fact generated by a virtual coexistence (i.e. inter-taxa coexistence that is real in time but not observed physically in the stratigraphic samples). The choice of the supposed badly oriented arc (or set of arcs) follows a “*majority rule*” (Guex 1991, p. 82; Galster et al. 2010, p. 244). This rule counts the number of arcs and their frequency in each direction separately, and then considers the most frequently observed direction as the correct stratigraphic order (Fig. 11.2d). Once all superpositional relationships between the maximal cliques have been resolved, one can construct a graph that exactly represents all these relationships (Fig. 11.2e).

Next, the method extracts the longest sequence (path) of superposed maximal cliques (Fig. 11.2f). Maximal cliques, which do not belong to the longest path, are merged (if possible) with contemporary maximal cliques of the path. Finally, one can transcribe the sequence of maximal cliques into the sequence of Unitary Associations (Fig. 11.2g). A unitary association is thus defined as a maximal set of mutually coexisting species, be it actually or virtually. The sequence of UAs is called

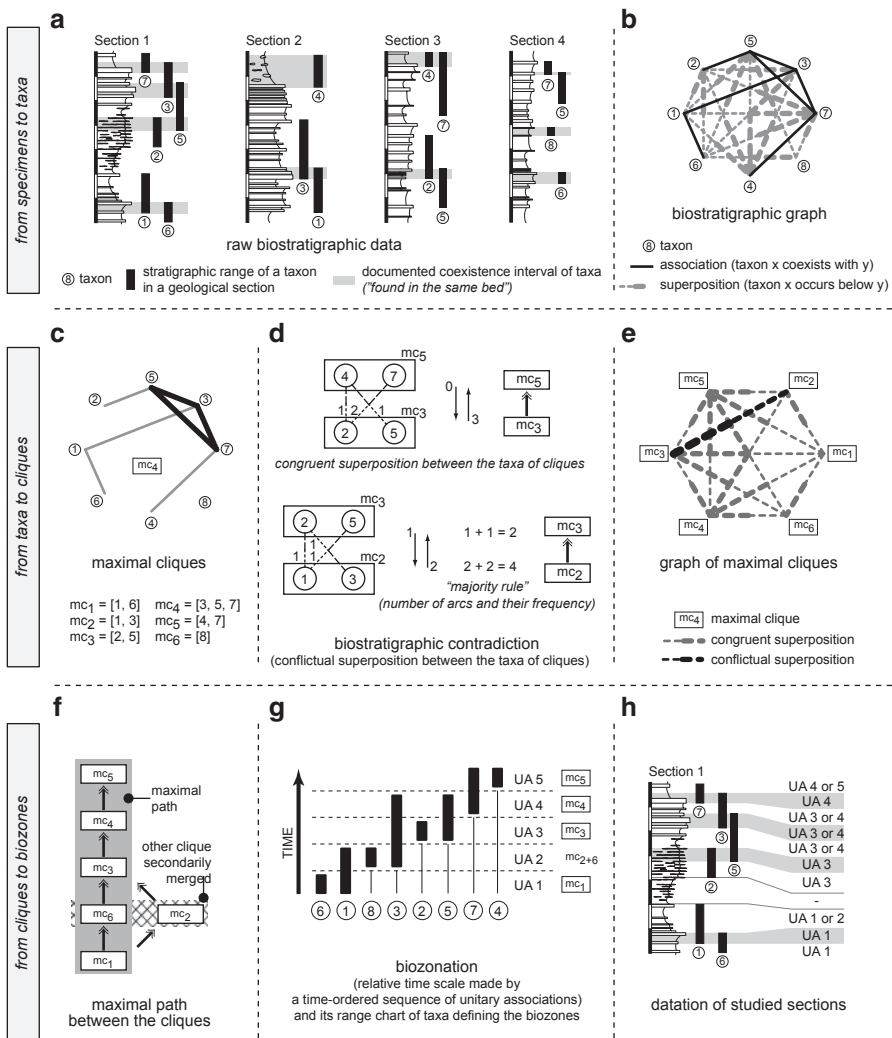


Fig. 11.2 Flow chart of the major analytical steps of the UA method (see text for explanation)

the “*protoreferential*” and along with the reproducibility matrix (a sections vs. UAs matrix), they constitute the zonation used to correlate the fossiliferous content of studied sections (Fig. 11.2h). Note that a strict association zone such as produced by the UAs is characterized either by the taxa occurring only within this zone or by the intersecting ranges of taxa observed within the zone: the FADs and LADs *per se* do not matter.

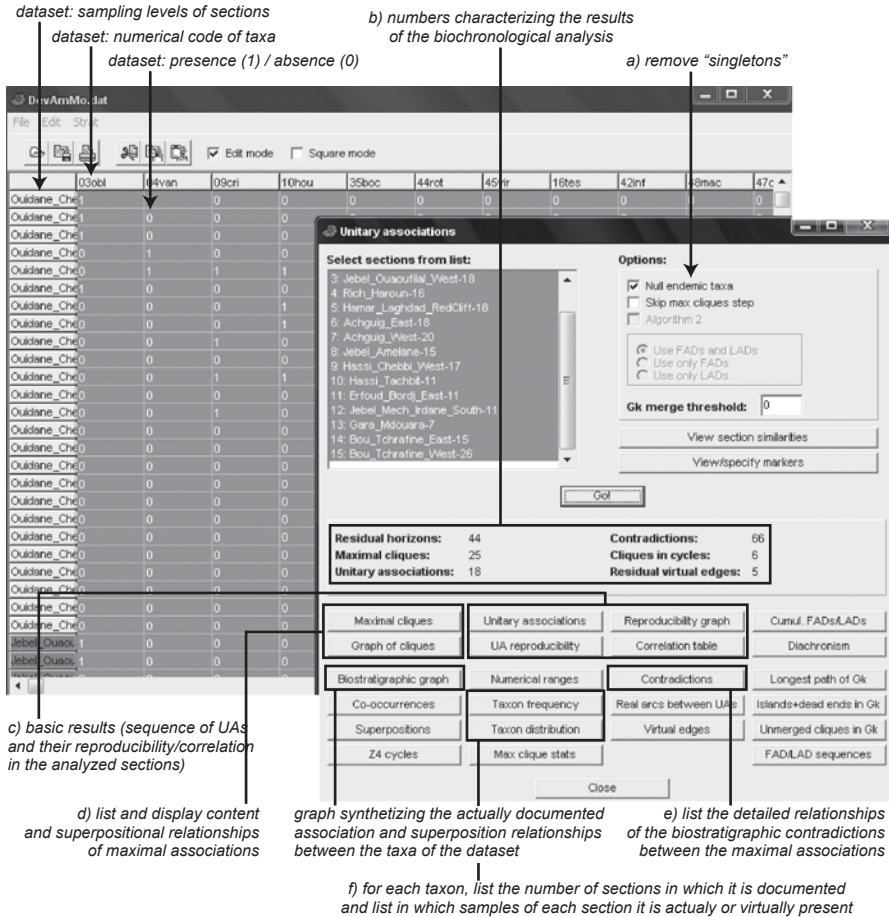


Fig. 11.3 Graphic user interface of UA-graph and tools provided with it (see text for explanation; letters are referred to in the text; after Monnet et al. 2011)

11.3.3 UA Tools and Interface

To perform a quantitative biochronological analysis by means of the UAs, one must use the software UA-graph (<http://folk.uio.no/ohammer/uagraph/>). This software is accompanied by a graphic user interface to ease its use as well as supplementary tools to analyze the dataset and results. Figure 11.3 reports and illustrates the graphic user interface of the software (version 0.28). For a recent and exhaustive application of the method on ammonoids by means of this interface, see Monnet et al. (2011); only the major points are listed here.

The biochronological analysis can be pre-processed with the removal of taxa found in only one section (Fig. 11.3a, "Null endemic taxa"). Such singletons are known to significantly increase the amount of biostratigraphic contradictions while

being of no help for correlation purposes (Boulard 1993; Savary and Guex 1999; Monnet and Bucher 1999). Once the analysis has been computed, the software directly reports some numbers (Fig. 11.3b), which characterize the results and the quality of the dataset (e.g., Boulard 1993; Monnet and Bucher 2002): e.g., the number of constructed UAs (here 18 biozones), the number of biostratigraphic contradictions (66) between the cliques (25), and the number of cliques involved in cycles (6). The major result of the biochronological analysis is a composite range chart representing the succession of the reconstructed discrete maximal sets of mutually coexisting species (UAs; Fig. 11.3c). This sequence synthesizes the association, superposition and exclusion relationships of the ammonoid taxa included in the analysis. This range chart, which thus defines the content of each UA, is complemented by its reproducibility matrix (Fig. 11.3c, “*UA reproducibility*”). It is a UA vs. section matrix, indicating, which UAs are identified in which sections. This enables assessment of the lateral (geographic) reproducibility of each UA, which is also a reflection of the variable completeness of each section and the degree of biogeographic differentiation (and/or the relative importance of facies control, depending on the geographic scale of the study). This set of information is important, because the goal of a biochronological analysis is to construct a zonation for correlations. Note that UA-graph automatically attributes (if possible) a UA or set of UAs to each sample of the dataset based on the resulting range chart produced by the method (Fig. 11.3c, “*Correlation table*”).

One of the major strengths of UAs and of its software UA-graph is the specific accompanying tools for evaluating the quality of the dataset and tracing back the possible origin of the conflicting stratigraphic relationships. For instance, the UA-graph has tools for providing the list of maximal cliques and their taxonomic content (Fig. 11.3d, “*Maximal cliques*”), for showing the relationships between these cliques (Fig. 11.3d, “*Graph of cliques*”), and for providing a complete list of the conflicting inter-taxon relationships (Fig. 11.3e, “*Contradictions*”). These sets of information can help to identify the possible origin of cycles and conflicting biostratigraphic relationships; see Monnet et al. (2011) for a detailed example. Additional information is available such as the number of sections, in which a taxon is documented and where it is present (Fig. 11.3f, “*Taxon frequency*” and “*Taxon distribution*”).

11.4 Example Applications

11.4.1 Early Triassic Ammonoids

About 252 Myr ago at the Permian/Triassic boundary, the Earth witnessed its major mass extinction of marine life of all time (Benton 2005; Shen et al. 2011). More than 90% of marine species disappeared abruptly and the biosphere previously was considered to recover its previous state only after several millions years (Kirchner and

Weil 2000; Erwin 2001). In this context, ammonoids were among the first marine organisms to diversify, with a first diversity peak less than 2 Myr after the Permian/Triassic boundary (Brayard et al. 2009b). However, the Early Triassic biotic recovery was not continuous but experienced several extinction and diversification cycles often associated with other events recorded by the sedimentary, geochemical and palynological records (Galfetti et al. 2007a; Hermann et al. 2011, 2012). Major environmental (in e.g., carbon cycle, ocean acidification, anoxia, productivity, sea-level changes) and climatic changes occurred repeatedly during the Early Triassic. In this context, large-scale ammonoid biodiversity changes are now relatively well documented (Brayard et al. 2009b). Notably, generic richness reached a first peak during the Smithian before collapsing anew at the Smithian/Spathian boundary (Fig. 11.4a). These evolutionary events are interpreted to reflect global climate changes (Brayard et al. 2006; Galfetti et al. 2007b; Romano et al. 2013). However, the long-distance and fine temporal correlation of these various events was hampered by poorly resolved previous biozonations.

To overcome these various biases and evaluate the temporal matching, causes and processes of the events, as well as investigate mechanisms of biotic recovery, a new biochronological scale of ammonoids has been constructed by means of the Unitary Associations method. This new biozonation shows a high resolution previously unmatched for the Triassic and consequently enables large-scale correlation (compare Jenks et al. 2015). For instance, the biochronological revision of the Smithian substage integrates several biostratigraphic records with abundant ammonoid faunas from basins spread all over the world (Brayard et al. 2013). Among these regions, the North Indian Margin (NIM) revealed abundant new ammonoid faunas that enabled construction of a high resolution ammonoid biozonation by means of UAs (Brühwiler et al. 2010). Indeed, a sequence of units defined by maximal set of (actually or virtually) coexisting species was reconstructed for each basin of the NIM. These local associations were then analyzed altogether by the same approach to deduce a new set of maximal associations at the NIM scale (Fig. 11.4b). This process enabled obtaining a robust ammonoid biozonation, free of biostratigraphic contradiction and reproducible over the entire NIM and even globally (Brayard et al. 2013).

Finally, known abiotic and biotic events were calibrated against this new ammonoid biozonation (Fig. 11.4c; Galfetti et al. 2007a, b; Brühwiler et al. 2010). Briefly, the analysis of dynamics of ammonoid biodiversity shows several marked patterns that were previously unknown, especially a diversification during the early Smithian followed by a global and synchronous extinction at the end-Smithian. Furthermore, the turnover of ammonoid faunas was extremely high during the middle Smithian. Indeed, the new ammonoid biozonation was calibrated by recent radioisotopic ages (Fig. 11.4a; Ovtcharova et al. 2006; Galfetti et al. 2007a; Brayard et al. 2009a, b; Brühwiler et al. 2010), which suggest an average mean duration of 17.5 kyr per UA, the separation intervals between UAs being included. This implies that rates of origination and extinction were of about 100 species per Myr and that the end-Smithian event was abrupt and took place with 2 UAs only. Thanks to this new UA-based biozonation applicable at the low paleolatitudes, the carbon and oxygen

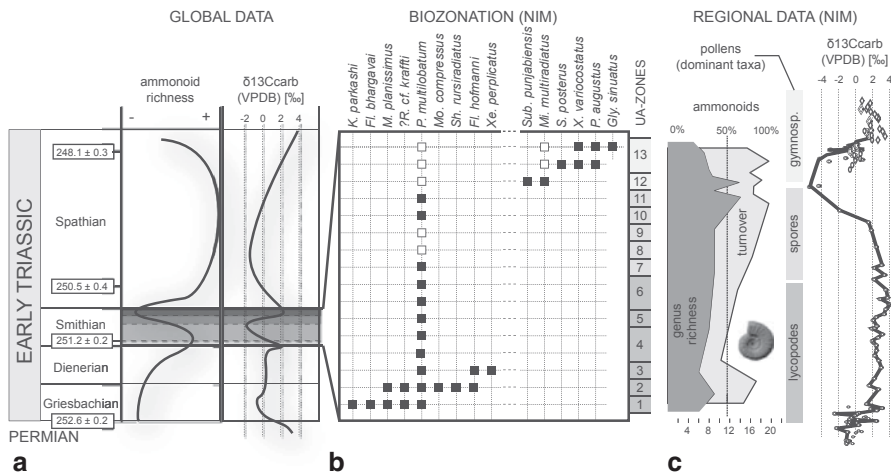


Fig. 11.4 Early Triassic ammonoid biochronology and calibrated biotic and environmental data. **a** Simplified global trends of ammonoid diversity and carbon isotope during the Early Triassic (after Brayard et al. 2009a). **b** Range chart of ammonoid species of the Smithian from the North Indian Margin (Salt Range, Spiti, and South Tibet) and biozones constructed by means of unitary associations (after Brühwiler et al. 2010). **c** Example of palynological and geochemical data calibrated towards this new UA-based biochronological scale

isotopic records and palynological records could be precisely dated and correlated in order to reconstruct a new extinction model linked with climate change (Romano et al. 2013).

11.4.2 Middle Triassic Ammonoids

Monnet and Bucher (2005a, b) synthesized and revised the ammonoid zonation of the Anisian (Middle Triassic) from North America. Their study focused on three basins, which were distributed along a latitudinal gradient (Fig. 11.5b): western Nevada (low paleolatitude, USA), British Columbia (mid- paleolatitude, Canada), and the Sverdrup Basin (high paleolatitude, Canada). They applied the UA method to reconstruct an ammonoid biozonation for each of the three basins, as well as the correlation between the three basins in a second, hierarchical step. This biochronological study benefited from recent and thorough taxonomic updates of Anisian ammonoids (Tozer 1994; Monnet and Bucher 2005a; Monnet et al. 2010, 2012, 2013).

Based on this quantitative analysis, the Anisian in the studied areas contains 13, 10, and 3 zones and a total of 174, 90, and 7 species, for western Nevada, British Columbia and the Sverdrup Basin, respectively (Fig. 11.5a). The use of such quantitative biochronological methods lead to new and more precise correlation. For instance, the *Buddhaites hagei* Zone (Canada) correlates only with the *Intornites*

mctaggarti Subzone (Nevada) and not with the entire *Acrochordiceras hyatti* Zone (Nevada) as previously empirically assumed by other authors (compare Figs. 11.5a, c). The *Tetsaoceras hayesi* Zone (Canada) appears to correlate with the *Unionvillites hadleyi* Subzone (Nevada) of the *hyatti* Zone and not with the *Nevadisculites taylori* Zone. The *Hollandites minor* Zone (Canada) correlates with the *taylori* Zone (Nevada), not with the *Balatonites shoshonensis* Zone as is usually acknowledged (Tozer 1994).

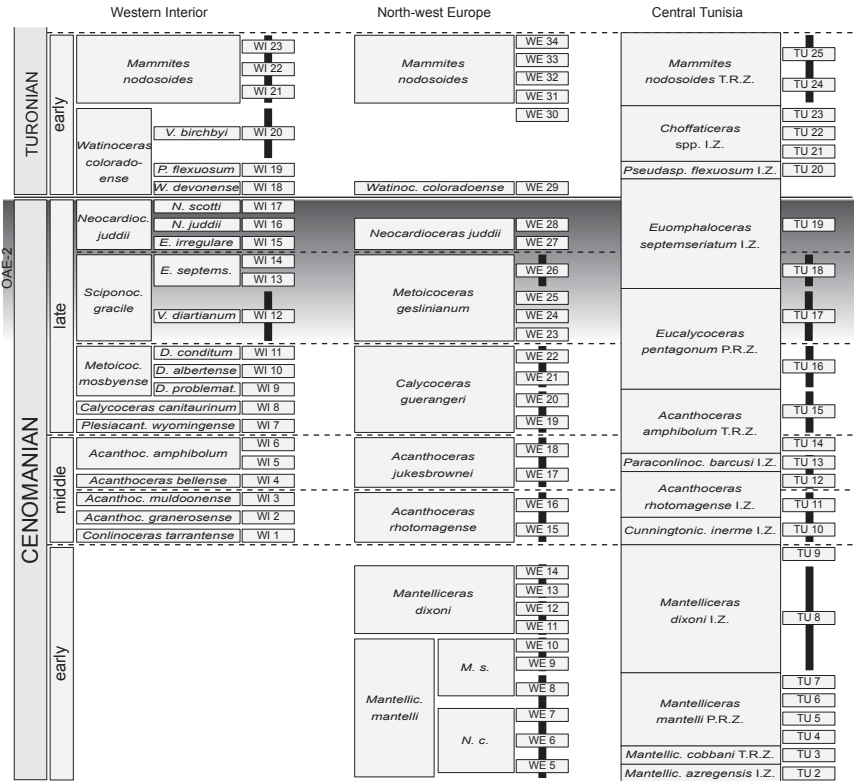
The UA method also enabled quantifying the diachronism of studied taxa. It appears that about 67% of the genera and 18% of the species common to Nevada and British Columbia have diachronous FOs or LOs (Fig. 11.5d). Therefore, this diachronism is significant and its impact on correlation should not be overlooked.

Finally, these revised biochronological zonations enabled quantifying biodiversity of Anisian ammonoids from North America. This analysis reveals that the major diversity peak occurred during the early Middle Anisian exact correlatives *hadleyi* Subzone in Nevada and *hayesi* Subzone in British Columbia. A closer look at the taxonomic composition of these correlatives reveals short-lived faunal exchanges between the usually latitudinally restricted middle and late Anisian faunas. This event may reflect significant changes in climate or oceanic circulation at that time (for more details, see Monnet and Bucher 2005b).

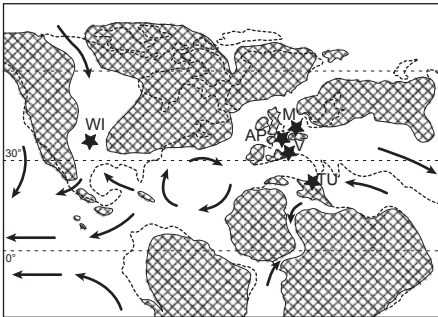
11.4.3 Late Cretaceous Ammonoids

The marine Cenomanian–Turonian is one of the best-studied stratigraphic intervals of the Cretaceous. Such focus has been prompted by several, more or less interwoven, biotic and abiotic events, such as a moderate mass extinction, the highest sea-level of the Mesozoic and a global oceanic anoxic event coupled with a high positive excursion in the carbon isotope record (references in Monnet 2009). In order to decipher these global events and their consequences during the mid-Cretaceous, a wealth of biostratigraphic data for this critical time interval has been generated. Hence, the biostratigraphic distribution of major ammonite genera and species during the Cenomanian–Turonian is relatively well known. In addition, empirical ammonoid zonations have been established for this interval in such distant basins as north-west Europe, central Tunisia and the Western Interior (e.g., Robaszynski et al. 1994; Cobban 1984; Wright and Kennedy 1984; Kennedy and Cobban 1991; Kennedy et al. 2004; Fig. 11.6b).

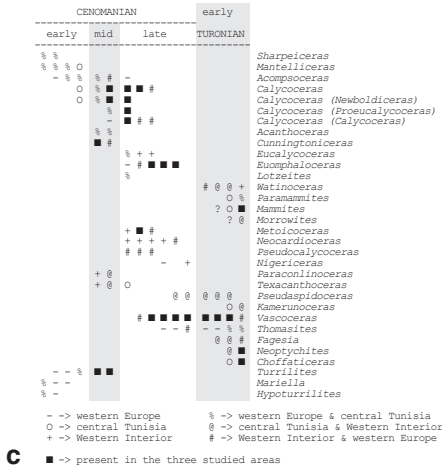
The biochronology of Cenomanian-early Turonian ammonoids from three key stratotype areas (north-west Europe, central Tunisia and the Western Interior of North America) has been thoroughly analyzed and revised by means of the UA method (Monnet and Bucher 1999, 2002, 2007; Figs. 11.6a, c). This review was based on a taxonomic homogenization of ammonoid faunas from these key areas. The Cenomanian and early Turonian comprises 30 UA-zones in north-west Europe, 24 UA-zones in central Tunisia and 23 UA-zones in the middle Cenomanian–early Turonian of the Western Interior Basin (Fig. 11.6a). The UA method leads to a two-fold increase in resolution of these ammonoid zonations compared to the standard,



a



b



c

Fig. 11.6 Ammonoid biochronology of the Cenomanian–early Turonian (Late Cretaceous). **a** Ammonoid zonation and correlation after Monnet and Bucher (2002, 2007) between the three studied areas and between the previous empirical zonation and the reconstructed UAs. **b** Paleogeographic location of the three studied areas (Western Interior, Central Tunisia, and north-west Europe, which includes the Anglo-Paris, Vocontian, and Münster Basins). **c** Biostratigraphic ranges and diachronism of ammonoid genera between the three studied areas (after Monnet and Bucher 2007)

synchronous datum known to date is the last occurrence (LO) of *Turrilites acutus*, which may thus be potentially used as a marker for the middle/late Cenomanian boundary, provided that it does not turn out to be diachronous in the light of any new data (Monnet and Bucher 2007).

Finally, these revised quantitative ammonoid biozonations enabled precise investigation of biodiversity patterns of ammonoids during the Cenomanian–Early Turonian in these areas (Monnet et al. 2003; Monnet 2009) and to evaluate these in the face of known abiotic changes during this time interval. The biodiversity patterns of ammonoids (species richness, origination/extinction, turnover, poly-cohort survivorship, and taxonomic distinctness) highlight that the mass extinction of the Cenomanian/Turonian boundary is restricted to Europe, as far as ammonoids are concerned. Only Europe documents an actual decrease of species richness during the late Cenomanian, which results mainly from decreasing originations. In Tunisia, where the onset of anoxic waters is synchronous with Europe, species richness increases during the late Cenomanian and reaches its highest values in the early Turonian. The Western Interior records relatively high species richness during the late Cenomanian with only a single minor extinction event. Furthermore, major changes in biodiversity patterns of ammonoids occurred around the middle/upper Cenomanian boundary, i.e. about 0.75 Myr before the onset of the Oceanic Anoxic Event 2 (OAE2). Although there is extensive evidence for widespread anoxia during the Cenomanian/Turonian boundary interval in deep sea environments, the biodiversity patterns of ammonoids in Europe, Tunisia, and the Western Interior rule out global anoxia as a direct causal mechanism for changes in ammonoid diversity (Monnet and Bucher 2007). These biodiversity patterns question the global scale character of the so-called Cenomanian/Turonian mass extinction. Observed biodiversity patterns of ammonoids strongly support the global warming of the late Cenomanian as evidenced by the northward migration of taxa typical of the Tethyan Realm. Changes in ammonoid diversity are compatible with the exceptional high sea level occurring at that time and with concomitant regional climate changes (Monnet 2009).

11.5 Conclusions

As demonstrated by their application on ammonoids, quantitative biochronological methods are very efficient and robust to produce highly resolved biozonations. For all these methods, free computer software is available. Among these methods, the Unitary Associations approach is probably the best for academic purposes in our opinion: Comparisons of empirical zones based on the maximum association principle to UAs processed from the same dataset shows up to a threefold increase in resolution. UAs allow identifying and processing the (often complex) biostratigraphic contradictions generated by the highly discontinuous records resulting from selective preservation, facies control, ecology, and sampling effort. The reconstructed robust and high resolution UA-biozonations can thus be used to precisely date

and correlate sections distributed across various geographic scales from a basinal to a global scope. Only UAs will not mask the limitations inherent to low quality datasets in term of resolution. The UA method offers additional powerful tools, which enable tracing back the origin of existing biostratigraphic contradictions to identify and evaluate the quality of the analyzed data. Last but not least, UA-biozones provide an ideal tool for the analysis of diachronism and biogeographic patterns. Rapidly evolving clades with a good quality record like ammonoids (or, e.g., conodonts) often lead the biostratigrapher to become somewhat overconfident in the *a priori* recognition of gradually evolving anagenetic lineages and the application thereof in dating. Among the phylogeny-free, quantitative biochronological methods, only UAs provide a logical and powerful tool for constructing reliable time frames without ignoring and masking the actual quality of the primary data.

Acknowledgments This work is a contribution to the team BioME of the UMR CNRS 6282; it was funded by the CNRS INSU Intervie. We thank Spencer Lucas and Jean Guex for insightful comments on this manuscript.

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