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Chapter 3

Evolutionary Trends within Jurassic Ammonoids

Pascal Neige and Isabelle Rouget

3.1 Introduction

Evolutionary trends have long been studied and discussed in evolutionary biology (e.g., Vrba 1983; McKinney 1990; McShea 1994, 2001; McNamara 2006; Gregory 2008). Such a trend may be defined as an identifiable pattern of a trait (e.g. body size, species richness, extinction rate) shifting in a given direction for a sufficiently long period of time to be detected. Traits that describe a trend may be expressed as “*state variables*” (McKinney 1990) and can be quantified using statistical point estimates (e.g. mean, maximum) or dispersion parameters (e.g. total variance). This concept of trends is central to evolutionary biology and can be studied at very different scales: from lineages to supraspecific clades (see McShea 2001 for a review).

It is common practice to divide trends into two kinds based on the nature of the dynamic underlying them (McShea 1994; Gregory 2008). The first kind, “*passive trends*”, exemplifies evolutionary patterns where a boundary (e.g. a design limitation) constrains fluctuations of the state variable. Consequently the state variable will generally fluctuate in two directions (e.g. increase or decrease in size) so approaching the boundary. However, there can be no fluctuations beyond the boundary (e.g., it is impossible to be smaller than a given “*boundary size*”). Consequently, lineages within the clade tend to vary in two directions but the clade as a whole varies in one direction only (e.g. the clade expands in the direction of larger size but only because any shift beyond minimum size is impossible). The second kind, known as “*driven trends*”, exemplifies evolutionary patterns where the state variable varies overall in one direction only and for most lineages

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(e.g., the clade expands in the direction of larger size and the smallest specimens also tend to be larger). Even if successful, it is worth noting that this terminology (“*passive*” vs. “*driven*”) does not imply any direct understanding of causes: passive does not mean random change any more than driven means adaptive change (McShea 1994; Wang 2001; and see Gregory 2008 for a synthesis). Therefore, a major problem in paleontology is to discover the causes generating the trends. As Gregory (2008) put it, trends are real phenomena and their underlying causes are rarely simple.

Obviously, before a trend can be identified and so before any attempt can be made to decipher the causes that trigger it, traits must first be quantified and then their fluctuations over time computed. This involves collating a robust bank of data and exploring it statistically. Such exploration is far from straightforward: different statistical parameters (e.g. mean, median, maximum) might reveal different patterns, as may studies at different scales (subclades vs entire clade). Even the first part of the agenda (constructing the database) is subject to difficulties: in the case of speciose clades, the number of species may be difficult to ascertain and the patterns observed may be skewed by various kinds of bias. For example, in a study based on Jurassic ammonoids, Nardin et al. (2005) show that the ratio between morphological disparity and species number tends to decline over historical time (i.e. the time over which the clade has been studied by paleontologists). This is attributed to the tendency of paleontologists to describe and name extreme forms before intermediate ones. Other biases such as the non-random geographic distribution of outcrops may affect the patterns observed (e.g. McGowan and Smith 2008; Vilhena and Smith 2013). However, in spite of bias, the fossil record provides a unique opportunity to study evolutionary trends extensively for different periods of time.

In this context, Jurassic ammonoids may be considered as a primary model. They benefit from a good fossil record (compared to other fossils), and they have been studied intensively for more than 200 years, yielding a comprehensive set of data in terms of geographic and stratigraphic species distribution. It is no surprise, then, to find an extensive literature about the evolutionary patterns of Jurassic ammonoids over time. Historically (and oversimplifying), scholars of Jurassic ammonoids focused first on evolutionary trends of lineages until the late twentieth century, and since then have favored broader sampling (i.e. macroevolutionary scale). In this paper we will focus largely on the latter. In a first part, we will review papers that explicitly attempt to reconstruct evolutionary patterns (thus potentially discovering trends) for Jurassic ammonoids. We exclude paleobiogeographic explorations of the type studied by Cecca et al. (2005) which are discussed elsewhere in this book. The second part will explore large-scale taxonomic patterns based on our own compilation of data published by various authors. Finally, we discuss limitations encountered in the study of evolutionary trends within Jurassic ammonoids.

3.2 The Jurassic System

Today, we consider that the Jurassic system encompasses more than 56 myr (Gradstein et al. 2012) from 201.3 Ma (base of its first stage: the Hettangian) to 145 Ma (top of its last stage: the Tithonian). The onset of the Jurassic was historically based on the large faunal turnovers brought about by the end-Triassic mass extinction (one of the five biggest Phanerozoic mass extinctions, Hallam and Wignall 1997). This mass extinction largely affects ammonoids: just three genera (*Choristoceras*, *Rhacophyllites*, *Eopsiloceras*) cross the Triassic/Jurassic boundary, and quickly become extinct (Yin et al. 2007; Smith et al. 2014). The Lower Jurassic limit is now formally recognized by a GSSP (Global boundary Stratotype Section and Point) located in the Karwendel Mountains, Austria (Hillebrandt et al. 2013; and see Ogg and Hinnov 2012a for a complete GSSP synthesis within the Jurassic), and the correlation event is the First Apparition Datum (FAD) of the ammonite *Psiloceras spelae*. The end of the Jurassic (i.e. the Jurassic/Cretaceous boundary) has generated dozens of debates and thousands of pages of publications. Today, its formal limit is still not fixed, and no GSSP is recognized yet. However, a possible correlation event for this limit may be the FAD of the ammonite *Berriasella jacobi* (Ogg and Hinnov 2012b).

The Jurassic system is subdivided into 11 stages. Their durations are far from equal: the Hettangian and the Bajocian are estimated to have lasted 2.0 myr whereas the Toarcian is estimated to span 8.6 myr. Ogg and Hinnov (2012a, p. 763) provide the most recent synthesis of the Jurassic Time Scale using different methods and data and recognize that “*the primary reference scales for most stage boundaries and other events in Jurassic stratigraphy are the ammonite zones [...]*”. These 11 stages form three large subdivisions (Lower, Middle, Upper) which together make up the complete Jurassic System. It is worth saying that studies of the Jurassic ammonoids have historically generated a tremendous number of concepts and results in various scientific fields such as biostratigraphy, paleogeography, paleoclimatology, sequence stratigraphy, and macroevolution. Celebrated geologists and paleontologists who contributed to this eighteenth- and nineteenth-century Jurassic “*epic*” include Alexander von Humboldt, who first recognized the Jurassic in 1795 when speaking of the “*Jura Kalkstein*” during a geological trip through southern France, western Germany, and northern Italy (and see Humboldt 1799); Alexandre Brongniart, who coined the name “*Terrains Jurassiques*” (1829); Leopold von Buch, who established the three-fold subdivision of the Jurassic (1839); Alcide d’Orbigny, who largely developed the idea of stages (“*étages*”) within mostly ammonoid-based Jurassic subdivisions (1852), and Albert Oppel, who developed the concept of biostratigraphic zone (1856–1858). More recently, Arkell (1956) synthesized what is known of the Jurassic in his *Jurassic Geology of the World*.

Besides the lower limit extinction of the Jurassic (first-order end Triassic mass extinction), several biotic events occurred during the Jurassic (Hallam and Wignall 1997). One such event was the Mesozoic Marine Revolution (Vermeij 1977). This revolution saw the restructuring of shallow marine benthic communities mainly

during the Jurassic and the Cretaceous. A particularly interesting event was the second-order extinction event at the Pliensbachian/Toarcian boundary: the so-called “*Early Toarcian Crisis*”, which largely affected marine faunas and microflora (see Dera et al. 2010 for a review). This appears to have been a multi-stage event and to have given rise to a rapid recovery for ammonoids (Dera et al. 2010). Finally, a second-order crisis, but less marked, occurred at the very end of the Jurassic (the “*Tithonian event*”, Hallam and Wignall 1997). Although less marked among ammonoids than previously thought (Sepkoski 1992; Hallam and Wignall 1997), this event has been recognized recently on a disparity-based approach which focuses on southern German ammonoids (Simon et al. 2010).

3.3 A Review of Macroevolutionary Patterns and Evolutionary Trends within Jurassic Ammonoids

Historically, identifying evolutionary trends was mainly process-oriented up to the last decades of the twentieth century (Rouget et al. 2004). As with many other groups, the first ammonoid evolutionary trends described in the literature were based on accepted laws which depend on the author’s concept of evolution, such as the biogenetic law (Waagen 1869; Hyatt 1889, 1897) or the irreversibility of evolution (Dollo 1922). The repeated occurrence of similar morphologies (including coiling, shell shape, and ornamentation) has long been known and led to the successful concept of iterative evolution (Salfeld 1913; Spath 1930). This concept postulates that evolution gave rise to a repetition of trends in distinct lineages at different times. This case of parallel evolution in a chronological sequence prevailed among ammonite workers during the first part of the twentieth century and has never been totally abandoned (Bayer and McGhee 1984; Landman et al. 1991). This concept was strikingly linked to the acceptance of the anagenetic process that impels all evolutionary trends. This was still the case in the 1980s when the study of heterochrony reappeared in evolutionary studies after being pioneered by such scholars as Schindewolf (1936). Ammonites were a highly suitable clade for such studies and provided many relevant examples of heterochronic trends: the so-called paedo- or peramorphocline (see Dommergues et al. 1989 and Dommergues 1990 for a large scope within Jurassic ammonites). These trends were mainly oriented by an anagenetic hypothesis, involving a low taxonomic rank level analysis (genus, species). In this context, Raup and Crick (1981), following Brinkmann (1929), published probably the most widely reported example of trend analysis within Jurassic ammonoids. Based on a biometric study of phyletic evolution in the Callovian genus *Kosmoceras* (including its four subgenera) through 14 m of the Peterborough section (lower half of the Oxford Clay Formation), they showed that some characters (e.g. adult shell diameter) display a non-random evolution (i.e. fewer reversals of a given state variable through time than would be predicted from a null hypothesis based on a random walk). They concluded that “*it is reasonable to interpret the low number of runs as indication of sustained trends in Zugokosmoceras [one of the subgenera*

of *Kosmoceras*] evolution”, and explained this trend as a non-random operation of natural selection. It is worth noting that trends in this example are far from systematic (depending on characters and/or sampling strategy along the studied section).

More recently, authors have described evolutionary patterns through time but without making assumptions about evolutionary processes. For example, House (1989) explores ammonoid taxonomic diversity fluctuations from the Devonian to the end of the Cretaceous by computing a large database at the family level. He relates the different fluctuation events (mainly extinctions) to sea-level fluctuations. In the same way, contemporary studies explore evolutionary patterns at very different taxonomic levels (from species to families), and generally—and contrary to the period when heterochronies were fashionable—do not focus on a single or a limited number of lineages. This corresponds to a macroevolutionary approach, and the traits explored are as different as body size, taxonomic richness, and morphologic disparity. Among these evolutionary patterns, trends may stand out.

We focus here on papers explicitly attempting to reconstruct evolutionary patterns for Jurassic ammonoids. However, this synthesis does not take into account all published papers dealing with Jurassic ammonoids. For example, Wiedmann and Kullmann (1981) focus on ammonoid suture trends throughout their evolutionary history. Therefore data for the Jurassic are very scarce and do not represent a pattern within the Jurassic period. On the same way, Boyajian and Lutz (1992) demonstrated that both the mean and range of suture complexity increased over the stratigraphic range of the Ammonoidea (from the Devonian to the end of the Cretaceous). However, no particular trends seem to occur for the Jurassic period. Similarly, Parent et al. (2010) explore size-shape relationships at the Mesozoic scale. Figure 3.1 shows a selective sample of published studies exploring macroevolutionary patterns of Jurassic ammonoids. These studies focus on different traits: body size, taxonomic richness (at the species, genus, or family levels), and shell morphology. Surprisingly, most of these studies make no attempt to find evolutionary trends, only a few of them doing so explicitly.

For example, Guex (2001) claims—in a study based on Toarcian ammonite lineages—that trends during ecologically stable periods are characterized by shell coiling change from evolute to involute, and those during episodes of stress are characterized by a reverse shell coiling change. O’Dogherty et al. (2006), exploring ammonoid taxonomic fluctuations within the southern Iberian paleomargin, claim that trends during ecologically stable periods also show the development of more complex ornamentation. In another example, Navarro et al. (2005) report that the trend toward more compressed forms of shell occur during the initial colonization of the Arctic Basin by the *Cardioceratidae* at the end of the Bajocian. This observation was based on a quantification of morphological disparity. Dommergues et al. (2002) explore shell size patterns of ammonoids through the Early Jurassic ammonite radiation using a database of 1236 ammonite species representing all known Early Jurassic faunas. Shell size patterns are studied for the entire period and then at the biozone scale for the first four stages of the Jurassic (28 myr), during which ammonites recovered from the crisis at the Triassic/Jurassic (T/J) boundary. They do not identify any global trend, but a sustained increase in size disparity at the beginning of the Early

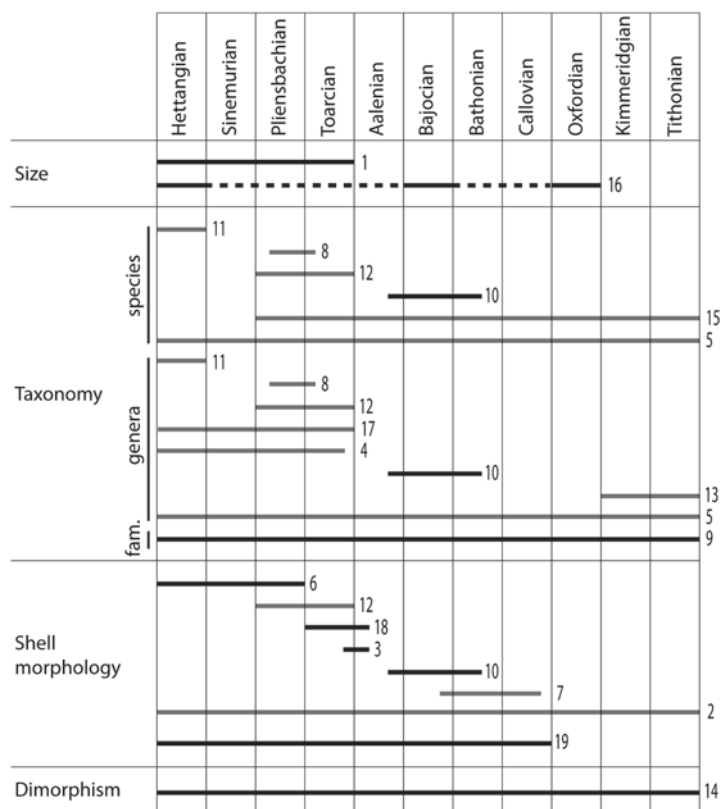


Fig. 3.1 Sample of published studies exploring macroevolutionary patterns of Jurassic ammonoids for different traits. *Black lines* represent worldwide studies. *Grey lines* represent geographically limited studies (geography or paleogeography named here in brackets according to original names of cited papers). (1 Dommergues et al. (2002), 2 Simon et al. (2010): Southern Germany, 3 Neige et al. (2001), 4 Hallam and Wignall (1997): Great Britain, 5 Sandoval et al. (2001): Betic Cordillera, data used partially by O'Dogherty et al. (2006), 6 Dommergues et al. (1996), 7 Navarro et al. (2005): Arctic, 8 Macchioni and Cecca (2002): Western Tethyan areas, 9 House (1989), 10 Moyne and Neige (2007), 11 Guex et al. (2012): NW European and Pacific realms, 12 Dera et al. (2010): NW Tethyan and Arctic domains, 13 Rogov (2012): Northern Hemisphere, 14 Davis et al. (1996), 15 Ruban (2007): Caucasus, 16 Stanley (1973), 17 Ziegler (1981): Southern Germany, 18 Guex (2001), 19 Smith et al. (2014))

Jurassic radiation: during the Hettangian up to the base of the Sinemurian (Fig. 3.2). They interpret this pattern as a passive evolutionary trend: ammonites at the beginning of the radiation were initially medium-sized and so amenable to changes in size in both directions (toward smaller and larger extremes) thus finally engendering a passive increase in size disparity. They also note that the minimum value of the coefficient of variation describing shell size disparity occurs during the Early Toarcian Crisis (*Tenuicostatum* zone), followed by an increase of size disparity during the Toarcian stage. However, in a global analysis of ammonoids during the recovery of the Lower Jurassic following the end-Triassic mass extinction, Dommergues

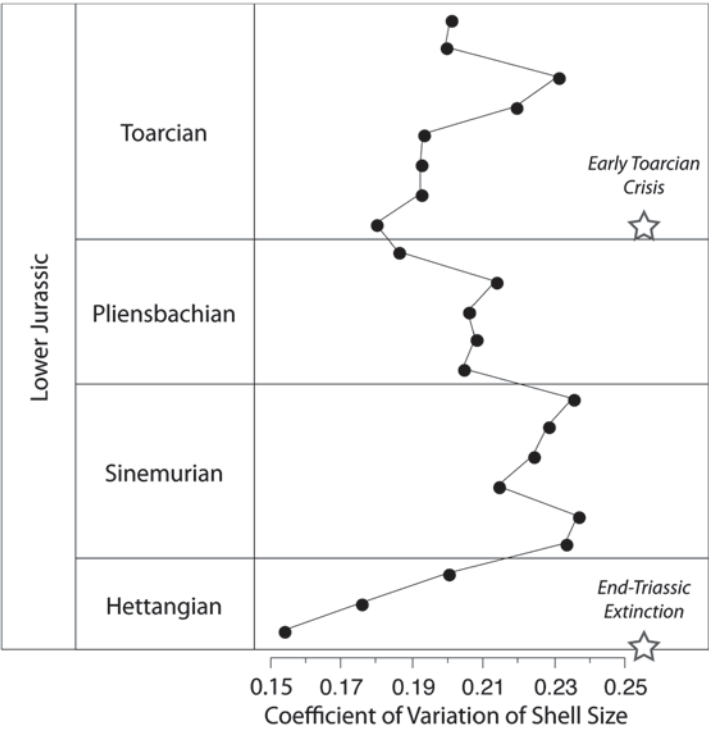


Fig. 3.2 Coefficient of variation in ammonite shell size throughout the Early Jurassic (one point per standard ammonite biozone). Stars indicate extinction events (modified from Dommergues et al. 2002)

et al. (1996) conclude that their disparity-based study of shell shape reveals a fairly homogeneous distribution with no significant trend. In a review paper, Davis et al. (1996) analysed dimorphism within ammonoids. A section of this paper focuses on patterns of dimorphism through time in the Jurassic, using a qualitative approach. For this period of time, dubious cases of sexual dimorphism appear as soon as the Hettangian, and obvious cases during the Toarcian among the Hildoceratinae (but see Davis et al. 1996 for a general discussion about sexual dimorphism recognition within ammonoids). After the Lower Jurassic, sexual dimorphism becomes a common ammonoid feature of nearly all Middle and Late Jurassic ammonoids.

3.4 Global Diversity Pattern

In this part, we begin a very preliminary exploration of Jurassic ammonoid macroevolutionary patterns. For that purpose, we constitute a database based on four publications offering a complete overview of Jurassic ammonoid evolution. These are the publications of four “primary” authors: Arkell (1957), Tintant et al. (1975),

Donovan et al. (1981), and Page (1996). Note that House (1989) who explored macroevolutionary patterns of the complete ammonoid clade (from the Devonian to the end of the Cretaceous) used data from Donovan et al. (1981) for the Jurassic. We admit that more recent data exist for different ammonoid groups, but the four publications used here synthesize the evolution of ammonoids during the Jurassic in a homogeneous way. As far as we know, no other publications are available covering the entire Jurassic and considering all ammonoid clades.

For our purpose, we simply report here FADs and LADs (Last Apparition Datum) of the different families during the Jurassic, given by these primary authors. Their data are available at stage level. A complementary and more precise compilation at the biozone level has been constituted based on the publication of Tintant et al. (1975). Others do not give sufficient temporal details. The biozone framework—based on ammonoids—used by Tintant et al. (1975) is episodically different from the chronozone scheme used nowadays (Page 2003), but we consider that these differences do not flaw the results. Our database may be biased in considering that some families are paraphyletic (Rouget et al. 2004). The use of paraphyletic groups for macroevolutionary studies is subject to debate (Sepkoski and Kendrick 1993). In our case, we assume that family level is a good proxy for scrutinizing Jurassic ammonoid biodiversity. This choice and its consequences will be discussed at the end of this study. The timeline used to represent the data is the last chronostratigraphical chart (Gradstein et al. 2012). Although numerical ages and stages duration are of different reliability during the Jurassic, this chart provide a relevant framework to characterize diversity pattern through time.

Spindle diagrams (number of taxa within each time bin) within ammonoid families for the four publications display very similar patterns (Fig. 3.3). First, we observe an increase in diversity from the beginning of the Jurassic up to the end of the Pliensbachian. This covers the recovery phase after the End-Triassic mass extinction and the continuation of the Early Jurassic Radiation phase. The Pliensbachian/Toarcian boundary is marked by a decrease in family numbers, corresponding to the Early Toarcian Crisis (second-order extinction event). After the Toarcian, we observe a new diversification phase, known as the Middle Jurassic Radiation: for Arkell (1957) and Page (2003) the maximum number of families is achieved during the Bajocian, whereas for Tintant et al. (1975) and Donovan et al. (1981) it is during the Callovian. Despite these slight differences, all the four spindle diagrams show a stable and less diverse Upper Jurassic.

Looking at this pattern at a finer time scale (i.e. biozone scale) offers a complementary view (Fig. 3.4). The Early Jurassic radiation is well marked. However, contrary to the preceding graphs (Fig. 3.3) it may be observed that the radiation reaches its peak at the beginning of the Pliensbachian. This difference is a simple effect of the temporal slicing used (stages vs biozones), the latter being more precise. The Early Toarcian Crisis appears less marked than previously. The Middle Jurassic radiation displays two successive phases: first is a marked upturn in diversity from the beginning of the Aalenian up to the end of the Bajocian then comes a more or less stable period up until the end of the Callovian. These two radiations (Early and Middle Jurassic) unfold in a very comparable duration of about 10 myr. They

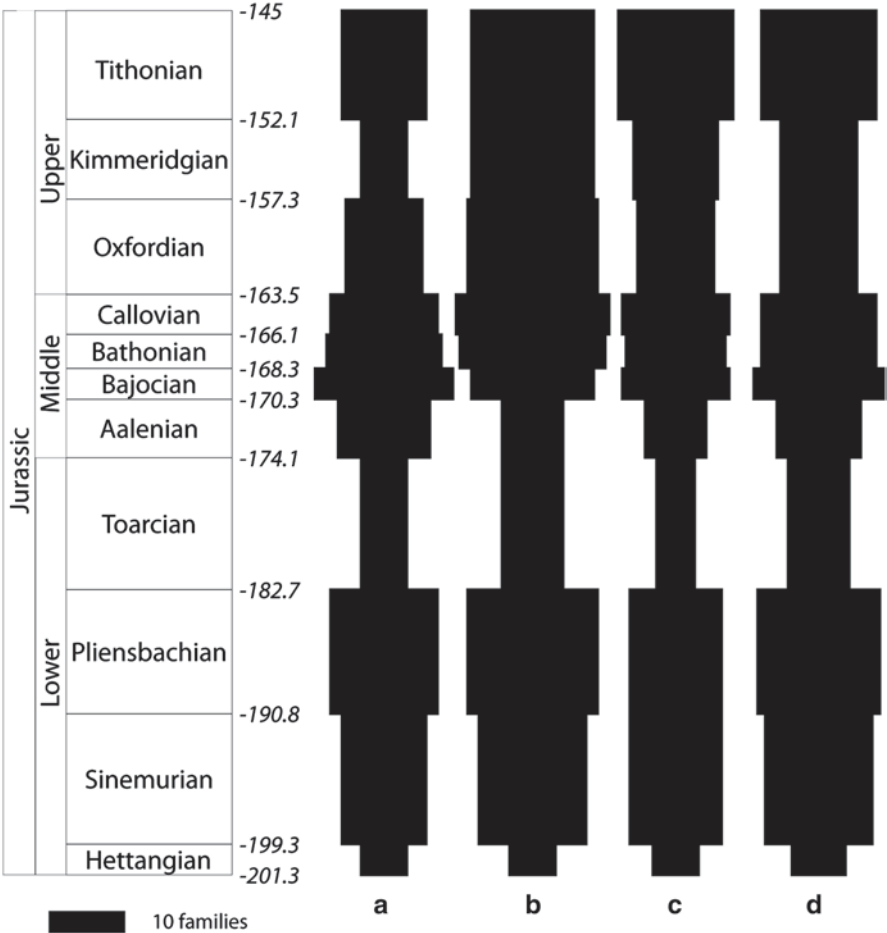


Fig. 3.3 Spindle diagrams for Jurassic ammonoids (number of families) according to four primary authors, at the stage level: **a** Arkell et al. (1957). **b** Tintant et al. (1975). **c** Donovan et al. (1981). **d** Page (1996). Numerical ages (Ma) from GTS2012, see Ogg and Hinnov (2012a)

consist in a sustainable increase in taxonomic diversity, which could be considered as a trend. Both the Early Jurassic and Middle Jurassic radiations observed in the present analysis concern drastic and profound changes in ammonoid diversity (i.e. changes in dominant clades), which has also been documented by cladistic and macroevolutionary studies (see Dommergues et al. 1996, 2001; Moyne and Neige 2004, 2007; Neige et al. 2013).

These two radiations are not temporally related in the same way to their preceding extinctions (Fig. 3.4b): the Early Jurassic Radiation immediately follows the first-order End-Triassic Extinction, whereas the Middle Jurassic Radiation is delayed relative to the second-order Early Toarcian Crisis. This is observed at the taxonomic scale of the family. At the species level, Dera et al. (2010) demonstrated

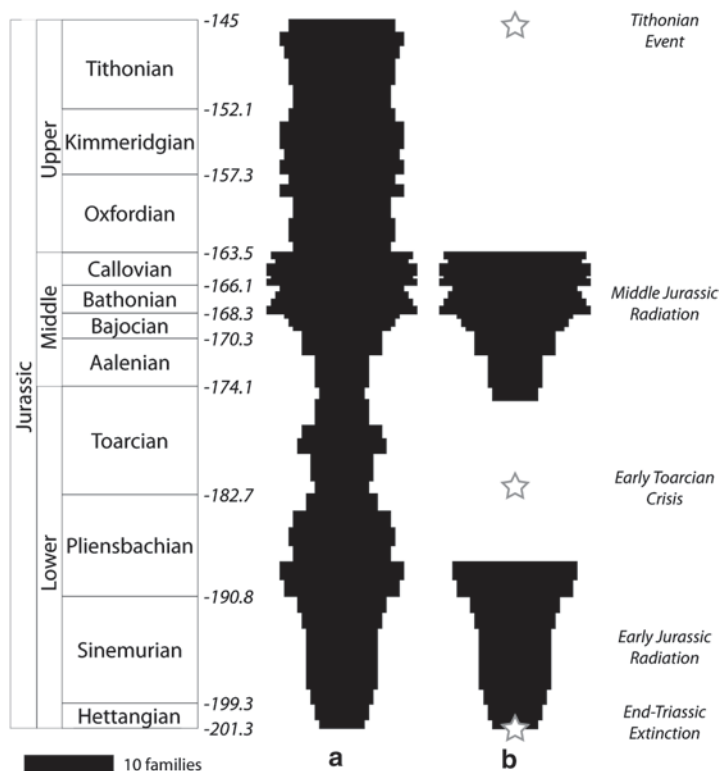


Fig. 3.4 **a** Spindle diagrams for Jurassic ammonoids (number of families) according to Tintant et al. (1975), at the biozone level, and main macroevolutionary events. Numerical ages (Ma) from GTS2012, see Ogg and Hinnov 2012a **b** Same but showing only evolutionary radiations (stars indicate extinction events)

a large and rapid recovery for ammonoids during the Toarcian, immediately after the Early Toarcian Crisis. In a recent paper, Neige et al. (2013) survey all main ammonoid clades during the Toarcian and Early Aalenian stages, using both taxonomic and disparity-based approaches. Results show that (1) one clade (the ‘hammatoceratids’, which engendered the Middle Jurassic radiation) has a fossil record that begins with low diversity and disparity but is superseded by a sustained radiation pattern, and (2) the rapid recovery after the crisis during the Toarcian is mainly due to clades that will rapidly become extinct. Therefore, the Middle Jurassic radiation is not strictly a consequence of the Early Toarcian Crisis. Even if first members of the root clade (the ‘hammatoceratids’) of the Middle Jurassic radiation are known just after this event, this clade radiates during the complete Toarcian stage to finally permit the Middle Jurassic radiation displaying the emergence of new clades (classified in different taxa: sonniniids, haploceratids, strigoceratids or stephanoceratids, perisphinctoids, see Moyne and Neige (2004) for a cladistics analysis of the Middle Jurassic radiation).

3.5 Conclusions and Prospects

Ultimately, this analysis of evolutionary trends within Jurassic ammonoids, exemplifies several main points:

- Jurassic ammonoids have been extensively studied and the evolutionary pattern of this clade is largely exemplified both at a global and local geographic scale;
- Searches for evolutionary trends within Jurassic ammonoids are not common within the literature;
- Only a few published cases at a large taxonomic and/or geographic scale attempt explicitly to decipher trends. These concern—for example—shell shape (i.e. evolute to involute, depressed to compressed), and adult shell size disparity;
- As far as we know, only Raup and Crick (1981), following Brinkmann (1929), attempted a statistical analysis of trends for Jurassic ammonoids but at a very local geographic scale (one section), and for a very short span of time (infra Callovian stage). They found few cases of trends and hypothesized that natural selection played a role;
- At the family level—and based on the analysis of four previously published synthetic papers about Jurassic ammonoids as a whole—we observe two trends in the context of increasing diversity for periods of time circa 10 myr: the Early Jurassic and the Middle Jurassic radiations;
- Observed at the family level, the Early Jurassic Radiation immediately follows the first-order End-Triassic Extinction, whereas the Middle Jurassic Radiation is largely delayed with respect to the second-order Early Toarcian Crisis.

Examples of demonstrated (or at least observed) evolutionary trends within Jurassic ammonoids are surprisingly few compared to the tremendous number of papers on Jurassic ammonoids. As previously stated, ammonoids, and particularly those from the Jurassic, offer a range of advantages for such a demonstration (good fossil record, fine chronostratigraphic framework, etc.). However, we must confess that this very good knowledge is drowned in confused high-rank taxonomic and phylogenetic frameworks. These taxonomic and phylogenetic uncertainties act as limiting factors when attempting to decipher evolutionary trends. For instance, in the present study, the four primary published papers that examine Jurassic ammonoids as a whole are based on the recognition of families that are mostly paraphyletic (Donovan 1994; Rouget et al. 2004; Neige et al. 2007 for explorations of taxonomic and phylogenetic practices among ammonoid and cephalopod scholars). This may lead to artificial patterns (e.g., pseudoextinctions). In this context, obtaining robust (i.e. character based) phylogenies is crucial to exploring trends at the lineage level. We attempted here to summarize these phylogenetic relationships among main ammonoid groups by a postulated phylogeny (Fig. 3.5). This phylogeny has not been obtained using a parsimony-based approach, but may be viewed as a summary of Jurassic ammonoid scholars point of views (and more precisely: Donovan et al. 1981; Guex 1995; House 1989; Page 1996; Moyne and Neige 2004; Tintant et al. 1975). To avoid any taxonomic confusion we used informal names

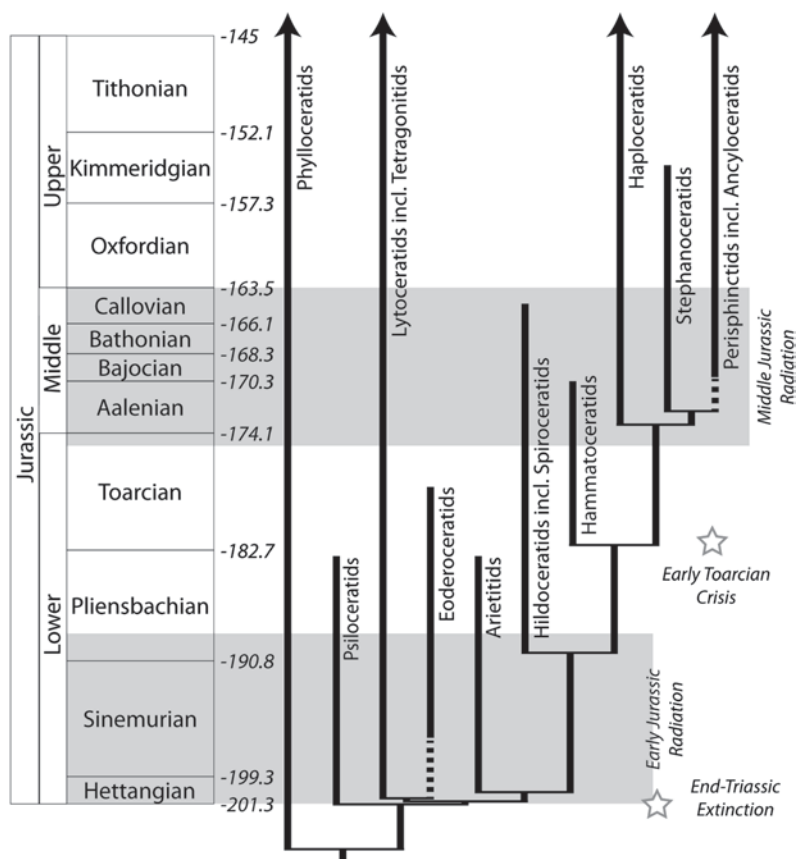


Fig. 3.5 Postulated phylogeny of Jurassic ammonoids assuming various sources of data (e.g., Donovan et al. 1981; Guex 1995; House 1989; Page 1996; Moyne and Neige 2004; Tintant et al. 1975). Dotted lines are supposed ghost lineages. (Note that informal names have been preferred to formal ones to avoid any taxonomic confusion)

(e.g. Psiloceratids instead of Psiloceratoidea). This phylogenetic tree can thus be considered as a first step toward a more formal (i.e. parsimony-based) one. It is not a surprise that the two radiation events (Lower and Middle Jurassic) appear in the phylogeny (Fig. 3.5, grey zones): Early Jurassic radiation is marked by the more or less synchronous emergence and diversification of numerous new clades (e.g. Psiloceratids, Eoderoceratids, Arietitids), whereas Middle Jurassic radiation is due the diversification of Hammatoceratids followed by the synchronous emergence of three clades (Haploceratids, Stephanoceratids and Perisphinctids). Increasing phylogenetic resolution among Jurassic ammonoids (i.e. obtaining good phylogenies for the each clade figured on Fig. 3.5) will definitely permits a better study of evolutionary trends. A second limiting factor when exploring evolutionary trends is to assign paleoecological conditions to ammonoids. The relationship between ammonoid shell shapes and their environment has long been discussed (see Westermann

1996 for an extensive review of arguments), the main debate being whether ammonoid habitats strongly influence their shapes compared to other factors such as phylogenetic inheritance, morphogenetic constraints, or developmental pathways. Increasing our knowledge of ammonoid habitat conditions would help greatly in interpreting evolutionary trends once established. In particular, this would permit fine interpretations between shell shapes and abiotic parameters such as sea-level changes, salinity, and temperatures. All in all, we believe that greater knowledge of the phylogeny and paleoecological conditions of Jurassic ammonoids would certainly give renewed impetus to evolutionary trend studies, and would reaffirm their value as a model in evolutionary paleontology.

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